Dear Colorado Parks and Wildlife Commissioners, Director Prenzlow, and Assistant Director DeWalt:

Please consider the following comments from the Center for Biological Diversity on the Colorado gray wolf restoration and management plan, and attached studies. The Center for Biological Diversity is a non-profit conservation organization dedicated to protecting and restoring endangered species and their ecosystems. Many of our over-36,000 members and supporters in Colorado volunteered their time to help in the 2020 passage of Proposition 114, which mandated wolf reintroduction and development of a wolf restoration and management plan.

This past February, along with three-dozen scientists, other notable individuals, and other conservation organizations, we sent (via email) a letter to each of you as well as to Governor Jared Polis, advising on how to carry out the process of developing this restoration and management plan with the utmost transparency and equity. We were disappointed that the Commission did not discuss the merits and any potential downsides of our recommendations prior to approving the ongoing, quite different process. However, recognizing that we proffered that letter spurred by no formal public comment process, we remain hopeful that you will carefully consider the following recommendations submitted during this initial official public comment period.


With the November 3, 2020 passage of Proposition 114, you became trustees and stewards of a historic public mandate to undo a societal mistake from our past and remedy the damage done. The first finding and declaration of the new law recounts that “[h]istorically, wolves were an essential part of the wild habitat of Colorado but were exterminated and have been functionally extinct for seventy-five years in the state.” Passage of Proposition 114 met a clarion call to address the extinction crisis and the central challenge for humanity in the 21st century: “Once restored to Colorado, gray wolves will help restore a critical balance in nature.”

Proposition 114, now Colorado Revised Statutes 33-2-105.8, requires the Colorado Parks and Wildlife Commission to develop a wolf restoration and management plan “using the best scientific data available.” That plan must include decisions on the “selection of donor populations of gray wolves,” on the “places, manner, and scheduling of reintroductions of gray
wolves,” on “[d]etails for the restoration and management of gray wolves, including actions necessary or beneficial for establishing and maintaining a self-sustaining population, and on “[m]ethodologies for determining when the gray wolf population is sustaining itself successfully and when to remove the gray wolf from the list of endangered or threatened species.”

The law also charges the CPW Commission with overseeing:

[T]he distribution of state funds that are made available to:
(I) Assist owners of livestock in preventing and resolving conflicts between gray wolves and livestock;
and
(II) Pay fair compensation to owners of livestock for any losses of livestock caused by gray wolves, as verified pursuant to the claim procedures authorized by sections 33-3-107 to 33-3-110 and, to the extent they are available, from moneys in the wildlife cash fund as provided in section 33-3-107 (2.5).

We comment below on these and closely-related matters.

I. The text of the law is antithetical to regulatory limits on wolf numbers or wolf distribution.

For three reasons, Colorado Revised Statutes 33-2-105.8, which the voters enacted through passage of Proposition 114, does not allow the gray wolf restoration and management plan to impose any limits on where wolves may be allowed to live in Colorado, nor to impose limits on how many wolves can live statewide or in specific areas.

First, the law requires the Colorado Parks and Wildlife Commission to “[d]evelop a plan to restore and manage gray wolves in Colorado, using the best scientific data available.” As we summarize in subsections below, scientific analysis of such data demonstrates that inclusion of population caps or wolf no-go zones would thwart statutory intent.

Second, the intent of the law is that “[o]nce restored to Colorado, gray wolves will help restore a critical balance in nature.” We show below that restoring a critical balance in nature comes down to restoring three tangible and, at least in part also measurable, ecological processes: Survival of the fittest, which shapes the evolution of both predator and prey; curtailment of the spread of infectious maladies within prey species, most notably chronic wasting disease; and trophic cascades that influence and sustain a variety of animal and plant species.

In order to achieve these proposed ecological goals – survival of the fittest, curtailment of infection and trophic cascades – over broad regions wolves must be at or near their natural abundance as determined by the availability and vulnerability of their wild prey animals. That precludes establishing an arbitrary population cap or restricting wolves’ distribution on the landscape.
Third, the law precludes the exclusion of wolves from any areas in Colorado because of the different parameters applying to reintroduction versus restoration. The law limits reintroduction geographically, but it explicitly applies restoration statewide.

This first section concludes with a discussion of the federal regulatory restrictions (enforced through wolf removals) on the distribution and abundance of endangered Mexican gray wolves. We show that those restrictions are not based on the best scientific data available. In Colorado too, there is no good reason to establish a wolf population cap or wolf no-go zones.

A. Survival of the fittest as an evolutionary influence on wolves and their prey.

Charles Darwin in the fifth (1869) edition of his classic book *On the Origin of Species By Means of Natural Selection*, adopted a concise phrase to encapsulate his overall thesis: “Survival of the fittest.” In the context of predation, survival of the fittest takes as a premise that disproportionate to their numbers in a population overall, more animals that succumb to predation are physiologically or behaviorally vulnerable and that, insofar as their vulnerabilities were genetically inherited and (except for the predation) would have been genetically transmitted to offspring, predation lessens such vulnerabilities among subsequent generations of the prey population.

Survival of the fittest also applies to predators. Predators with genetically transmissible traits that lessen their likelihood of successfully killing and consuming their prey, or that increase the likelihood that through efforts at predation they will suffer significant injuries, pass such deleterious traits to subsequent generations at lower rates than would occur at random.

Survival of the fittest as it applies through predation ensures the critical balance in nature through shaping the evolution of prey and predator species over multiple – dozens, hundreds and even thousands and millions – of generations. Over time, physiological and behavioral advantages acquired by either predator or prey are countered by the other species’ adaptations – creating a long-term balance – as vividly envisioned by poet Robinson Jeffers:

> What but the wolf’s tooth whittled so fine
> The fleet limbs of the antelope?
> What but fear winged the birds, and hunger
> Jewelled with such eyes the great goshawk’s head?

The first finding or declaration in C.R.S. 33-2-105.8 chronologically contextualizes the CPW Commission’s charge (in the third finding or declaration) to restore a critical balance in nature. That first finding strongly suggests that the long-term influence of wolves is necessary to help achieve that balance: “Historically, wolves were an essential part of the wild habitat of Colorado but were exterminated and have been functionally extinct for seventy-five years in the state.” Of course, history reaches a lot further back than just the last 75 years and includes oral histories from Native American societies going back thousands of years. The best and likely the only regulatory mechanism available to you to incorporate this important historical perspective.

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into the restoration and management plan, is establishing as a goal that the long-term process of survival of the fittest guide evolution of both wolves and their prey in Colorado.

Establishing survival of the fittest as an ecological goal in the restoration and management plan requires allowing wolves to prey on ungulates such as deer and elk to the extent of the wolves’ natural capacities in relation to such prey animals’ natural capacities.

In contrast, curtailing predation by limiting the number of wolves or the distribution of wolves would diminish the effects of survival of the fittest among prey animals, since predation would be proportionately less of an influence on their populations. For example, if the restoration and management plan was to ban wolves east of the continental divide, wolf predation would not affect deer and elk throughout the Front Range and the eastern plains. But most if not all of those deer and elk would still retain genetic connections, direct or mediated, to others of their kind on the Western Slope. Excluding the eastern animals from survival of the fittest in relation to wolves would dilute and thereby lessen the effects of survival of the fittest among deer and elk further west.

Moreover, capping the number of wolves could only be accomplished through killing wolves in excess of the cap. Such killings would have no relation to the wolves’ capacities to successfully hunt their prey. Instead, such killings would extinguish the gray wolf genes that are both beneficial and deleterious to survival of the fittest, and thereby outweigh and lessen and even nullify the evolutionary effects that would otherwise lead to extinguishment of harmful physiological and behavioral traits and proliferation of salutary traits.

To put it simply, either banning wolves from any area of the state or capping their numbers would interfere with the survival of the fittest, and therefore also undercut the statutory intention to restore a critical balance in nature informed by a historical perspective. Conversely, establishing a goal of facilitating survival of the fittest would clarify the incompatibility of the law with any limits on wolf numbers or distribution.

B. Curtailment of the spread of infectious maladies within prey species.

Survival of the fittest cannot be the sole standard by which restoring a critical balance in nature should be achieved and measured, because discerning some of the future evolutionary changes stemming from wolf predation and survival and the countervailing survival of prey animals may not be possible over the course of a single human lifetime. Policy as well as measurement of the effects of policy must be oriented at least in part to the polity that enacts it and cannot serve exclusively to benefit an indefinite future.

Affecting the exigent present-day, there may be no more dramatic illustration of the need to restore a critical balance in nature than the increasingly frequent rise of pandemics – most tragically for our species in the emergence of (and epidemiological conquest by) Covid 19, but also heartbreakingly noticeable in increasingly common and lethal epizootics.

Whether observed in the phenomenon of bat populations declining precipitously due to white-nose syndrome or in amphibians similarly crashing in numbers and some even going
extinct due to chytrid fungus, nothing bespeaks a world out of balance more than the triumph of newly-evolved and/or newly-proliferating microbes over venerable, longstanding vertebrates. Researchers have found evidence that “changes in predator communities may have cascading impacts that facilitate the emergence of zoonotic diseases,” suggesting that such changes (primarily past wolf extermination) contributed to such emergences— and thereby indirectly suggesting at least part of the cure. Other researchers found that “predator abundance may have cascading effects on tick-borne disease risk.” Yet, among a teeming microscopic universe that includes fungi, bacteria and viruses, there is no more insidious and intractable malady than the prions that cause chronic wasting disease in deer and elk, including in Colorado.

We recommend that the restoration and management plan include as a goal and metric in restoring the critical balance of nature, the extinguishment of chronic wasting disease in deer and elk in Colorado. A secondary and related goal and metric should be the curtailment of Rocky Mountain spotted fever, a bacterial ailment transmitted through ticks. Success or partial success in either or both of these endeavors would aid in ecological resiliency as well as in maintaining the health of Colorado’s human residents and visitors. We focus below on the means by which wolf restoration could curb chronic wasting disease in Colorado.

A 2006 analysis developed for the National Park Service examined the potential effect of wolves on the prevalence of chronic wasting disease in elk within Rocky Mountain National Park. The background to the model explains the premises:

Increasing mortality rates in diseased populations can retard disease transmission and reduce disease prevalence (Barlow 1996, Lafferty and Holt 2003, Packer et al. 2003, Ostfeld and Holt 2004). Increasing mortality slows transmission via two mechanisms. First, it reduces the average lifetime of infected individuals. Reduced lifespan, in turn, can compress the time interval when animals are infectious, thereby reducing the number of infections produced per infected individual. The effect of reduced intervals of infectivity is amplified by reductions in population density that occur as mortality increases, reductions that cause declines in the number of contacts between infected and susceptible individuals. Both of these mechanisms retard the transmission of disease. If these mechanisms cause the number of new infections produced per infected individual to fall below one, then the disease will be eradicated from the population.

Any elevation in mortality rate has the potential to cause these effects, however, reductions in transmission rates and disease prevalence can be particularly large if mortality rates are elevated in the infected portion of the population to a greater extent than in the susceptible portion. This explains why diseases that cause rapid death fail to persist. However, other, non-disease agents of selective mortality can exert the same, beneficial effect. For example, if predators prey selectively on diseased individuals, it is

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reasonable to expect that they might reduce disease prevalence much more rapidly than would occur if mortality were non-selective.

Here, I use a simple mathematical model to evaluate the potential for selective predation by wolves to reduce or eradicate chronic wasting disease in populations of elk in Rocky Mountain National Park.\textsuperscript{4}

The model incorporated 14 parameters: Maximum per capita rate of recruitment, per capita natural mortality rate, per capita mortality rate from CWD, transmission rate, excretion rate, turnover rate of infectious material, population number where recruitment is 0, initial number of susceptibles, initial mass of infected material, initial number of infecteds, number of wolves, maximum kill rate, inflection point of functional response, and compensation between predation and natural mortality.\textsuperscript{5} Notwithstanding the limited geographic purview of this model, the results provide an encouraging basis for including in the upcoming wolf restoration and management plan the goal of eradicating chronic wasting disease in elk throughout Colorado, through wolf restoration:

In the absence of disease the model predicted that the elk population would reach an ecological carrying capacity of 1044 animals over about 35 years (Figure 1). Adding disease in year 1 produced oscillatory dynamics typical of epidemics (Figure 2 A, B). Adding wolves in year 50 caused relatively rapid decline in the prevalence of CWD, leading to eradication 19 years after introduction (Figure 3 A, B). The time required to eradicate the disease was sensitive to assumptions on vulnerability of infected animals and compensation between predation and mortality due to disease and natural causes (Figure 4). Increasing vulnerability of infected animals accelerated the rate of eradication but did not influence the number of susceptible elk at steady state, which was approximately 240 animals, regardless of vulnerability.\textsuperscript{6}

Those oscillatory dynamics typical of epidemics figuratively express the need to restore a critical balance in nature. But the model showed that not just the presence of wolves in Rocky Mountain National Park, but also the number of them, would determine whether chronic wasting disease among elk in the park would be eradicated or merely curtailed:

Time to eradication declined as the population size of wolves increased (Figure 6). For any given wolf population size, times to eradication increased with increases in the extent of compensation between predation and disease mortality. When compensation between disease mortality and predation mortality was high (i.e., .75), there was a threshold population size of wolves somewhere between 10 and 15 animals where eradication of CWD was infeasible (causing the truncation of the .75 compensation curve in Figure 6). When the wolf population size dropped below this threshold, predation simply pushed the prevalence of the disease to a new, lower steady state in the elk population. Near this threshold, time to eradication declined dramatically with increasing numbers of wolves.

\textsuperscript{5} Hobbs (2006), p. 4, Table 1.
\textsuperscript{6} Hobbs (2006), p. 4.
However, when the wolf population size exceeded 20, further increases in numbers of wolves had much less dramatic effects on time to eradication (Figure 6).\(^7\)

Notwithstanding uncertainty, the report discussed the range of implications:

Results from simulations suggest that predation by wolves has the potential to eliminate CWD from an infected elk population. Although the time required to achieve this result depends in a fundamental way on assumptions about prey vulnerability, the nature of compensation among different sources of mortality, as well as parameters regulating disease transmission, it appears that eradication within two or three decades would be feasible by maintaining a constant population of approximately 20 wolves.

This result must be tempered with the very important caveat that the elk population is closed to infection from outside sources. If infection is continually reintroduced, then eradication may not be feasible. However, model results suggest that even of [sic] open populations, wolf predation will substantially reduce prevalence. Moreover, the model does not represent a potentially large benefit of predation, the removal of carcasses as sources of infection. Although I did not have any way to estimate parameters for transmission from carcasses, such transmission is known to occur in mule deer.

Selective predation does not allow a larger population of susceptible animals relative to the non-selective case because wolves are assumed to consume more susceptible animals as infected ones become rare.

Model experiments reveal that uncertainties in estimates of values of parameters for transmission and excretion rates cause substantial uncertainty in estimates of time required to eradicate CWD from elk populations. Thus, the quantitative result from the simulations described here is not strong—we cannot specify with confidence how long it might take for predators to eliminate CWD from an elk population. Moreover, there are combinations of parameters for which eradication is infeasible. In particular, if transmission and excretion rates are high, it appears unlikely that predation by wolves will cause eradication within any reasonable period of time.

These results suggest that predation by wolves could have potent effects on disease prevalence under certain conditions. Although non-selective predation, as might occur with culling for example, may also be effective in eradicating the disease in a closed population, our results suggest that natural predation could substantially reduce the time required to eliminate the disease.\(^8\)

This 2006 report to the National Park Service shows that, while eradicating chronic wasting disease in elk cannot be guaranteed, a regulatory limit on the abundance of wolves would impair that possibility and quite likely thwart eradication. Similarly, the “very important caveat that the elk population is closed to infection from outside sources” shows that a regulatory limit on wolf distribution anywhere where there are elk in Colorado would also thwart

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eradication; it would allow for a reservoir of chronic wasting disease to persist in the elk that live where the wolves would not be allowed, and they would recurrently reinfect elk in the areas where wolves would otherwise be eradicating the disease.

Could wolf restoration also curtail or eradicate chronic wasting disease in deer? Biologists including the author of the 2006 report to the National Park Service that we summarize above, analyzed this possibility in a 2011 peer-reviewed paper. The backdrop to their research was the contemporary disruption of the critical balance in nature: “Ecologic imbalances can diminish the resilience of host species to natural fluctuations in pathogens and the host’s capacity to resist or recover from pathogen introductions.”9 They repeated the hypothesis from the 2006 report that “if predators prey selectively on diseased individuals, it is reasonable to expect that they might reduce disease prevalence much more rapidly than would occur if mortality were nonselective.”10 And they suggested logical reasons for why predators would prey selectively on diseased individuals:

[Pre]dators’ high success with diseased prey may be due to poorer body condition of the prey and consequently prey’s slower avoidance behavior, decreased awareness, or reduced stamina. Studies have suggested that predators may also use visual pattern, scent, or behavioral cues to select compromised prey.11

These biologists also summarized some of the “widely observed” evidence supporting the notion that, indeed, “predators have a greater selectivity for diseased prey.”12 Those examples drew from multiple taxa including ungulates:

[D]iseased moose (Alces alces; Joly and Messier, 2004a) and bison (Bison bison; Joly and Messier, 2004b) appeared to be more susceptible to predation by wolves than apparently healthy animals. White-tailed deer (Odocoileus virginianus) killed by wolves may appear normal to human inspection, but subtle alterations may be present as demonstrated by the correlation of fawn and subadult survival to maternal and grand-maternal nutrition (Mech et al., 1991). Further, Krumm et al. (2009) recently reported that mountain lions (Puma concolor) prey selectively on prion-infected mule deer (Odocoileus hemionus) in Colorado, USA.13

The study pertaining to mountain lion predation on prion-infected mule deer in Colorado (published in 2010 and not 2009 as quoted above) is instructive. Biologists led by a researcher for the Colorado Division of Wildlife (predecessor to Colorado Parks and Wildlife) captured nine mountain lions on the northern Front Range and outfitted them with GPS collars. Over the course of subsequent years, periodic sedentary behaviors of the mountain lions enabled the researchers to locate the mountain lions' kills and thereby obtain and analyze samples of mule deer killed by them to determine whether those deer had been infected by prions. They located

“54 lion-killed deer carcasses that were greater than or equal to 2 years of age, had suitable tissue available and had greater than or equal to three associated vicinity kills.”\(^\text{14}\) Those associated vicinity kills consisted of mule deer killed by human hunters within three kilometers, a control group which enabled comparison between the infected statuses of the deer killed by mountain lions versus those killed by hunters. They found that “[a]dult mule deer killed by mountain lions were more likely to be prion-infected than were deer killed more randomly in sympatric populations, suggesting that mountain lions were selecting for infected individuals when they targeted adult deer.”\(^\text{15}\)

Noting that mountain lions in Colorado selectively preyed on prion-infected deer but that chronic wasting disease has not been extinguished, the authors of the 2011 study wanted to build on that finding with a further-reaching but (now it turns out) practical inquiry:

Although mountain lions do appear to preferentially prey on mule deer infected with CWD (Krumm et al., 2009), epidemics persist in mule deer herds in the presence of mountain lion predation (Miller et al., 2008; Krumm et al., 2009). Based on the subtlety of the behavioral changes early in the course of CWD infection, we would expect coursing predators like wolves to show even greater potential selective capability than ambush predators like mountain lions; however, wolves were extirpated and packs are presently absent from the areas in North America where CWD is endemic in deer, so field data are not available for comparison. Consequently, to assess this possibility we developed and explored the behavior of models representing the effects of selective predation by wolves and compared these with nonselective predation, such as through harvest or culling, on CWD dynamics in deer.\(^\text{16}\)

The study came to similar conclusions regarding deer as did the 2006 report predicting effects of wolves on the prevalence of prion-infected elk in Rocky Mountain National Park:

Although the time required to achieve results depends in a fundamental way on assumptions about prey vulnerability to selective predation and the nature of compensation among different sources of mortality, as well as parameters regulating disease transmission, it appears that prevalence could be halved within a decade and eliminated within the century through sustained predation by a pack of wolves that removed 15% of deer per year in a closed population. Although uncertainty in parameter estimates limits our confidence in predicting the precise timeframe required for control or elimination of disease, these time estimates provide a basis for comparison of approaches. What is most clear is a consistent and robust trend toward decreasing CWD prevalence in populations subject to predation, particularly selective predation, over a range of parameter estimates (Fig. 2). A similar decreasing trend would be predicted in a population subject to predation where CWD was repeatedly introduced at low levels (i.e., an open population); however, the slope of decline would be variable and elimination

might never be achieved because high rates of disease reintroduction may offset selective predation of CWD-positive individuals.\(^{17}\)

As with the 2006 model on wolves and prion-infected elk in Rocky Mountain National Park, the difference between eradicating chronic wasting disease from deer and merely reducing the prevalence of the disease in deer populations depends in large part on whether the wolf population is abundant and well distributed across the landscape – which would not be the case in the event that the restoration and management plan were to impose a maximum number of wolves or to delineate areas the wolves would not be allowed to live. The 2011 study also found that:

Simulation results suggested that selective predation could also dampen or eliminate the emergence of CWD in new locations (Fig. 3), adding support to speculation that the absence of large predators presents an amplification risk factor for establishment of CWD (Samuel et al., 2003).\(^{18}\)

That shows that regulatory wolf no-go zones in Colorado would enable not just possible persistence of chronic wasting disease in the deer living in those areas, but also the emergence of the disease in those areas even if their deer are not currently infected. And thus any limit on the distribution of wolves in Colorado would undermine achievement of our proposed ecological goal of eradicating chronic wasting disease in Colorado through wolf restoration – a goal that is supported by the statutory intent to restore a critical balance in nature.

C. Trophic cascades.

Survival of the fittest and curtailment of infectious maladies must be complemented with at least one other standard and goal because these first two standards and goals apply largely to the wolves and their prey and not to the multitudinous other manifestations of nature.

Because Colorado Revised Statutes 33-2-105.8 identifies wolves as an “essential part of the wild habitat of Colorado” and declares that “[o]nce restored to Colorado, gray wolves will help restore a critical balance in nature,” the effects of that restoration must be achievable and measurable beyond the effects on the wolves and their prey, beyond even the effects on other animals, and should be achieved and measured in part through future effects on wild habitat and on nature overall. Habitat and nature extend beyond the wolf’s prey species, to other animals as well, and clearly also include the plants.

That brings us to the third necessary manifestation of restoring a critical balance in nature which, like the re-establishment of survival of the fittest and the curtailment of infectious maladies, would also be undercut and made unachievable through regulatory limits on wolf numbers or distribution. Since the 1980’s, biologists have identified specific population-level effects of trophic cascades precipitated by predators. Trophic cascades is the scientific term for the ripple effects on diverse animal and plant species stemming from predatory behaviors. Those ripple effects consist of the influencing of various animals’ behaviors, distributions and

abundance, and even of the distribution and abundance of plants, in ways that ultimately favor the persistence of all animals and plants in an ecosystem through maintaining the specific conditions to which each species has evolutionarily adapted.

Largely due to the research opportunities afforded through reintroduction of wolves to Yellowstone National Park in 1995, in addition to other investigations, scientists have attributed multiple examples of trophic cascades to wolves. Incorporating the creation and maintenance of trophic cascades into a goal in the wolf restoration and management plan stems logically from the language of C.R.S. 33-2-105.8. In fact, compliance with the law will not be achieved if the plan would thwart the ability of Colorado’s future population of wolves to restore and maintain trophic cascades.

The widespread extirpation of wolves throughout the course of the development of the U.S. disrupted trophic cascades nationwide, including in Colorado. Wolves must be restored in sufficient abundance and density on the landscape to help to re-precipitate trophic cascades, which are central to maintaining the balance of nature. A 2011 review by 34 scientists concluded that “Top-down forcing must be included in conceptual overviews if there is to be any real hope of understanding and managing the workings of nature.”19 The best-known example of trophic cascades stems from wolf reintroduction to Yellowstone National Park, where biologists discovered that alongside some of the larger waterways where steep terrain blocks elk’s ability to spot approaching wolves, cottonwood and willow trees have proliferated where previously elk browsing kept them from maturing; the elk had learned to avoid such areas where wolves can surprise them. These riparian trees provide food and dam construction materials for beaver that are far more common than before wolf reintroduction.20 The dams that the beavers construct provide habitat for a wide variety of fish, amphibians, and reptiles.21

A scientist associated with the Colorado Natural Heritage Program in Colorado (who is also on the emeritus faculty of the Department of Environmental Science and Engineering at Colorado School of Mines) wrote in the Colorado Native Plant Society newsletter last summer that wolves reintroduced to Colorado could have similar beneficial effects on the degraded vegetative communities that he is familiar with in Colorado:

The most noticeable damage occurs in aspen groves and in riparian willow carrs, particularly if elk use these resources year-round or if unmanaged livestock overgraze these systems. When healthy, both ecosystems support a high diversity of sub-dominant plant species, as well as diverse animal communities including mammals, birds, and invertebrates. This diversity declines with prolonged heavy grazing. In Rocky Mountain National Park, excessive grazing of alpine tundra plants by elk may have contributed to the decline of ptarmigan numbers.

Aspen groves—typically clones in which the trees are interconnected by a common root system—produce shoots, or suckers, from the root system to expand the grove or to replace ageing or diseased trees. When the shoots are heavily browsed by elk and other herbivores, the groves fail to mature. Elk also gnaw the bark of aspen trees during late winter and early spring, and that can lead to infection of the tree by various diseases. Both situations in concert can eventually lead to the death of the entire clone.

Riparian willow carrs, particularly those in broader valley bottoms, are commonly occupied by beavers. Willows and beavers are codependent. Beavers use the willows for food and building materials for their dams and lodges. Beaver dams raise the water table, providing shallow ground water that willows need. When willows are browsed heavily by elk, beavers leave due to over-competition with elk, beaver dams are no longer maintained, and streams and rivers begin to run straight and fast. This results in downcutting of the channel, a drop in the water table, and further demise of the willows. Sedges, grasses, and smaller shrubs that help to maintain channel stability are also affected by heavy elk browsing.\(^{22}\)

However, restoring the critical balance in nature in the case of such vegetative changes would only occur with sufficient numbers of wolves in the state:

The reintroduction of wolves to Colorado is likely to have mostly subtle and indirect effects on our native plant communities. Those effects will probably not occur after until wolf populations increase to ecologically effective numbers and stabilize.\(^{23}\)

A cap on the abundance of wolves would prevent there being enough of them to be ecologically effective and would therefore thwart the needed trophic cascades that would help to restore a critical balance in nature. Such an absence of wolf-caused trophic cascades was documented in the Apache National Forest of east-central Arizona where endangered Mexican gray wolves were reintroduced in 1998, and should serve as a warning to Colorado of the adverse ecological effects of limiting wolf numbers. The reason for that absence was insufficient wolf numbers – which illustrates precisely the effect that a wolf population cap would cause in Colorado. (It would also be caused by heavy-handed management in the absence of a numeric cap, a management that we argue against in other sections of this letter below.) Researchers in 2009 selected three mixed-conifer sites on the Apache National Forest to characterize long-term age structure of aspen and to check for the possible occurrence of a tri-trophic cascade involving Mexican wolves, elk and aspen, as the same researchers had previously documented was occurring in Yellowstone National Park. The abstract to the study describes the sites and the long-term and more recent effects of elk herbivory within them:

These mixed-conifer sites included (a) a refugium site, (b) an old-growth site, and (c) a site thinned in 1991–1992. The refugium site was inaccessible to elk and cattle whereas the old-growth and thinned sites were accessible to elk, but not cattle. Age structure results indicated that aspen recruitment (i.e., the growth of sprouts/seedlings into tall


saplings, poles, and eventually trees) at the refugium site had been ongoing over a period of many decades. In contrast, aspen recruitment at the old-growth and thinned sites decreased significantly (p < 0.05) during the two most recent decades when elk populations, as indexed by annual harvest levels, were relatively “high”. From 2000 to 2008, only 2.9 Mexican wolves per 1000 elk were present on the Apache National Forest compared to 9.3 western gray wolves (Canis lupus occidentalis) per 1000 elk in Yellowstone National Park where tri-trophic cascades involving wolves, elk, and aspen have been reported. The low number of Mexican wolves relative to their primary prey (elk) suggests that an ecologically effective density of wolves has not become established in east-central Arizona. Furthermore, the lack of recent aspen recruitment in stands accessible to elk indicates an absence, to date, of a tri-trophic cascade.\(^2\)

These researchers attributed that absence to there not being enough wolves on the landscape:

Soule et al. (2003) indicate an ecologically effective density of highly interactive species (such as wolves in terrestrial ecosystems) is one that would maintain critical ecological interactions and help ensure against ecosystem degradation. With regard to a tri-trophic cascade involving wolves, elk, and aspen, this would be a predator density sufficient to mediate the behavior and/or density of native herbivores thus regulating potential impacts to plant communities. The relatively low ratio of Mexican wolves per 1000 elk on the Apache National Forest, in comparison to gray wolves in northern Yellowstone (Fig. 6a) and other areas of north America (Fig. 6b), appears to indicate that Mexican wolves have not achieved an ecologically effective density in Arizona.\(^2\)

They concluded that Mexican wolves “appear to not yet have attained an ecologically effective density as we were unable to document a trophic cascade (i.e., improved aspen recruitment). Unless wolf densities increase, it is possible that the potential ecological benefits of these apex predators in the mixed-conifer forests of east-central Arizona will not be achieved.”\(^2\)

The context to the Mexican wolves not having attained an ecologically effective density in 2009 when that study was conducted is that 2009 represented the demographic nadir in a four-year downturn in the number of Mexican wolves in the wild in Arizona and New Mexico. After reintroduction in 1998, the population had peaked at 59 animals in 2006.\(^2\) But the previous year, 2005, decision-making authority over removing wolves from the wild in Arizona was effectively delegated from the U.S. Fish and Wildlife Service to the Arizona Department of Game and Fish through standard operating protocol 13 on control of Mexican wolves. Between 2005 and 2009, federal employees removed 71 wolves from the population.\(^2\) As a consequence, by 2009 the bi-state wolf population had been reduced by over 28% to 42 animals including 27 in Arizona. That year, there were only two successful breeding pairs (a male wolf and a female

\(^{27}\) Minimum population estimate, minimum breeding pair estimate, and population estimate numbers per state within the MWEPA, 1998 - 2019: www.fws.gov/southwest/es/mexicanwolf/pdf/popestimateweb9819%20final.pdf
wolf that produced two or more pups that survived through December 31 of the year of their births) in the combined states of Arizona and New Mexico.\textsuperscript{29} (In December 2009, the Fish and Wildlife Service entered into a settlement agreement with conservation organizations including the Center for Biological Diversity in which the federal agency committed to no longer allowing the states to decide on removing wolves. The population began to grow again in ensuing years.) Learning from wolf mismanagement in the Southwest and the impacts on aspen, it is critical that the Colorado gray wolf restoration and management plan not limit wolf numbers, in order to enable wolf restoration to help restore a critical balance in nature.

The process of trophic cascades also plays out through wolf attacks on coyotes, which the larger wolves treat as territorial rivals. As a result, other mammals on which the coyotes prey benefit in the presence of wolves. For example, after wolves were reintroduced to Yellowstone National Park and expanded their range southward, pronghorn in Grand Teton National Park rebounded from a significant decline that had been caused by coyote hunting of the pronghorn fawns.\textsuperscript{30} Similarly, red foxes and gray foxes in Minnesota and Wisconsin are more prevalent in areas with wolves than in areas with few or no wolves and a corresponding abundance of coyotes.\textsuperscript{31} And in the absence of wolves in Utah, in order to minimize dangerous proximity to coyotes, kit foxes avoid suitable habitats and thereby lessen their access to prey.\textsuperscript{32} In Yellowstone, rodents such as voles thrive where there are wolves.\textsuperscript{33} By killing coyotes in Wisconsin, the presence of wolves led to an increase in snowshoe hare numbers, which in turn may benefit Canada lynx.\textsuperscript{34}

Many of these same species in Colorado would similarly benefit from the presence of wolves, including endangered Canada lynx.\textsuperscript{35} So might black-footed ferrets and swift foxes as well – for the same reason; the latter two are also preyed upon by coyotes.\textsuperscript{36} Notably, were wolves in Colorado to be banned from the grasslands ecosystems inhabited by black-footed ferrets or swift foxes, those benefits derived through trophic cascades would not accrue to these much smaller and also imperiled carnivores. This shows another instance in which curtailing the distribution of wolves in Colorado would run counter to the statutory intent to restore a critical balance of nature.

\textsuperscript{29} Minimum population estimate, minimum breeding pair estimate, and population estimate numbers per state within the MWEPA, 1998 - 2019: www.fws.gov/southwest/es/mexicanwolf/pdf/popestimateweb9819%20final.pdf
Again, the example in reintroduction of the Mexican wolf to Arizona and New Mexico should serve to caution the CPW Commission against limiting wolf abundance through the Colorado gray wolf restoration and management plan. A 2018 M.S. thesis examined through the placement of 18 camera traps in three plots in eastern Arizona – cameras which over the course of 4,517 trap nights took 38,820 photographs, 1,224 of which were independent photos of wildlife species – whether Mexican wolves can influence the distribution of elk, mule deer, coyotes and gray foxes. Two of the plots were within wolves’ core home ranges while the third was in an area without sustained wolf activity. Detection rates for coyotes, gray foxes, elk and mule deer were not statistically different in the plots, “which means there is no indication that the Mexican wolves are influencing the distribution of coyotes, gray foxes, elk, or mule deer in the region.”

The thesis suggested three possible explanations – the first of which is likely most influential and which we quote here:

One plausible explanation for the lack of significance may be due to the Mexican gray wolf population size and range. In 2016, the Mexican gray wolf population was estimated to be around 113 wolves occupying 41,735 km², primarily in New Mexico (US Fish and Wildlife Service, 2016) whereas the wolf population of approximately the same size in Yellowstone National Park occupied 8,989 km² (Smith et al. 2017). For a landscape of fear to be instituted in coyotes, gray foxes, elk, and mule deer, these species have to encounter the Mexican wolves, in either a competitive or preyed upon manner, often enough for the Mexican wolves to be incorporated into each species’ optimal foraging strategy (Lima and Dill 1990, Brown, Laundré, and Gurung 1999) as happened in the Yellowstone National Park system (Ripple and Beschta 2004a). If these species were to encounter the Mexican gray wolf on a consistent basis, it would be reasonable to assume a modified distribution of these species, as measured by detection rate, such that a lower detection rate is observed for coyotes, elk, and mule deer, but a higher detection rate for gray foxes, in areas consistently occupied by Mexican wolves. If, however, a Mexican gray wolf is encountered only occasionally, not consistently, then the risk of predation/competition by the Mexican gray wolf would not be incorporated into the species’ optimal foraging strategy. Therefore, in this case, we should not see differences in distribution of these species as measured by detection rate. According to our analyses there is no statistically significant difference in detection rate between plots with Mexican wolves and plots without, thus we suggest that a landscape of fear has not been instituted in the Blue Range Wolf Recovery Area.

For additional context on the 113 Mexican wolves that were estimated to survive in Arizona and New Mexico in 2016, which throughout that year (as has the wolf population in every other year in this century) inhabited almost exclusively the Gila National Forest, Apache National Forest

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37 Hoskinson, J.S.. 2018. Mexican gray wolves and the ecology of fear: a comparative assessment of community assemblages in Arizona. Thesis submitted to the faculty of the Department of Ecology and Evolutionary Biology in partial fulfillment of the requirements for the degree of Master of Science in the graduate college of the University of Arizona; p. 17.
and Fort Apache Indian Reservation, it is worth noting that the carrying capacity of the two national forests was calculated at 468 wolves based on the biomass of elk and deer on those forests, and not counting other animals that the wolves may eat such as jackrabbits and javelina.\textsuperscript{40} In other words, even if all those 113 wolves had lived in the two national forests, and even if they eschewed preying on smaller animals and only fed on deer and elk, their numbers were fewer than 25% of the carrying capacity, which helps explain why they apparently did not influence the distribution of elk, mule deer, coyotes and gray foxes in the thesis study quoted above. Again, the lesson for development of the Colorado gray wolf restoration and management plan must be that the abundance of wolves should not be limited.

Our proposed goal of re-establishing the processes of trophic cascades should be built with several of the aforementioned known effects of wolves elsewhere serving as metrics in Colorado, and establishing the procedures to measure such effects through baseline research prior to and following wolf restoration.

\textit{D. Restoration must be statewide.}

Colorado Revised Statutes 33-2-105.8 requires that the wolf restoration and management plan “must include . . . [t]he places, manner, and scheduling of reintroductions of gray wolves by the division [i.e. Colorado Parks and Wildlife], with such reintroductions being restricted to designated lands.”

The law defines “designated lands” as “those lands west of the continental divide in Colorado that the commission determines are consistent with its plan to restore and manage gray wolves.”

In broader contrast, the law defines “restore" or "restoration" as “any reintroduction, as provided for in section 33-2-105.7 (1)(a), as well as post-release management of the gray wolf in a manner that fosters the species' capacity to sustain itself successfully.”

While the law only refers to those geographically constrained “designated lands” twice, including the instance quoted above, the law refers eight times to “restore” and “restoration,” the terms encompassing a broader mandate and conspicuous for not being delineated geographically. Notably, that broader mandate is invoked in the finding and declaration that “[o]nce restored to Colorado, gray wolves will help restore a critical balance in nature.” But the broader intention in the word \textit{restore} also appears in the charge to the CPW Commission to “[d]evelop a plan to restore and manage gray wolves in Colorado.”

Had the law empowered the commission to develop a plan that would limit the distribution of wolves in Colorado – which it does not – that last statement would have substituted “within Colorado” for the actual “in Colorado;” but the law does not authorize developing a plan to restore and manage wolves \textit{within} Colorado.

Instructively, in separately delimiting the permissible locales for wolf reintroductions while in eight other passages affirming wolf restoration as either a statewide goal or at least not a goal that is not limited by geography, the law makes clear that the wolf restoration and management plan may not arbitrarily limit the distribution of wolves within the state. Such limitations may only serve the purpose of, in part of the definition of restoration, “post-release management of the gray wolf in a manner that fosters the species' capacity to sustain itself successfully.” Limiting the range of wolves would not foster the species capacity to sustain itself successfully. Instead, through the definition of *restore* and *restoration*, the law makes clear that the benefits of wolf restoration must apply statewide (notwithstanding that different areas in the state can support wolves at varying capacities). Statewide application of the law means that no area of the state can be deprived of having wolves, and wolves cannot be deprived of the benefits of occupying any area within Colorado.

**E. A spurious rationale for limiting wolf numbers and distribution.**

It is worth the CPW Commission learning from the ongoing mistakes in the U.S. Fish and Wildlife Service’s Mexican gray wolf recovery program, whose regulations require that endangered wolves be limited in their numbers and curtailed in their distribution, and bind the Service to enforce those population caps and geographic restrictions. (The U.S.D.A. Animal and Plant Health Inspection Service and its branch, Wildlife Services, conducts most of the wolf removals, as directed by the Fish and Wildlife Service.) The 1998 final rule for the reintroduction of the Mexican wolf as an experimental, non-essential population under section 10(j) of the Endangered Species Act, justified imposing the initial geographic restriction on the wolves in this statement:

> A limited and defined area is considered necessary to allow the wolf the highest degree of acceptance and recovery and to allow the Service and cooperating agencies to plan for wolf management. Allowing the recovery areas to expand out continually would defeat this purpose. However, if the Service determined it was necessary to survival and recovery of the reintroduced population, it is possible that after thorough evaluation the Service could recommend changes to the recovery area boundaries. These would have to be proposed as a revision to the final Mexican Wolf Experimental Population Rule and be subject to formal agency and public review under rulemaking procedures and the National Environmental Policy Act. Language has been added to the rule to clarify that members of wolf packs whose territories consist of public lands lying both within and outside designated recovery areas would not routinely be captured and translocated.  

To reach this goal of providing the Mexican wolf the “highest degree of acceptance and recovery,” the Fish and Wildlife Service through regulation pledged to remove any wolf (including those not in conflict with livestock) whose home territory lay wholly outside of two national forests and also not on any contiguous private or tribal lands where the landowner or tribe had requested the wolf be allowed to stay. Elsewhere, including on any BLM public lands and on nearby other national forests, the wolves had to be removed no matter the circumstances. That ultimately confined the wolves to approximately 1.1 million acres on the Apache National Forest, 3.3 million acres on the Gila National Forest, 1.7 million acres on the Fort Apache Indian

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Reservation and 157,000 acres on the Ladder Ranch owned by the Turner Endangered Species Fund – amounting to over 6.2 million acres in one bloc across two states.

For a wide-ranging subspecies such as the Mexican wolf, this constrained recovery prospects considerably. A 2001 independent scientific review of the Mexican wolf reintroduction program recommended that the Service “[i]mmediately modify the final rule to allow wolves that are not management problems to establish territories outside” the two national forests, in part because the restrictive provision “needlessly excludes habitat that could substantially contribute to recovery.”\textsuperscript{42} In 2007, the American Society of Mammalogists passed a resolution on reintroduction and recovery of the Mexican wolf that urged the Fish and Wildlife Service to “allow wolves to roam freely throughout the Southwest.”\textsuperscript{43}

The intended acceptance and recovery stemming from this geographic restriction and from other provisions allowing for the live-removal as well as the killing of depredating wolves, was supposed to ensure that more wolves ended up left alive:

Designation of the released wolves as nonessential experimental is considered necessary to obtain needed State, Tribal, local, and private cooperation. This designation also allows for management flexibility to mitigate negative impacts, such as livestock depredation. Without such flexibility, intentional illegal killing of wolves likely would harm the prospects for success.\textsuperscript{44}

In 2015, the Fish and Wildlife Service amended the 1998 experimental population rule to allow Mexican wolves to inhabit and establish territories in approximately 17 times as much area as they previously were allowed, to eventually encompass (in chronologic stages) all lands south of Interstate 40 in Arizona and New Mexico. Again, the Service bound itself by pledging to always remove Mexican wolves that breached these boundaries in the U.S. The Service also added a pledge to remove from the wild in Arizona and New Mexico (through live removals or killing) all Mexican wolves in excess of the number 325. The rationale was essentially the same as in 1998.\textsuperscript{45}

In 2018, in response to a lawsuit by the Center for Biological Diversity and our allies, the U.S. District Court in Arizona held the 2015 Mexican wolf experimental population rule to be unlawful, in part for its provision limiting the distribution of wolves and not allowing them to live north of I-40. The court has ordered the rules to be revised by July 2022, and the analysis process for that revision is underway.

In the meantime, it is clear that the caps on wolf numbers and curtailment of their distribution, as well as the other provisions allowing for the killing and live-removal of wolves, failed in their intended purpose of allowing the wolf “the highest degree of acceptance and recovery.” A peer-reviewed study published this year tested “[t]wo opposing hypotheses” that “implementing lethal management may decrease poaching incidence (killing for tolerance) or

\textsuperscript{42} Paquet et al (2001), pp. 65, 66.
\textsuperscript{44} 63 Fed. Reg. 1755 (Jan. 12, 1998).
increase it (facilitated illegal killing)” through analyzing mortality and disappearance data pertaining to Mexican wolves. They wanted to know whether wolf poaching (reported and unreported) in Arizona and New Mexico responded to changes in policy that reduced protections to allow more wolf-killing. They employed advanced biostatistical survival and competing risk methods to data on individual resightings, mortality and disappearances of collared Mexican wolves, supplemented with Bayes factors to assess the strength of evidence. Their abstract summarized results:

We find inconclusive evidence for any decreases in reported poaching. We also find strong evidence that Mexican wolves were 121% more likely to disappear during periods of reduced protections than during periods of stricter protections, with only slight changes in legal removals by the agency. Therefore, we find strong support for the ‘facilitated illegal killing’ hypothesis and none for the ‘killing for tolerance’ hypothesis. That demonstrates that policies to remove wolves, including because they are in locales where they are not permitted or because their numbers have exceeded a population cap, did not save wolves from illegal killings – and might even have helped motivate some people to choose to break the law and kill wolves. Similarly, there is no reason to believe that setting regulatory and enforceable limits on where wolves can live in Colorado, or on how many can live in Colorado or any region within the state, would have any benefit for the wolves. It would not serve the statutory purpose in restoration to foster the Colorado wolf population’s “capacity to sustain itself successfully.”

In conclusion, the Colorado gray wolf restoration and management plan must actively facilitate the capacity of a population of wolves to restore Colorado’s critical balance in nature. To do that, the plan should enshrine three ecological goals. The first goal, assuring the multiple-generational predation-induced process of survival of the fittest, can practically effect (and to a limited extent be measured in) the ungulate prey of the wolves and the wolves themselves. The second ecological goal, which is the extinguishment and curtailment of infectious maladies with a focus on chronic wasting disease, can be achieved and measured in ungulate prey species. The third goal, broader in scope, the restoration and maintenance of trophic cascades, can effect (and be precisely measured in) a variety of animal and plant populations. All of these goals stem naturally from the language of C.R.S. 33-2-105.8. Each of these individually, and certainly all of them together, illuminate the utter incompatibility of the law with establishment of any arbitrary cap on the number of wolves or limit on the distribution of wolves within Colorado.

II. Criteria for removing the gray wolf from the state endangered species list.

Colorado Revised Statutes 33-2-105.8 requires that the gray wolf restoration and management plan include “[m]ethodologies for determining when the gray wolf population is sustaining itself successfully and when to remove the gray wolf from the list of endangered or threatened species.”

Three conditions should guide when the gray wolf should be removed from Colorado’s endangered species list. First, the gray wolf in Colorado should not be imperiled due to the threat of killing by people. Second, the gray wolf in Colorado should have sufficient numbers and connectivity to other wolf populations to remain genetically viable. And third, the gray wolf should be influencing trophic cascades according to a variety of metrics described in Section I, above, and should have successfully extinguished chronic wasting disease from elk and deer in Colorado, or suppressed its incidence to negligible amounts.

A. Viability

It has long been known that populations suffer loss of viability through genetic drift and inbreeding depression stemming from small and/or fragmented populations. But how many animals (or plants) are necessary for viability has been determined in a variety of ways and with refinements in methodologies. A scientist in 1995 calculated that effective populations of around 5,000 organisms (i.e. that number of reproducing animals -- not equaling the total number of animals) would be necessary to stave off deleterious mutations leading to inbreeding and other genetic ills.47

In 2003, a study noted that population size is a major determinant of extinction risk and used population viability analysis to estimate minimum viable populations for 102 species, with a mean estimate of 7,316 organisms and median estimate of 5,816 adults. They advised that conservation programs for wild vertebrate populations conserve habitat capable of supporting approximately 7,000 adults in order to ensure long-term persistence.48

Then a 2007 meta-analysis of population viability studies for 212 disparate species, determined that the median minimal viable population was 4,169 organisms.49 And in 2009 researchers found that “thousands (not hundreds) of individuals are required for a population to have an acceptable probability of riding-out environmental fluctuation and catastrophic events, and ensuring the continuation of evolutionary processes.”50

A 2011 critique challenged the universal applicability of a single number as a threshold for population viability. This set of scientists agreed that in many instances “multiple populations totaling thousands (not hundreds) of individuals will be needed to ensure long-term persistence” and “realistic MVPs might well be in the thousands for many life histories,” but argued that “uncertainty around any guideline figure would be of a similar order of magnitude” because “estimates both among and within species show striking variation for many reasons. The fundamentally contingent nature of MVPs means that we cannot support a universally applicable

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MVP threshold.” Noting the importance of population trend in extinction risk, they determined that had a previous meta-study (Brook et al 2006) of 1,198 populations, which found a median minimal viable population number at 1,181 organisms, instead excluded populations with a significant declining trajectory, then the median for viability would drop to just 355 organisms.

Not all wolves in a family pack breed; generally, just two animals do so. With a median pack size of ten, that means that 20% of the wolves contribute genetically, serving as an effective population. Since wolf numbers in Colorado will be increasing with reintroduction, even these minimal 355 breeding animals would have to represent five times that many wolves overall to be genetically viable – in other words 1,775 wolves. However, it is possible that number is above the wolf carrying capacity of Colorado’s ecosystems. A 1994 congressionally-chartered wolf reintroduction feasibility study found that 1,128 wolves could live on Colorado’s seven national forests based on the biomass of elk and deer. The assessment did not assess carrying capacity on other lands.

To stay within the ballpark of that roughly-estimated and very old calculation of carrying capacity – 1,128 wolves – and to ensure that the minimal viable number we propose as a recovery goal to assess genetic viability be based on the science but also actually be achievable, we propose that criterion be met through a minimum presence over three successive years of 750 wolves, with a growing population each year and with connectivity through natural migration to and from wolves in the northern Rocky Mountains and Mexican gray wolves in the Southwest, such that at least one immigrant wolf into Colorado from each of these regions, north and south, successfully reproduce and raise at least two pups to age two in Colorado, every two years, for at least six years prior to delisting. That would amount to an effective population of just 150 wolves within the state, but the connectivity to wolf populations outside of Colorado would ensure that genetic drift and inbreeding do not doom Colorado’s wolves.

B. Ecological goals.

Genetic viability goals are not sufficient to determine at what point the gray wolf should be removed from the endangered species list in Colorado. The finding and declaration in Colorado Revised Statutes 33-2-105.8 to restore a critical balance in nature should be incorporated into recovery criteria, as a means to ensure that purpose is fulfilled. Researchers argued in a 2015 review that viability-based standards in recovery plans do not suffice, and that ecosystem-focused criteria “are important not only for ensuring sufficient habitat quantity, quality, and connectivity, but also for restoring the ecological function of species by maintaining abundance at a level that provides a particular ecosystem function,” particular “for strongly interactive species that are key to ecosystem structure and function such as keystone species, foundation species, ecosystem engineers, and top predators.”

A population of wolves that is large enough and sufficiently well-distributed throughout Colorado so as to selectively prey on prion-infected elk and deer sufficiently to extinguish or nearly extinguish (with an explanation as to why wolves cannot suffice to fully extinguish) chronic wasting disease in elk and deer in Colorado, should be one of the ecological criteria for gray wolf recovery in Colorado and removal from the state endangered list.

Another ecological criterion should be a population of wolves that is large enough and sufficiently well-distributed throughout Colorado so as influence the behavior and/or distribution of elk sufficient to restore or nearly restore (with an explanation as to why wolves cannot fully restore) the natural riparian and hydrological functioning of significant stretches (to be defined further) of the state’s rivers, streams and other wetland habitats.

A third ecological criterion should be a population of wolves that is large enough and sufficiently well-distributed throughout Colorado so as to reduce the number and/or change the distribution of coyotes sufficiently to increase populations and/or aid the sustainability of each of the following species: pronghorn, swift fox, black-footed ferret, and Canada lynx.

These ecological criteria should be additional to the viability criterion in the subsection above.

III. Protecting livestock from wolves, and protecting wolves from the consequences of irresponsible livestock husbandry.

Wolf recovery is a public priority and wolves should not be killed as a consequence of killing livestock on public lands.

In general, livestock owners should take responsibility, assisted by Colorado Parks and Wildlife and other state and federal agencies, in protecting their animals from wolves through scaring the wolves away and deterring their presence in the immediate vicinity of cattle, sheep, horses and other domesticated animals, without injuring or killing any wolves. That responsibility of the livestock owner should be most absolute on public lands, and wolves should not pay any price for any human inadequacy in protecting livestock on public lands.

On both private and public lands, ranchers should be required to properly dispose of carcasses of stock that die from non-wolf causes, so as to render them entirely unpalatable to wolves and thereby prevent scavenging and ensuing predation on live stock.

Livestock die before they are destined for slaughter for a variety of causes, including from illness, birthing problems, eating poisonous plants, and predation by mountain lions, black bears and coyotes. Once wolves scavenge on carrion from domestic animals, they may stay closer to the area where they found such food, and therefore may be more likely to end up preying on vulnerable nearby livestock.

A 2001 independent scientific review of Mexican wolf reintroduction program recommended that the U.S. Fish and Wildlife Service require livestock owners to take responsibility for carcass removal or disposal, noting that at least three packs had been removed
from the wild because they first scavenged on dead livestock left on national forest land.\textsuperscript{55} The American Society of Mammalogists reiterated this recommendation for Mexican wolf recovery in 2007.\textsuperscript{56} In 2011, researchers who examined wolf scavenging on livestock carrion and their predation behaviors in Alberta, Canada, recommended “sanitary disposal of dead livestock to prevent wolves from becoming accustomed to feeding on livestock.”\textsuperscript{57}

Oregon and Washington both provide some degree of protection for wolves by premising potential removal actions on the wolves not having been baited. In Oregon, the wolf management plan requires that “[n]o identified circumstances exist that are attracting wolf-livestock conflict” before wolves can be targeted for removal.\textsuperscript{58} In Washington, the management plan similarly premises the killing of wolves on “no evidence of intentional feeding or unnatural attraction of wolves by the livestock owner.”\textsuperscript{59}

In reintroducing northern Rocky Mountain gray wolves to Yellowstone National Park and central Idaho in 1995, the Fish and Wildlife Service premised the removal of depredating wolves on their not having been attracted to livestock in the place where they were depredating:

The Service and authorized agencies of the Service would use the following conditions and criteria to determine the status of problem wolves within the non-essential experimental population area . . . (2) No evidence of artificial or intentional feeding of wolves can be present. Improperly disposed of livestock carcasses located in the area of depredation will be considered attractants.\textsuperscript{60}

For restoration of wolves to Colorado, in order to prevent wolves from scavenging, livestock carcasses can be doused in gasoline and burned, when there is snow on the surrounding ground or otherwise it is safe. With road access, carcasses can be removed or buried by backhoe. A carcass can even be exploded into pieces too small to attract a wolf via dynamite. But perhaps the most versatile technique is to dump lime, which can be brought in on horseback, on the carcass to immediately decompose it. Colorado Parks and Wildlife and other agencies can help livestock owners to accomplish these tasks. The expenses to the public would be lower than in reimbursing ranchers for their losses after wolves potentially begin to hunt livestock as a possible consequence of having scavenged.

Requiring that owners of domestic livestock remove or render inedible the remains of their animals that die of non-wolf causes before any wolves scavenge on them, should be required in the Colorado gray wolf restoration and management plan. And in part to ensure enforcement, as well as equity, wolves that scavenge on domestic livestock that died of non-wolf causes should not be killed for killing livestock afterwards. Owners of stock who have allowed

\textsuperscript{55} Paquet et al (2001), pp. 67-68.


\textsuperscript{58} Oregon Wolf Conservation and Management Plan, p. 51.


\textsuperscript{60} 59 Fed. Reg. 60272 (Nov. 22, 1994).
wolves to scavenge on carrion of their animals, should not be reimbursed for ensuing predation losses to those same wolves.

Moreover, on both private and public lands, ranchers should be required to have a human presence appropriately close to their stock to be able to protect their animals from wolves without injuring or killing any wolves. Alternately, if a human presence to scare away and deter wolves is not feasible, ranchers should be required to take equivalent or close-to-equivalent non-injurious and non-lethal measures to protect their livestock. Those who do not take such measures should not receive reimbursement for their livestock killed by wolves.

IV. Mexican wolves should be introduced in southwestern Colorado.

Gray wolves taken from areas in Wyoming, Idaho and/or Montana where these animals are subject to widespread killing by people, should be captured alive and released in west-central and northwestern Colorado.

Endangered Mexican gray wolves should be released in the San Juan Mountains of southwestern Colorado, as recommended by scientists who advised that Mexican wolf recovery will require a population of this subspecies in the southern Rocky Mountains, which would have connectivity to the existing population at the southeastern edge of the Mogollon Plateau in Arizona and New Mexico, and also would have connectivity to a conceivable future population of Mexican wolves in the Grand Canyon ecoregion. These three connected populations would provide the genetic diversity and resilience to ensure recovery.61

Occasional interbreeding of wolf subspecies in Colorado would benefit the existing Mexican wolf population in southwestern New Mexico and southeastern Arizona, which would be connected through long-distance dispersing wolves. The benefit would come in the form of diversifying an impoverished gene pool of the current Mexican wolf population, without doing so to such an extent as to swamp with northern wolf genes the gene pool of the Mexican wolf where it exists in the wild in the Southwest today.62

Thank you for your consideration.

Sincerely,

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Contributed Papers

Mutation and Conservation

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Abstract: Mutation can critically affect the viability of small populations by causing inbreeding depression, by maintaining potentially adaptive genetic variation in quantitative characters, and through the erosion of fitness by accumulation of mildly detrimental mutations. I review and integrate recent empirical and theoretical work on spontaneous mutation and its role in population viability and conservation planning. I analyze both the maintenance of potentially adaptive genetic variation in quantitative characters and the role of detrimental mutations in increasing the extinction risk of small populations. Recent experiments indicate that the rate of production of quasisneutral, potentially adaptive genetic variance in quantitative characters is an order of magnitude smaller than the total mutational variance because mutations with large phenotypic effects tend to be strongly detrimental. This implies that, to maintain normal adaptive potential in quantitative characters under a balance between mutation and random genetic drift (or among mutation, drift, and stabilizing natural selection), the effective population size should be about 5000 rather than 500 (the Franklin-Soulé number). Recent theoretical results suggest that the risk of extinction due to the fixation of mildly detrimental mutations may be comparable in importance to environmental stochasticity and could substantially decrease the long-term viability of populations with effective sizes as large as a few thousand. These findings suggest that current recovery goals for many threatened and endangered species are inadequate to ensure long-term population viability.

Mutación y conservación

Resumen: La mutación puede afectar críticamente la viabilidad de poblaciones pequeñas al causar la depresión de endocria, mantener la variación genética potencialmente adaptativa en caracteres cuantitativos, y por medio de la erosión de la condición por acumulación de mutaciones levemente perjudiciales. En el presente estudio revisé e integré trabajos empíricos y teóricos recientes sobre mutaciones espontáneas y su papel en la viabilidad de las poblaciones y la planificación para la conservación. Se analizó tanto el mantenimiento de la variabilidad genética potencialmente adaptativa en los caracteres cuantitativos como el papel de las mutaciones perjudiciales en el incremento de riesgo de extinción de las poblaciones pequeñas. Experimentos recientes indican que la tasa de producción de varianza genética quasisneutra y potencialmente adaptativa en los caracteres cuantitativos es de un orden de magnitud menor que la varianza mutacional total debido a que las mutaciones con efectos fenotípicos pronunciados tienden a ser fuertemente perjudiciales. Esto implica que a efecto de mantener el potencial adaptativo normal en los caracteres cuantitativos bajo un balance entre mutación y deriva génica al azar (o entre mutación, deriva génica y selección natural estabilizadora), el tamaño poblacional efectivo debe ser de aproximadamente 5000 y no 500 (número de Franklin-Soulé). Resultados teóricos recientes sugieren que el riesgo de extinción debido a la fijación de mutaciones levemente perjudiciales podría ser comparable en importancia a la estocasticidad ambiental y podría reducir substancialmente la viabilidad a largo plazo de las poblaciones con un tamaño poblacional efectivo de solo unos pocos miles. Estos descubrimientos sugieren que las metas de recuperación para muchas especies en peligro y amenazadas son inadecuadas para asegurar la viabilidad poblacional a largo plazo.

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Introduction

Mutation is the ultimate source of all genetic variation (Dobzhansky 1970). Different kinds of genetic variation can critically affect population viability, especially in small populations. Deleterious (partially) recessive mutations, such as recessive lethal alleles, contribute to inbreeding depression in fitness, which increases the risk of extinction. Mildly detrimental mutations accumulate and can become fixed by random genetic drift, gradually eroding fitness and increasing extinction risk. Quasineutral, potentially adaptive genetic variance in quantitative characters maintained by mutation becomes diminished by inbreeding and random genetic drift, reducing the ability of a population to adapt and persist in a changing environment.

Measurements of the rates at which different types of mutations arise spontaneously have been used in conjunction with population genetic theories to suggest minimum population sizes for different goals in species conservation, such as avoiding inbreeding depression, maintaining potential for adaptive evolution, and avoiding genetic erosion of fitness from the accumulation of detrimental mutations (Franklin 1980; Soulé 1980; Lynch & Gabriel 1990; Lynch et al. 1993). I review and integrate recent experimental and theoretical work on spontaneous mutation and discuss how this affects our understanding of conservation goals for threatened and endangered species. Following a brief review of the genetic basis of inbreeding depression, I summarize information on spontaneous mutations affecting fitness and quantitative (polygenic) characters. Drawing from recent experimental and theoretical results, I then reconsider the role of mutation in the maintenance of potentially adaptive genetic variance in quantitative characters and the risk of population extinction from fixation of new detrimental mutations.

Inbreeding Depression

Decrease in the mean value of a character upon inbreeding is known as inbreeding depression, which results from the segregation of partially recessive mutations within populations. In historically large outbreeding populations, rapid inbreeding decreases the mean of characters—such as body size—and of major fitness components—such as seed yield in corn or litter size in mice and pigs—by a few percentage points to 10% or more for every 10% increase in the inbreeding coefficient (Falconer 1989; Ralls & Ballou 1983). In most naturally outbreeding species, close inbreeding—as by brother-sister mating—results in rapid extinction of a high percentage of lines (Soulé 1980).

A typical human or Drosophila fly carries one or two nearly recessive lethal or sublethal mutations in heterozygous form, while in some species of coniferous trees individuals may be heterozygous for five to ten recessive lethal equivalents (Sorenson 1969; Dobzhansky 1970). Habitual inbreeding decreases this hidden (recessive) genetic load by eliminating recessive lethal and sublethal mutations from the population when they are expressed in homozygous form. Predominantly self-fertilizing plant species therefore manifest reduced levels of inbreeding depression for fitness (Lande & Schemske 1985; Charlesworth & Charlesworth 1987).

The genetic basis of inbreeding depression for fitness has been studied more carefully in Drosophila than in other species. Using special genetic techniques available in Drosophila, chromosomes have been sampled intact, without recombination, from wild populations and tested in homozygous and in heterozygous form. The distribution of egg-to-adult viability in chromosomal heterozygotes is approximately normal, with a standard deviation of several percent of the mean. In chromosomal homozygotes, egg-to-adult viability has a strongly bimodal distribution, with a lethal and sublethal mode and a quasinormal mode that has a smaller mean and larger variance than that of chromosomal heterozygotes (Dobzhansky 1970). Genetic and statistical analysis shows that about half of the inbreeding depression in viability is caused by rare, nearly recessive lethal and sublethal point mutations, with the remainder attributable to numerous mildly detrimental mutations of small, more nearly additive effect (Simmons & Crow 1977). There is little evidence that overdominance (heterozygote advantage) contributes substantially to inbreeding depression (Charlesworth & Charlesworth 1987, 1990; Crow 1993).

The amount of inbreeding depression manifested by a population depends on the rate of inbreeding and the opportunity for selection to purge recessive lethal and semilethal mutations; this important point is neglected in some recent models that therefore overestimate the impact of inbreeding depression on population viability (Sener 1980; Halley & Manasse 1993; Mills & Smouse 1994). Gradual inbreeding by incremental reductions in population size over several or many generations allows selection to eliminate at least the lethal and sublethal mutations when they become homozygous (Falconer 1989). In contrast, the component of inbreeding depression from more nearly additive mutations of small effect may be difficult or impossible to purge by inbreeding, and even habitually self-fertilizing plants show considerable inbreeding depression manifested as heterosis (increased fitness) upon crossing different lines (Lande & Schemske 1985; Charlesworth & Charlesworth 1987; Charlesworth et al. 1990; Hedrick 1994).

Mutation Rates

In Drosophila melanogaster about 5000 lethal-producing loci mutate at an average rate of \( \mu = 2 \times 10^{-6} \) per allele per generation, giving a gametic mutation rate of...
10^{-2} per generation. Lethal and sublethal mutations are not completely recessive, decreasing the fitness of heterozygotes by about 2% on average (Simmons & Crow 1977). In large populations, selection keeps such strongly deleterious mutations at low equilibrium frequencies (≈ 4 × 10^{-6}). The expected frequency of slightly dominant lethal and sublethal mutations in a population of constant size is approximately independent of population size, provided that the effective population size, N_e, is large enough for selection to keep them at low frequency (N_e >> 2) (Crow & Kimura 1970:448-449). N_e refers to an ideal population of constant size, reproducing by random union of gametes, that gives the same rate of random genetic drift as an actual population of size N. Because of temporal fluctuations in population size, greater than Poisson variance in reproductive success, and unequal sex ratio, N_e is generally substantially less than N (Wright 1969; Crow & Kimura 1970; Lande & Barrowclough 1987).

Mildly detrimental mutations in Drosophila melanogaster have a heterozygote disadvantage of about one-third to one-half that of homozygotes (Mukai et al. 1972; Crow & Simmons 1983). Upper bounds for the average homozygous effect of mildly detrimental mutations are 4%-5% for viability (Simmons & Crow 1977; Crow & Simmons 1983) and about twice as large for fitness (Houle et al. 1992). These estimates are upper bounds because they neglect variation in selection coefficients among new mutations, which would decrease the estimated average effect by a factor of 1/(1 + c^2). c is the coefficient of variation (standard deviation/mean) of the effects of mildly detrimental mutations on fitness (Crow & Simmons 1983), which is likely to be substantial, perhaps of order 1 (Keightly 1994; Lande 1994). We therefore assume that mildly detrimental mutations have additive effects with an average heterozygous fitness loss of 2.5%. Such slightly deleterious mutations arise frequently, with total genomic mutation rates on the order of U = 1 per generation (Mukai et al. 1972; Mukai 1979), and they have a much higher probability of fixation than do mutations of large effect if N_e exceeds a few individuals.

The rate of phenotypic divergence by random genetic drift among replicated, highly inbred lines, and/or the rate of response in the mean phenotype to artificial selection on a highly inbred line, can be used to measure the genomic mutation rate and the production of genetic variance by spontaneous mutation in quantitative characters. For typical quantitative traits of plant and animal morphology, in excess of one in a hundred gametes contains a new mutation with an effect on any character (Sprague et al. 1960; Russell et al. 1963; Hoi-Sen 1972). Thus, the (diploid) genomic mutation rate summed over all loci producing mutations that affect a particular character, U = 2Σμ_p, is typically about 0.02 per generation. For a variety of quantitative characters in plants and animals, the additive genetic variance created each generation by spontaneous mutation, V_m, is roughly 10^{-3} times the environmental (nongenetic) variance in the character that would be expressed in a vigorous inbred line, V_e (Lande 1975; Lynch 1988). Assuming that mutational changes are symmetric (equally often increasing and decreasing the character), the average squared mutational effect is then about \alpha^2 = 0.05V_e. Recent experiments with Drosophila indicate that nearly half of these mutations, especially those with large phenotypic effects, are highly detrimental (recessive lethal), and that the rate of production of quasinuclear mutational variance per generation, denoted as \tilde{V}_m (which is likely responsible for much of the standing variation in quantitative traits of natural populations), is roughly an order of magnitude lower, \tilde{V}_m ≈ 10^{-4}V_e (Mackay et al. 1992; López & López-Fanjul 1993a, 1993b). Thus, in comparison to the total set of mutations affecting a typical quantitative character, the genomic mutation rate is about half as large for quasinuclear mutations, U = 0.01, and the mean squared mutational effect is about one-fifth as large, \alpha^2 = 0.01V_e.

**Maintenance of Potentially Adaptive Genetic Variance**

Franklin (1980) and Soulé (1980) proposed that N_e = 500 is sufficient for long-term maintenance of genetic variability in quantitative characters, and this number was quickly adopted as the basis of management plans for captive as well as wild populations (Lande 1988). The Franklin-Soulé number was derived by assuming a balance between mutation and random genetic drift and by using experimental measurements of mutability of quantitative characters to determine an effective population size sufficient to maintain typical amounts of heritable variation and adaptive potential (Lande & Barrowclough 1987). Explicit connections between additive genetic variance, adaptation, and population persistence were later analyzed by Lynch and Lande (1993), Bürger and Lynch (1994) and Lande and Shannon (1995).

**Mutation in a Finite Population**

Quantitative characters of morphology, physiology, and behavior are of great importance in adaptation to natural environments. The rate of evolution of the mean phenotype in response to directional natural selection is proportional to the additive genetic variance (the heritable portion of the genetic variance responsible for the resemblance between relatives) when selection acts on a single character (Falconer 1989), or to the additive genetic variance-covariance matrix when selection acts on a set of correlated characters (Lande & Arnold 1983).

Let V_{as} be the (purely) additive genetic variance in a quantitative character. Assuming a wide range of possi-
ble allelic effects at each locus, with a constant rate and distribution of mutational changes to altered allelic effects on the character, the input of additive genetic variance from mutation each generation is a constant, \( V_m \). In a diploid randomly mating population, the expected rate of loss of heterozygosity, or additive genetic variance in a quantitative trait, due to random genetic drift in the absence of selection is \( 1/(2N_e) \) per generation (Wright 1931; Lande & Barrowclough 1987). Measuring time, \( t \) in generations, the expected value of the additive genetic variance, \( V_g \), under random genetic drift and mutation obeys the dynamics
\[
\frac{dV_g}{dt} = \frac{V_g}{2N_e} + V_m^\ast.
\]
(1)

At equilibrium between mutation and random genetic drift, the expected genetic variance is \( V_g^\ast = 2N_e V_m^\ast \). The heritability of a character is the proportion of the total phenotypic variance due to additive effects of genetic variation. For quantitative characters of morphology, physiology, and behavior, excluding major components of fitness such as viability and fecundity, heritabilities usually range between 0.2 and 0.8 (Mousseau & Roff 1987; Falconer 1988). Assuming a typical heritability of 0.5, so that \( V_g^\ast = V_e \), using \( V_m^\ast = 10^{-3}V_e \) and solving for the effective population size gives \( N_e = 500 \).

If we incorporate the finding that only about 10% of the spontaneous mutational variance is quasineutral (López & López-Fanjul 1993a, 1993b), we should substitute \( V_m = 10^{-4}V_e \) for \( V_m^\ast \) into the above formulas, and the Franklin-Soulé number would have to be increased by a factor of 10, to \( N_e = 5000 \).

**Mutation and Stabilizing Selection in a Finite Population**

Natural selection on quantitative characters (other than major components of fitness) generally favors an intermediate optimum phenotype that may fluctuate with time. Weak stabilizing selection on a quantitative character can be described by a bell-shaped (Gaussian) curve giving the fitness per generation as a function of the individual phenotype. The strength of stabilizing selection is measured by \( V_e \), the “width” (or variance analog) of the fitness function. Stabilizing selection acting directly on a given character and indirectly on correlated characters (Lande & Arnold 1983) decreases the phenotypic variance of a typical trait within a generation by a few to several percent (Johnson 1976; Endler 1986). The total strength of (direct + indirect) stabilizing selection on a typical character is therefore about \( V_e = 25V_e \).

The expected additive genetic variance maintained by mutation in a finite population for a quantitative character under stabilizing selection is accurately described by the formula
\[
V_g = \frac{2N_e V_e V_e(\infty)}{2N_e V_e + V_g(\infty)}.
\]
(2)

\( V_g(\infty) \) is the additive genetic variance that would be maintained at mutation-selection equilibrium in an infinitely large population (Bürger & Lande 1994). Two approximations for the amount of additive genetic variance maintained in an infinite population under the polygenic mutation model described above are known as the house-of-cards model and the Gaussian allelic model.

The house-of-cards model assumes a large number of loci, \( n \), and low mutation rates per locus, \( \mu \), such that with a typical strength of stabilizing selection each locus has one common “wild-type” allele in high frequency and rare mutant alleles with relatively large effects. Under the house-of-cards approximation, \( V_g(\infty) \approx 4n\mu V_e \) (Turelli 1984; Kightley & Hill 1988; Bürger et al. 1989; Houle 1989).

The Gaussian allelic model assumes a relatively small or moderate effective number of loci, \( N_e \), with high per-locus mutation rates such that each locus has several or many segregating alleles per locus, with an approximately Gaussian distribution of small phenotypic effects. Under the Gaussian allelic approximation, \( V_g(\infty) \approx \sqrt{(2n\mu V_e V_m)} \), where \( n \) is typically around 5 or 10 (Kimura 1965; Lande 1975, 1981).

In the house-of-cards approximation, the additive genetic variance maintained in an infinite population with \( V_e = 25V_e \) and \( U = 2n\mu \) is 0.02 is \( V_g(\infty) = 1.0V_e \). In the Gaussian allelic approximation, with \( V_e = 25V_e \), \( V_m = 10^{-3}V_e \), and \( n_e = 10 \), a somewhat lower additive genetic variance is maintained in an infinite population, \( V_g(\infty) = 0.71V_e \). These correspond, respectively, to heritabilities of 0.50 and 0.42, both of which are in the typical range for quantitative characters (0.2 to 0.8; Mousseau & Roff 1987; Falconer 1989).

If we exclude recessive lethal mutations and include only the quasineutral, potentially adaptive mutations, the additive genetic variance maintained in an infinite population under the house-of-cards approximation becomes \( V_g(\infty) = 0.50V_e \) and under the Gaussian allelic approximation, assuming \( n_e \) remains at 10, the additive genetic variance becomes \( V_g(\infty) = 0.225V_e \). These correspond, respectively, to the reduced heritabilities of 0.33 and 0.18. It should be noted, however, that mutation is only one of several factors contributing to the maintenance of potentially adaptive genetic variance, including gene flow among differentiated populations, and density- and frequency-dependent competition (Felsenstein 1977; Slatkin 1979). The segregation of rare excessive lethal mutations contributes only a small fraction of the additive genetic variance in most quantitative characters (Falconer 1989).

Figure 1 shows the expected additive genetic variance maintained by mutation as a function of \( N_e \) for typical quantitative characters under the two approximations. The effective population size at which the expected additive genetic variance is equal to a proportion \( p \) of that
Figure 1. Expected additive genetic variance, $V_e^a$ relative to environmental variance, $V_e^I$, maintained by mutation in a typical quantitative character under stabilizing selection in a finite population: house-of-cards approximation (a) and Gaussian allelic approximation (b). Dashed lines include all mutations; solid lines include only quasineutral mutations, excluding recessive lethals.

Maintained in an infinitely large population is from equation 2, $N_e^* = \frac{[p/(1 - p)]V_e^I/(2V_m)}$. Table 1 gives numerical values of $N_e^*$ corresponding to different values of $p$ under both approximations. For example, under the house-of-cards approximation, including all mutations (ignoring recessive lethal effects), a population with $N_e = 1000$ is expected to maintain 67% of the additive genetic variance maintained in an infinite population; under the Gaussian allelic approximation, a population with $N_e = 707$ is expected to maintain 67% of the additive genetic variance maintained in an infinite population. Including only quasineutral mutations $N_e^*$ would have to be five times larger (5000) in the house-of-cards approximation and 3.15 times larger in the Gaussian allelic approximation (2236) to maintain 67% of the additive genetic variance in an infinite population.

The house-of-cards approximation is most accurate for loci with relatively large effects and low mutation rates, and the Gaussian allelic approximation is most accurate for loci with relatively small effects and high mutation rates. Because both types of loci probably contribute to variance of quantitative characters, the actual amounts of additive genetic variance maintained by mutation are likely to be between these two approximations. Excluding recessive lethal mutations, and whether or not we include stabilizing selection, it therefore appears that the effective population size necessary to maintain a high proportion of the potentially adaptive, additive genetic variance that would occur in a large population requires effective population sizes an order of magnitude larger than the original Franklin-Souède number, increasing the management goal from $N_e = 500$ to $N_e = 5000$.

**Extinction from Fixation of New Mutations**

Small populations risk extinction from a variety of genetic and demographic factors, including inbreeding depression as well as the fixation of new detrimental mutations. For large populations that have been reduced suddenly to a small size, inbreeding depression based on segregating detrimental mutations carried by the founders constitutes an important risk of rapid extinction (Souède 1980). For populations that are reduced in size more gradually, the fixation of new detrimental mutations poses a more serious risk of eventual extinction. In this section I examine how the risk of extinction from fixation of new mutations scales with population size and how this compares with the risks from stochastic demographic factors.

Most mutations are either quasineutral or detrimental. In populations with effective sizes larger than a few individuals, fixations of new, mildly detrimental mutations are far more important in causing loss of fitness and eventual extinction than are new, lethal and semilethal mutations. This is because strongly detrimental mutations have an exceedingly low chance of fixation in comparison to selectively neutral mutations, which have a relatively high chance of fixation but do no damage to the population. Lande (1994) analyzed the fixation of new, mildly detrimental mutations in a randomly mating population of constant size. Mildly detrimental mutations were assumed to have additive effects on Malthusian fitness. Table 1. Effective population sizes, $N_e$, required to maintain an expected additive genetic variance equal to a given fraction $p$ of that in an infinite population including either all mutations or only quasineutral mutations (excluding recessive lethals).

<table>
<thead>
<tr>
<th>Mutations</th>
<th>Approximation</th>
<th>0.50</th>
<th>0.67</th>
<th>0.75</th>
<th>0.80</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>house-of-cards</td>
<td>500</td>
<td>1000</td>
<td>1500</td>
<td>2000</td>
</tr>
<tr>
<td></td>
<td>Gaussian allelic</td>
<td>354</td>
<td>707</td>
<td>1061</td>
<td>1414</td>
</tr>
<tr>
<td>Quasineutral</td>
<td>house-of-cards</td>
<td>2500</td>
<td>5000</td>
<td>7500</td>
<td>10,000</td>
</tr>
<tr>
<td></td>
<td>Gaussian allelic</td>
<td>1118</td>
<td>2236</td>
<td>3354</td>
<td>4472</td>
</tr>
</tbody>
</table>
ussian fitness (population growth rate), with a fitness decrement of \( s \) per heterozygote and \( 2s \) per mutant homozygote. He found that the magnitude of selection coefficient that minimizes the mean time to extinction is about \( \tilde{s} = 0.4/N_e \), which is close to the border between neutrality and selection defined by Wright (1931, 1969), \( s \leq 1/(2N_e) \). For this reason, and because they arise at much higher spontaneous rates than do recessive lethal mutations, mildly detrimental mutations on the border of neutrality are the most damaging to population viability.

**Risks of Extinction from Genetic Stochasticity**

To analyze the risk of population extinction from fixation of new mutations, and to compare this to extinction risks from demographic factors, Lande (1994) modeled a randomly mating population with no demographic or environmental stochasticity. Population size was assumed to remain constant as long as the mean Malthusian fitness, \( r \) (the intrinsic rate of increase of the population), is positive. This model accounts only for unconditionally detrimental mutations. Stochastic fixation of mildly detrimental mutations gradually erodes the mean Malthusian fitness until \( r \) becomes negative—the population then can no longer replace itself and declines relatively rapidly to extinction (Lynch et al. 1993). Lande (1994) derived analytical approximations for the mean time until the population becomes genetically inviable (or extinct) in the situation where all mildly detrimental mutations have the same selection coefficient, \( s \) against heterozygotes and \( 2s \) against homozygotes. Lynch et al. (1995a) analyze this situation in more detail and perform computer simulations to check the analytical results. Lande (1994) also analyzed the influence of variance in selection coefficients among new mutations. The results on the scaling of mean time to extinction with effective population size are as follows.

With a constant selection coefficient against new mutations, \( s \), the mean time to extinction, \( \tilde{T} \), is a nearly exponential function of effective population size, \( N_e \). Because the mean time to extinction is such a rapidly increasing function of \( N_e \) (see Fig. 2), with values of \( s \) around a few percent, this indicates that the fixation of new mutations poses little risk of extinction for populations with effective size about 100 individuals (Lande 1994). This conclusion is in agreement with extensive simulation results of Charlesworth et al. (1993). However, the inclusion of variance in selection coefficients in the model drastically decreases the mean time to extinction.

With variance in \( s \), the mean time to extinction increases as a power of population size. If \( s \) is exponentially distributed, then \( \tilde{T} \) is asymptotically proportional to \( N_e^2 \). This more gradual increase in \( \tilde{T} \) with population size, shown in Figure 2, indicates a much greater risk of extinction than in the case of a constant selection coefficient. For reasonable variance in \( s \) (a coefficient of variation of about \( c = 1 \)), it appears that fixation of new, slightly deleterious mutations poses a considerable risk of extinction for populations as large as a few thousand individuals. Numerical examples appear in Table 2. These results, in conjunction with data on the rate and magnitude of mildly detrimental mutations in *Drosophila melanogaster*, indicate that the long-term viability of even moderately large populations, with effective sizes of a few thousand (and actual sizes of several or many thousands), may be substantially reduced by the fixation of new mutations.

**RELATIVE RISKS FROM GENETIC AND DEMOGRAPHIC FACTORS**

It is illuminating to compare the risks of population extinction from genetic stochasticity, due to fixation of new mutations, with the risks from demographic and environmental stochasticity. The relative risks of population extinction from different stochastic factors can be assessed by comparing asymptotic scaling relationships describing how the average time to extinction, \( \tilde{T} \), increases with equilibrium population size (or carrying capacity) under each stochastic factor alone. Although the actual extinction risk for a population of a given effec-
Table 2. Scaled mean times to extinction, \((U/r_0)\bar{T}\), in generations (from Lande 1994).

<table>
<thead>
<tr>
<th>Effective Population Size, (N_e)</th>
<th>((U/r_0)\bar{T}) (x^*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>constant s 44 49</td>
</tr>
<tr>
<td>5</td>
<td>constant s 52 65</td>
</tr>
<tr>
<td>10</td>
<td>constant s 69 99</td>
</tr>
<tr>
<td>20</td>
<td>constant s 128 193</td>
</tr>
<tr>
<td>50</td>
<td>constant s 1179 677</td>
</tr>
<tr>
<td>100</td>
<td>8.8 \times 10^4 2149</td>
</tr>
<tr>
<td>200</td>
<td>9.7 \times 10^4 7690</td>
</tr>
<tr>
<td>500</td>
<td>4.1 \times 10^5 4.4 \times 10^5</td>
</tr>
<tr>
<td>1000</td>
<td>1.1 \times 10^5 1.7 \times 10^5</td>
</tr>
<tr>
<td>2000</td>
<td>1.4 \times 10^6 6.7 \times 10^5</td>
</tr>
</tbody>
</table>

\(x^*\) is the expected population growth rate (or mean Malthusian fitness); \(r_0\) is the initial Malthusian fitness (intrinsic rate of increase), and \(\bar{T}\) is the general time. The selection coefficient, \(s\), against mildly deleterious mutations either is constant or has an exponential distribution with \(s = 0.025\). For most species, the scale factor \(r_0\bar{T}\) is likely to be in the range of about 1 to 10.

Table 3. Asymptotic scaling laws for mean time to extinction, \(\bar{T}\), as a function of the equilibrium population size, \(N\), or effective population size, \(N_e\), for demographic and genetic risk factors.

<table>
<thead>
<tr>
<th>Risk Factor</th>
<th>Proportional Scaling of (\bar{T})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Demographic Stochasticity</td>
<td>((1/N_e)^{2\nu/V_i})</td>
</tr>
<tr>
<td>Environmental Stochasticity</td>
<td>(N^{2\nu-V_i-1})</td>
</tr>
<tr>
<td>Fixation of New Mutations</td>
<td>constant s (1/N_e) (x^{4N_e})</td>
</tr>
<tr>
<td></td>
<td>variance in s (N_e^2 + 1/c^2)</td>
</tr>
</tbody>
</table>

\(x^*\) is the expected population growth rate (or mean Malthusian fitness); \(V_i\) is the demographic variance in Malthusian fitness among individuals; \(\bar{T}\) is the mean population growth rate; \(V_e\) is the temporal environmental variance in population growth rate; \(c = \sigma_s/s\) is the coefficient of variation of \(s\) among new mutations.

for mildly detrimental mutations to become fixed and the final decline of the population after \(r\) has become negative are both short in comparison to the mean time to reach genetic inviability, provided that the initial intrinsic rate of increase per generation \(r_0\bar{T}\) is substantially positive and \(N_e\) is not very small (Lynch et al. 1995b). Partial recessivity of detrimental mutational effects would increase the probability of fixation and decrease the mean time to extinction. Synergistic epistatic interactions among mildly detrimental mutations, which has been documented for viability in *Drosophila melanogaster* (Mukai 1969), slows the loss of mean fitness if all mutations have the same selection coefficient (Charlesworth et al. 1993), but substantial variance in selection coefficients among new mutations is likely to minimize this effect (Lande 1994). Large populations may never become genetically inviable due to fixation of mildly detrimental mutations because selection against them is more efficient and the erosion of mean fitness may be counteracted by reverse and advantageous mutations. Finally, compensatory mutations at different loci are common, especially for quantitative characters under stabilizing selection (Fisher 1958:44–48), and even strongly deleterious mutations with major morphological effects can be gradually compensated for by the evolution of minor modifiers (Lewontin 1974:91).

Nevertheless, there may be a large class of mildly detrimental mutations that cannot be readily compensated, such as delections of nonessential but fitness-enhancing loci that may compose the majority of single-copy genes (Cavalli-Smith 1985). The theory remains valid if the genomic mutation rate is multiplied by the proportion of mildly detrimental mutations that are unconditionally deleterious. If the fitness effects of a substantial fraction of all mildly detrimental mutations are unconditional, this would not change the result that with variance in selection coefficients the mean time to extinction is asymptotically proportional to a low power of \(N_e\); one would still conclude that the risk of population extinction from fixation of new mutations is potentially of

LIMITATIONS OF THE MODELS

Several factors could modify the mean persistence times of populations in this simple model. The time required
comparable importance with that from environmental stochasticity.

Discussion

Mutation has been used in two different ways in the evaluation of population viability and the design of conservation plans. Quasineutral, potentially adaptive mutations have been used to establish minimum effective population sizes for the maintenance of typical levels of additive genetic variance in quantitative characters, which are known to be of great importance in adaptive evolution. Harmful mutations also have been used to set minimum effective population sizes for avoiding the immediate consequences of inbreeding depression and for preventing the erosion of fitness by accumulation of mildly detrimental mutations.

Recent experiments accumulating spontaneous mutations in *Drosophila melanogaster* indicate that the rate of production of quasineutral, genetic variance in quantitative characters is an order of magnitude smaller than the total mutational variance in the characters, because mutations with large effects tend to be strongly detrimental (recessive lethals). This suggests that the effective population size of about 5000, rather than the Franklin-Soule number of 500, is necessary to maintain normal levels of potentially adaptive genetic variance in quantitative characters under a balance between mutation and random genetic drift. Including stabilizing selection toward an intermediate optimum phenotype does not much affect this conclusion. Of course, $N_e = 5000$ should not be regarded as a magic number sufficient to ensure the viability of all species, because of differences among characters and among species in genetic mutability and differences in environmental fluctuations and selective pressures to which populations are exposed. Maintenance of potentially adaptive genetic variation in single-locus traits (such as major disease resistance factors), which have mutation rates on the order of $10^{-6}$ per allele per generation, may require much larger effective population sizes, on the order of $10^4$ or $10^5$ (Lande & Barrowclough, 1987; Lande 1988).

In stable populations, mildly detrimental mutations on the border of neutrality do the most damage to population viability because they arise far more frequently and have a much higher chance of fixation than strongly deleterious mutations. Accounting for the high variance in selection coefficients likely to exist among new mutations, the fixation of new, mildly detrimental mutations may be comparable in importance to environmental stochasticity and could substantially reduce the long-term viability of populations with effective sizes as large as a few thousand. In contrast to the rapid extinction caused by inbreeding depression in populations suddenly reduced to a few individuals (Soule 1980), the fixation of mildly detrimental mutations in a stable population, even of very small size, produces only a gradual erosion of fitness that is likely to take many generations to cause extinction.

When listed, threatened and endangered species typically have actual population sizes on the order of 100 (plants) to 1000 (animals) (Wilcove et al. 1993), and population recovery goals frequently are not much larger than at the time of listing (Tear et al. 1993, 1995; Schemske et al. 1994). The above results cast doubt on whether populations of many threatened and endangered species will maintain adequate evolutionary potential and long-term genetic viability unless they recover to much larger sizes. Effective population sizes generally are substantially lower than actual population sizes because of fluctuations in population size, high variance in reproductive success, and unequal sex ratios (Wright 1969; Crow & Kimura 1970; Lande & Barrowclough 1987); maintaining effective population sizes of several thousand in the wild therefore will usually require average actual population sizes on the order of $10^4$ or more. Synergistic interactions among different genetic and demographic factors contributing to the risk of population extinction (Gilpin & Soulé 1986) are likely to cause the minimum population sizes for long-term viability of many wild species to be much larger than $10^3$.

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MEXICAN WOLF RECOVERY: THREE-YEAR PROGRAM REVIEW AND ASSESSMENT

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1. **INTRODUCTION**

Herein we assess the progress of efforts to reestablish Mexican wolves (*Canis lupus baileyi*) in the Blue Range Wolf Recovery Area (BRWRA). This review is a direct result of an Environmental Impact Statement (EIS) concluded by the U.S. Fish and Wildlife Service (USFWS) in 1996 (U.S. Fish and Wildlife Service 1996). The EIS and associated final rule (Parsons 1998) call for the USFWS to reestablish Mexican wolves to the BRWRA. The recovery area encompasses 17,752 km² (6,854 mi²) of the Apache National Forest in southeastern Arizona and the Gila National Forest in southwestern New Mexico.

Specifically, the U.S. Department of Interior has authorized the USFWS to reintroduce about 15 wolves every year for 3 to 5 years in the BRWRA primary recovery zone. The primary recovery zone comprises about 2,664 km² (1,029 mi²) of the Apache National Forest (Groebner *et al.* 1995). The remainder of the Apache National Forest and all the Gila National Forest make up the secondary recovery zone. The USFWS may conduct re-releases in the secondary recovery zone and wolves that move from the primary recovery zone can inhabit the secondary zone.

The USFWS began reintroductions with the release of 11 wolves in March 1998. From then until March 2001 the USFWS released another 45 individuals on 61 occasions. An Interagency Field Team comprising employees from the USFWS, Wildlife Services (U.S. Department of Agriculture), Arizona Department of Game and Fish, and New Mexico Department of Game and Fish carried out the releases and associated fieldwork.

The final rule governing the reintroduction project (Parsons 1998) and the 1998 Mexican Wolf Interagency Management Plan both require the USFWS to conduct a comprehensive review of the project at the end of the third year (i.e., March 2001). The full evaluation must include recommendations regarding continuation, modification, or cancellation of the reintroduction effort. If appropriate, the evaluation may include recommendations on whether and how to use the White Sands Wolf Recovery Area.

The primary goal of the reintroduction effort is to restore a self-sustaining population of about 100 wild Mexican wolves distributed over 12,950 km² (5,000 mi²) of the BRWRA. Such an objective is consistent with the 1982 Mexican Wolf Recovery Plan (U.S. Fish and Wildlife Service 1982 (EIS). The 1998 Mexican Wolf Interagency Management Plan projects that about 9 years will be required to achieve this objective. Wolves in the BRWRA are to be managed to reduce negative impacts and maximize positive influences on the lifestyles and economy of local residents.

The USFWS contacted the Conservation Breeding Specialist Group (CBSG) to conduct the specified review. CBSG is ideally suited for the task because of extensive worldwide experience with small population restoration, conservation, and management. On behalf of CBSG, Paul Paquet assembled an expert review team composed of John Vucetich, Michael Philips, and Leah Vucetich. The team review is based on data provided by the USFWS data collected in the first 3 years of the reintroduction project.
2. **ISSUES FOR WHICH ASSESSMENTS WERE REQUESTED**

Our assessment addresses the following questions as outlined by the 1998 Mexican Wolf Interagency Management Plan.

- Have wolves successfully established home ranges within the designated wolf recovery area?
- Have reintroduced wolves reproduced successfully in the wild?
- Is wolf mortality substantially higher than projected in the EIS?
- Is population substantially growth lower than projected in the EIS?
- Are numbers and vulnerability of prey are adequate to support wolves?
- Is the livestock depredation control program effective?
- Have documented cases of threats to human safety occurred?

We were not asked to address the following 2 additional questions identified in the 1998 Mexican Wolf Interagency Management Plan:

- Is effective cooperation occurring with other agencies and the public?
- Are combined agency funds and staff adequate to carry out needed management, monitoring and research?
3. OUR APPROACH

Although a paucity of data compels us to speculate on many biological issues, we do so using the best available information about wolf ecology. The lack of information reflects the short time the Program has been underway. Where necessary and appropriate we infer from published studies conducted elsewhere, our own experiences, and the experience of other researchers and managers. Throughout the report, we are careful to distinguish fact from inference, speculation, and professional opinion. Our conclusions and recommendations reflect our current knowledge and the fundamental principles of Conservation Biology.

Conclusions and recommendations depend on the likelihood of the assumptions underlying the assessment. Therefore, we reviewed several principles of conservation biology, which apply to restoring and maintaining a viable population of wolves. Some of these principles are established generalizations, some are testable hypotheses, and others are practical guides that we assessed as important in developing our recommendations.

- The fewer data or more uncertainty involved, the more conservative conclusions must be.
- To be comprehensive, an assessment must be concerned with multiple levels of biological organizations and with many different spatial and temporal scales.
- Species well distributed across their native range are less susceptible to extinction than species confined to small portions of their range.
- Large blocks of habitat containing large populations of a target species are superior to small blocks containing small populations.
- Maintaining viable ecosystems is usually more efficient, economical, and effective than a species by species approach.
- Viability of wild populations depends on the maintenance of ecological processes.
- Human disturbances that mimic or simulate natural disturbances are less likely to threaten restoration efforts than disturbances radically different from the natural regime.

We note that how we measure and perceive the success or failure of wolf recovery is contextual. Accordingly, our focus is on wolf ecology and how the quality of management affects the persistence of the reintroduced Mexican wolf population. Specifically, we are concerned with the viability of the population as affected by habitat quality, population size, population isolation, and agency management. Although a viable wolf population could affect people’s lives and the economy, we do not consider social and economic issues in this report.

Finally, our protocol for assessment was to:
- Review pertinent scientific literature
- Use available data provided by the Interagency Field Team
- Review pertinent regulations, polices, and rules
- Evaluate data quality
- Identify data gaps
- Analyze and interpret data
- Compare progress with program goals
- Evaluate program success & failures
• Develop data collection, data management & conservation recommendations
4. ECOLOGICAL BACKGROUND

a. RESILIENCY

Resilience has been defined as the ability to absorb disturbance and still maintain the same relationship between populations or state variables (Holling 1973) and the degree to which an entity can be changed without altering its minimal structure (Pickett et al. 1989). Thus, resilience can be thought of as a property of a system, whereas persistence is the outcome (Weaver et al. 1996).

Wolves evolved in environments that included prevailing disturbance regimes with certain ecological characteristics and boundary conditions. Disturbance varied in frequency, duration, extent, and intensity, thereby resulting in different spatio-temporal patterns of change. Behaviors and life history traits conferred resilience that enabled wolves to absorb these intrinsic disturbances and persist. Modern humans, however, have presented new regimes of disturbance that could be considered exotic because they are qualitatively novel or quantitatively atypical.

Three mechanisms of resilience at different hierarchical levels are: individual - plasticity in foraging behavior that ameliorates flux in food availability; population - demographic compensation that mitigates increased exploitation; and metapopulation dispersal - that provides functional connectivity among fragmented populations. Accordingly, flexible food habits, high annual productivity, and dispersal capabilities enable wolves to respond to natural and human-induced disturbances (Weaver et al. 1996). However, environmental disturbances at various temporal and spatial scales may exceed the ability of wolves and systems that support them to absorb disturbance (Weaver et al. 1996).

Wolves display remarkable behavioral plasticity in using different prey and habitats (Mech 1991). They are able to substitute one resource for another in the face of environmental disturbance (Weaver et al. 1996). Specifically, wolves specialize on vulnerable individuals of large prey [elk (Cervus elaphus) and moose (Alces alces)] yet readily generalize to common prey [usually deer (Odocoileus sp.)] (Weaver et al. 1996).

Wolf populations are able to compensate demographically for excessive mortality. Under certain circumstances this compensation enables wolves to respond to increased rates of juvenile or adult mortality with increased reproduction and/or survival, thereby mitigating demographic fluctuations (Weaver et al. 1996). Dominant wolves are able to reproduce at a very young age and usually reproduce every year thereafter (Weaver et al. 1996). Age at reproductive senescence has not been well documented but few females survive to reproduce past age 9 (Mech 1988). Wolves also display remarkable ability to recover from exploitation. For example, during a wolf reduction program in the Yukon, wolves recovered to pre-reduction densities within 5 years (Hayes and Harestad 2000). Wolves immigrated into the study area during early recovery, followed by increases in pack size from reproduction (Hayes et al. 2000).

The final mechanism that confers resilience to wolf populations is dispersal. When dispersal is successful, vanishing local populations are rescued from extirpation (Brown and Kodric-Brown 1977) and functional connectivity of metapopulations is established (Hansson 1991). Wolves have tremendous dispersal capabilities and as a result, “connectivity” of populations can be high. Dispersing wolves typically establish territories or join packs within 50-100 km of the pack in which they were born (Fritts and Mech 1981, Fuller 1989, Gese and Mech...

### b. THE PERILS OF SMALL POPULATIONS

Small populations, because of random normal variability in demographics, are more likely to become extinct than larger populations (Schonewald-Cox *et al.* 1983). Moreover, these small populations are thought to be vulnerable because of deleterious effects of inbreeding (Wright 1977) and chance environmental disturbances such as forest fires, disease or infestations that affect a species or its prey (Franklin 1980). In theory, the interaction of these factors increases the probability of extinction (Shafer 1987).

Small insular populations may have a restriction of genetic variation because they represent a very small subset of the total population (i.e., a few individuals). As populations become smaller a further reduction in genetic variation results in decreased survival (i.e., increased mortality). Increased mortality leads to additional reduction in genetic variation resulting in an "extinction vortex." Biologists theorize that because of this self-amplifying cycle the rate of extinction for small populations is higher than predicted from the population size alone (cf. Caro and Laurenson 1994).

### c. USE OF HABITAT AND PATTERNS OF TRAVEL

Throughout its broad geographical distribution the gray wolf is considered an ecosystem and prey generalist. However, populations are adapted to local conditions and are, therefore, specialized concerning den site use, foraging habitats, and prey selection. In mountain regions, the effects of physiography, weather, prey distribution, and prey abundance combine to concentrate activities of wolves into forested valley bottoms (Paquet 1993, Paquet *et al.* 1996, Paquet *et al.* 1996, Weaver 1994, Singleton 1995, and others).

Elevation can also govern seasonal movements of wolves. In mountainous areas with high snowfall, use of low elevation valleys increases during winter, where frozen rivers and lakes, shorelines, and ridges are preferred because of ease of travel. Ski trails, snowmobile trails, graded roads, and packed roads can artificially enhance the range and efficiency of winter forays (Paquet 1993). Singleton (1995) has suggested that variation in pack size, variation in home range size, and interactions with sympatric predators may influence habitat use and travel patterns. He further speculated that turning frequency or travel route complexity are likely to vary depending on whether an animal is within a patch of concentrated resource availability (e.g., deer winter ranges), moving between known patches, or exploring new areas.

### d. INFLUENCE OF WOLVES ON THE BIOLOGICAL COMMUNITY

Generally we understand that the ecology of predators, prey, and scavengers, is intertwined. However, the details of these relationships, and the general role of predation in shaping the structure of ecological communities is poorly understood. Changes in predator-prey relationships may affect species other than wolves and their prey. Disruption of top predators can affect interspecific associations by disrupting relationships within food webs. This, in turn, may cause unanticipated ripple effects in populations of other species (Paine 1966, 1969, 1980; Terborgh and Winter 1980, Frankel and Soulé 1981, Wilcox and Murphy 1985, Wilcove *et al.* 1986, Valone and Brown 1995), which markedly alter the diversity and composition of a
community (Paine 1966). Multi species effects often occur when changes in a third species mediate the effect of one species on a second species (or analogous higher-order interactions). For example, a wolf can affect a grizzly bear (*Ursus arctos*) by reducing the availability of a limiting resource (possibly an ungulate). Also a secondary carnivore such as a coyote (*C. latrans*) can affect the degree to which a herbivore's lifestyle is influenced by a primary carnivore such as a wolf. Ecologists have only begun to develop theory that attempts to explain the coexistence of prey in terms of predator-influenced niches ("enemy-free space").

Terborgh and Winter (1980) noted that we know little about the loss of top carnivores in terrestrial environments, and predicted a wave of extinctions following the loss of any key species. For example, if species interact as competitors, as predator and prey, or as facilitators in successional processes, then the presence of one species may influence the extinction probability of another "linked" species.

Recent evidence suggests the importance of cascading trophic interactions on terrestrial ecosystem function and processes. Research has documented differences within systems from which large predators have been removed or are missing (Glanz 1982, Emmons 1984, Terborgh 1988, Leigh *et al.* 1993, Terborgh *et al.* 1999). Accordingly, the ecosystem impacts of wolves may be more profound than previously expected. For example, on Isle Royale, Michigan wolf predation on moose has been shown to influence positively biomass production in trees of boreal forest (McLaren and Peterson 1994). Growth rates of balsam fir (*Abies balsamea*) were regulated by moose (*Alces alces*) density, which in turn was controlled by wolf predation (McLaren & Peterson 1994). When the wolf population declined for any reason, moose reached high densities and suppressed fir growth. This top-down "trophic cascade" regulation is apparently replaced by bottom-up influences only when stand-replacing disturbances such as fire or large windstorms occur at times when moose density is already low (McLaren & Peterson 1994). This is strong evidence of top-down control of a food chain by wolves (Terborgh *et al.* 1999). Research elsewhere suggests elk (*Cervus elaphus*) populations not regulated by large predators affect negatively the growth of aspen (*Populus tremuloides*) (Kay 1990, Kay and Wagner 1994, White *et al.* 1992, D. Smith pers. comm.), though information remains equivocal (L. Morgantini pers. comm.).

In addition to the obvious interactions between wolves and prey, wolves provide a regular supply of carrion to scavengers. Less obvious community dynamics might include the relationships between different predators, and how wolves influence these relationships. For example, how do wolves modify the relationships between coyotes and foxes?

Interest in the role of wolves in the broader ecosystem is not new. From 1939-1944 Adolf Murie (1944) conducted field studies in Denali Park Alaska to determine "...the ecological picture centering about the wolf of Mount McKinley National Park". Here, he entertained questions about the relationships between park wolves and other wolves, between wolves and their prey, and between wolves and other predators. Few studies, however, are available to yield insights into many of the relationships between wolves and other ecosystem components.

e. RESPONSE OF WOLVES TO HUMAN ACTIVITIES

The seriousness of human disturbance is ultimately a human judgement and, as such, some may consider any alteration of the normal activities of wolves to be undesirable. The ecological issue is how the probability of persistence changes with habitat degradation, small population size,
and population isolation. The management issue is what probability of persistence and environmental quality is compatible with legislation and acceptable to society. Interpretation of the wolf-human interaction is confounded by multiple factors that influence how wolves use the landscape and react to people (Mladenoff et al. 1995, L. Boitani pers. comm., L. Carbyn pers. comm., E. Zimen pers. comm.). Because of the wolf’s inherent behavioural variability, it is unlikely that all wolves react equally to human induced change. Moreover, many extraneous factors contribute to variance in behaviour of individual wolves. Because we have developed no reasonable expression of those differences, assessments are usually applied at the pack and population levels.

The specific conditions in which wolves are ‘disturbed’ (i.e., distribution, movements, survival, or fecundity are impaired) are believed to be highly variable. The extent and intensity of disturbance appear to vary with environmental and social context, and the individual animal (L. Boitani pers. comm.). Though wolves are sensitive to human predation and harassment (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989, Mech 1989, Purves et al. 1992, Fuller et al. 1992, Mech 1993, Mech 1995, Thurber et al. 1994, Mladenoff et al. 1995. Paquet et al. 1996), we have limited empirical information on tolerance to indirect human disturbance. Several studies suggest the main factor limiting wolves where they are present and tolerated by humans is adequate prey density (Fuller et al. 1992). Although human activities have been shown to influence the distribution (Thiel 1985, Fuller et al. 1992, Paquet 1993, Mladenoff et al. 1995) and survival of wolves (Mech et al. 1995, Mladenoff et al. 1995, Paquet 1993. Paquet et al. 1996), human-caused mortality is consistently cited as the major cause of displacement (Fuller et al. 1992, Mech and Goyal 1993, and others).

Studies that have quantified wolf-human interactions have shown wolves avoid humans or are displaced via human induced mortality (Paquet et al. 1996). Avoidance is temporal (Boitani 1982) and spatial (Mladenoff et al. 1995, Paquet et al. 1996). Several studies that used road densities as an index of human influence concluded that human activities associated with roads affect the survival and behaviour of wolves. Interpretation, however, was confounded because many human activities associated with roads result in the death of wolves. Thus, absence of wolves in an area may not be the result of behavioural avoidance per se. Data from Ontario, Wisconsin, Michigan, and Minnesota suggest that wolf survival is usually assured at road densities below 0.58 and 0.70 km/km² (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989, Mech 1989, Fuller et al. 1992). A study in Alaska concluded that wolves avoid heavily used roads and areas inhabited by humans, despite low human caused wolf mortality (Thurber et al. 1994). Landscape level analysis in Wisconsin found mean road density was much lower in pack territories (0.23 km/km² in 80% use area) than in random non pack areas (0.74) or the region overall (0.71). Few areas of use exceeded a road density of >0.45 km/km² (Mladenoff et al. 1995).

Recent reports suggest wolves in Minnesota tolerate higher levels of disturbance than previously thought possible. Wolves, for example, are now occupying ranges formerly assumed to be marginal because of prohibitive road densities and high human populations (Mech 1993, Mech 1995). Legal protection and changing human attitudes are cited as the critical factor in the wolf’s ability to use areas that have not been wolf-habitat for decades. If wolves are not killed, they seem able to occupy areas of greater human activity than previously assumed (Mech 1993, Fuller
Mexican wolf review . . . Paquet et al. 2001

Wolves from the Midwestern United States have hybridized with coyotes (Canis latrans) (Wayne et al. 1991, Wayne et al. 1992, Lehman et al. 1991), be red wolves, or red wolf hybrids (Wilson et al. 2001), which may affect their behaviour (Fox 1971) and their relationship with humans. Consequently, extrapolating information from Minnesota, Michigan, Minnesota, and Ontario may be inappropriate for the Rocky Mountains. Wolves in the Rocky Mountains show no introgression of coyote genes (Forbes and Boyd 1996).
road and/or human population density, wolves were completely absent. Overall, habitat alienation resulted in altered predator/prey relationships.

The observed patterns of displacement suggest the presence of humans repulses wolves, although a strong attraction to highly preferred habitats increases a wolf’s tolerance for disturbance. As conditions become less favorable, the quality of habitat likely takes on greater importance. Tolerance thresholds are unknown but, as noted, in the Bow River Valley changes in patterns of habitat use were evident when human activity exceeded 100 people/month. Nearly complete alienation of wolves occurred when more than 10,000 people/month used an area.

f. HUMAN INFLUENCE ON HABITAT USE BY WOLVES

The degree of human influence probably varies according to the environmental context. If a particular habitat is highly attractive, wolves appear willing to risk exposure to humans, at least within some limits (Chapman 1977). As levels of disturbance increase, favorableness of habitat likely takes on greater importance. For example, we know that wolves select home sites near intense human activity when denning areas are limited, or where innocuous human activity occurs (Chapman 1977). The presence of artificial food sources (e.g., carrion pits, garbage dumps) also attracts wolves and reduces avoidance of human activity (Chapman 1977, L.D. Mech pers. comm., Paquet 1996, Krizan 1998). In the Bow River Valley, wolves denned within 500 m of the Trans Canada highway when Parks Canada was dumping carrion in the area. Wolves abandoned the home site after Parks stopped dumping of the carrion.

The tension between attraction and repulsion is probably expressed differently by individuals, packs, and populations. Attraction to an area is a complex sum of physiography, security from harassment, positive reinforcement (e.g., easily obtained food), population density, and available choice. Moreover, the response to a particular disturbance seems to depend on disturbance-history (E. Zimen pers. comm.); a critical concept in understanding the behaviour of long-lived animals that learn through social transmission (Curatolo and Murphy 1986, S. Minta pers. comm.).

We can group human influence into effects on wolf habitat and populations. Habitat disturbance can be short or long term and can include direct loss of habitat (i.e., vegetation removal, vegetation change, or isolation and removal of prey). Direct habitat loss does not include the loss of habitat due to temporal or spatial alienation (sensory disturbance) or from fragmentation of habitat. Indirect losses will occur due to habitat alienation, where wolves abandon habitat because of nearby disturbances or are spatially isolated from using them because of impediments to movements. Changes in population can occur directly through alterations in habitat and indirectly because of disturbing activities.

The major impacts of human induced changes are, in order of decreasing importance, physical loss of habitat, loss of prey species, fragmentation of habitat, isolation of habitat, alienation of habitat, alteration of habitat, changes in original ratios of habitat, and changes in juxtaposition of habitats. These effects combine to have local and population level influences by altering the composition of biological communities upon which wolves are dependent, restricting movements, reducing foraging opportunities, and limiting access to prey. Obstructing movements also increases the vulnerability of wolves to other disturbances as they attempt to learn new travel routes.
The degree to which human activities disrupt wildlife reflects the type and extent of disturbance, which interacts with the natural environment to affect environmental quality. In mountainous landscapes wildlife often responds markedly to disturbances that occur at small spatial scales. This is because the topography amplifies the effects of disturbances by concentrating activities of humans and wildlife into valley bottoms. The forced convergence of activities limits spatially the range of options wildlife have for coping with disruption, reducing resilience to anthropogenic disturbance (Weaver et al. 1996, Alaska Department of Fish and Game unpublished data).

Indirect human influences can affect an animal’s chance to survive and reproduce. As wolves approach their limits of tolerance, they become increasingly susceptible to what would otherwise be minor influences. In the mountainous terrain, natural landforms and the condensed arrangement of habitats make wolves highly susceptible to the adverse effects of human disturbance. Because most development occurs in areas preferred by wolves, human activities unavoidably increase the risk of death and injury for wolves, decrease opportunities for wolves to move freely about, displace or alienates wolves from preferred ranges, and interrupt normal periods of activity. In less physiographically complex environments multiple travel routes link blocks of wolf habitat. Destruction or degradation of one or 2 routes is not usually critical, because safe alternative routes are available. In contrast, wolves living in mountains cannot avoid valley bottoms or use other travel routes without affecting their fitness. Therefore, tolerance of disturbance is probably lower than in other human dominated environments where wolves can avoid disturbed sites without seriously jeopardizing survival.

g. RESPONSE OF WOLVES TO LINEAR DEVELOPMENTS

The security of wolf populations in the many regions may be tenuous, because linear developments heavily dissect wolf ranges (i.e., highways, secondary roads, railways, and power line corridors). Highway mortality has become a primary cause of wolf mortality and there is accumulating evidence of habitat loss, fragmentation, and degradation related to roads (Purves et al. 1992, Paquet 1993). Ensured connectivity of quality habitats is important for survival of large carnivores (Beier 1993, Paquet and Hackman 1995, Doak 1995, Noss et al. in press), especially for those that face a high risk of mortality from humans or vehicles when travelling across settled landscapes (Noss 1992, Beier 1993).

There are several plausible explanations for the absence of wolves in densely roaded areas. Wolves may behaviourally avoid densely roaded areas depending on the type of use the road receives (Thurber et al. 1994). In other instances, their absence may be a direct result of mortality associated with roads (Van Ballenberhe et al. 1975, Mech 1977, Berg and Kuehn 1982). Besides fragmenting and consuming critical habitat, linear developments provide access to remote regions, which allows humans to deliberately, accidentally, or incidentally kill wolves (Van Ballenberhe et al. 1975, Mech 1977, Berg and Kuehn 1982). Despite legal protection, 80% of known wolf mortality in a Minnesota study was human-caused (30% shot, 12% snared, 11% hit by vehicles, 6% killed by government trappers, and 21% killed by humans in some undetermined manner) (Fuller 1989). Mech (1989) reported 60% of human-caused mortality in a roaded area (even after full protection), whereas human caused mortality was absent in an adjoining region without roads. On the east side of the Central Rockies between 1986 and 1993, human caused
mortality was 95% of known wolf death. Thirty-six percent (36%) of mortality was related to roads (Paquet 1993).

Wolves also experience higher mortality in areas with higher road density. On Prince of Wales Island, Alaska, researchers report a significant jump in wolf mortality (kill/259 km²) in areas where road densities exceed 25 km/km². While wolf mortality in the category of most densely roaded areas is highest, the variance is also high. The authors suggest that at some threshold of road density or human activity, wolves may abandon an area, resulting in decreased trapping and hunting mortality (Alaska Department of Fish and Game, unpublished data).

Linear developments may also be physical and/or psychological impediments to wolf movement. Road density and human density have been inversely correlated with viable populations of wolves in several areas. Along the Ontario-Michigan border, distribution of breeding packs occurred only in Ontario. Except for Cockburn Island, only lone wolves were found in areas close to the border or in Michigan. In Ontario, the density of roads in areas not occupied by wolves was greater than in areas occupied by wolves. Mean road density in Michigan, where no wolves resided, was also greater than in wolf-occupied areas of Ontario. High human densities, represented by road densities of > 0.6 km/km², were believed to be a barrier to wolf dispersal into Michigan (Jensen et al. 1986).

Studies in Wisconsin, Michigan, Ontario, and Minnesota have shown a strong relationship between road density and the absence of wolves (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989). Wolves generally are not present where the density of roads exceeds 0.58 km/km² (Thiel 1985 and Jensen et al. 1986, cf. Fuller 1989). Landscape level analysis in Wisconsin, Minnesota, and Michigan found mean road density was much lower in pack territories (0.23 km/km² in 80% use area) than in random non-pack areas (0.74) or the region overall (0.71). Road density was the strongest predictor of wolf habitat favorability out of 5 habitat characteristics and 6 indices of landscape complexity (Mladenoff et al. 1995). Few areas of use exceeded a road density of >0.45 km/km² (Mladenoff et al. 1995). Notably, radio collared packs were not bisected by any major federal or state highway. In Minnesota, densities of roads for the primary range, peripheral range, and disjunct range of wolves were all below a threshold of 0.58 km/km². These results, however, probably do not apply to areas on which public access is restricted. Mech (1989), for example, reported wolves using an area with a road density of 0.76 km/km², but it was next to a large, roadless area. He speculated that excessive mortality experienced by wolves in the roaded area was compensated for by individuals that dispersed from the adjacent roadless area. Wolves on Prince of Wales Island, Alaska currently use areas with road densities greater than 0.58 km/km². Core areas, however, are generally in the least densely roaded areas of the home range, and wolf activity that does occur in densely roaded areas occurs primarily at night. This behavioral response may reflect the limited options wolves have to relocate when they live on islands or insularized landscapes.

The response of wolves to different road types and human presence at the boundaries of Kenai National Wildlife Refuge, Alaska, was examined in a study of radio-collared wolves (Thurber et al. 1994). Wolves avoided oilfield access roads open to public use, yet were attracted to a gated pipeline access road and secondary gravel roads with limited human use. Thurber et al. speculated that roads with low human activity provide easy travel corridors for wolves. The response of wolves to a major public highway was equivocal. They thought wolf absence from settled areas and some roads were caused by behavioral avoidance rather than direct
attrition resulting from killing of animals. In Montana, Singleton (1995) found that wolves preferred areas 0.5-1 km from open roads for travel routes. He speculated that wolves did not select locations more distant from open roads because of the distribution patterns of wintering ungulates and the barrier provided by the river. Overall, wolves preferred areas with 0.01-2 mi/mi² for travel routes.
5. HAVE WOLVES SUCCESSFULLY ESTABLISHED HOME RANGES WITHIN THE DESIGNATED WOLF RECOVERY AREA?

a. BACKGROUND

Biologists usually define the home range of a wolf as an area within which it can meet all of its annual biological requirements. Seasonal feeding habitat, thermal and security needs, travel, denning, the bearing and raising of young, are all essential life requirements. The manner in which habitats for these requirements are used and distributed influences home range size and local and regional population distributions. Generally, wolves locate their home ranges in areas where adequate prey are available and human disturbance minimal (Mladenoff et al. 1995, 1997, Mladenoff and Sickley 1998). Wolves use areas within those home ranges in ways that maximize encounters with prey (Huggard 1993a, b).

Newly colonizing wolf pack might shift home ranges in response to climate, food availability, human disturbance, and other factors. A colonizing pack might have a larger, more fluid, home range than a pack surrounded by other wolf packs (Boyd et al. 1996). Some evidence suggests that wolf packs colonize areas that were first “pioneered” by dispersing lone wolves (Ream et al. 1991).

In mountainous areas, topographic position influences selection of home ranges and travel routes (Paquet et al. 1996). Wolf use of valley bottoms and lower slopes correspond to the presence of wintering ungulate prey and snow depth in these areas (Singer 1979, Jenkins and Wright 1988, Paquet et al. 1996). In areas of higher prey density pack sizes increase (Messier 1985) and home range size is closely correlated with pack size (Messier 1985, Peterson et al. 1984).

b. DATA SUMMARY

We assessed home ranges using locations from radio-collared animals. Radio-telemetry data (>7000 locations) were provided in an Excel database (Monitor). These data include all telemetry locations from 3 March 1998 to 3 March 2001. Each location was appended by wolf identification, date, time, and pack membership. Although locations were qualitatively ranked for accuracy, no quantitative assessment of telemetry error was available. Thus, we classified locations into 4 categories, which corresponded to the database provided. Class 1, 2, 3, and 4 locations were those within 100 m, 100-250 m, 250-450 m, and greater than 450 m from the true location, respectively. Only class 1 aerial and ground locations were used in the home range analysis.

c. METHODS

Our objective was to quantitatively describe areal distribution of reintroduced Mexican wolves within the recovery region. In a few cases, however, subjective determination of the home range was more appropriate.

Using ArcView Spatial Analyst, we plotted all class 1 locations. We discarded locations deemed to be recording errors, extraterritorial forays, and dispersals. We assumed a wolf dispersed if it permanently left its original pack and formed a new pack or joined an existing one (Messier 1985b).
Locations of individual wolves were grouped by pack affiliation. We defined a pack as 2 or more wolves that traveled together more than 1 month (Messier 1984). For each pack we used one wolf/year to represent the annual home range of the pack. This is a reasonable assumption if a high degree of association exists between pack members (Kolenosky and Johnston 1967, Fuller and Keith 1980, Fritts and Mech 1981, Ciucci et al. 1997). We confirmed pack affiliations by examining telemetry locations of wolves believed to be associating and through visual observations of the wolves by the field crew.

We used Home Range and Ranges V® software (Kenward and Hodder 1996) to calculate annual (1 Apr–31 Mar) and seasonal 95% minimum convex polygons (Mohr 1947) for individual packs and the entire free ranging wolf population within the primary zone and recovery area (Apache/Gila N.F.). Home range is an extension of ArcView Spatial Analyst. We assumed home ranges were defined when the observation-area curve formed an asymptote (Kenward and Hodder 1996) and locations were obtained throughout the year.

Accuracy of aerial and ground locations for the entire study was estimated to be 250 m, which is the highest mean error of telemetry obtained by researchers on other wolf projects. To account for the 250-m error, we changed the fix resolution from the RangesV® software default of 1 m to 250 m. This resolution is used to set the width of the boundary strip that is included in polygon edges and areas (Kenward and Hodder 1996, R. Kenward, pers. comm.). We left the scaling parameter at the software default of 1 m, which means that each coordinate unit was 1 m from the next.

d. RESULTS

From 1998 through 2001, 9 wolf packs were identified by name in the telemetry database. However, the criteria for specifying packs were not always biological. Release sites, geographic locations, and affiliations with other wolves influenced pack designation. Packs, pack compositions, and configurations of home ranges changed as reintroduced wolves encountered other wolves, and established new territories. In addition, the frequent removal and reintroduction of wolves confounded the assignment of individual wolves to specific packs.

The number of recorded aerial and ground locations varied among wolf packs (Figure 1). For the most part, the frequency of locations reflected the time that radio collared wolves were free-ranging, rather than differential effort by the field crew. Time of year, however, affected the number of locations acquired (Figure 2). Discussions with the field team confirmed that for logistic reasons they reduced monitoring activities in winter. We identified some locations that were far outside the reintroduction area. Many of these were recording or data entry errors (Figure 3). Several, however, were from wandering or dispersing wolves.

The proportion of telemetry locations within the primary recovery zone (Apache N.F.) and within the Blue Range wolf recovery area (Apache/Gila N.F.) varied among packs (Figure 4). Temporal trends in the proportion of telemetry locations (pooled across all packs) within the primary zone and within the recovery area also varied (Figure 5). The approximate area occupied by free-ranging Mexican wolf population changed over time as did the density of wolves. This was partially a reflection of periodic releases and recaptures of wolves, and also free-ranging wolves shifting centers of activity as they established pack affiliations and home ranges (Figures 6, 7, 8).
Many individuals and packs showed home range fidelity typical of wolves with established territories (Figure 9). However, frequent social disruption via mortality, recaptures, and re-releases may have altered the natural territorial behavior of packs. Wolves are long-lived social carnivores that transmit information between generations and among individual pack members. In this regard, the establishment, location, and maintenance of home ranges likely depend on a stable pack structure and the persistence of traditional pack knowledge. The home range behavior of reintroduced wolves may be highly susceptible to social disruption because they lack a cognitive map of the area. Moreover, lack of familiarity with the landscape may have a stronger influence on captive reared animals than wild born.
Figure 1. Summary of Mexican wolf radio telemetry data, 1998-2001. Numbers in parentheses are telemetry locations recorded.

Figure 2. Monthly radio-telemetry locations of reintroduced Mexican wolves, Arizona, 1998-2001.
Figure 3. Many telemetry locations resulted from data entry errors. For example, numerous locations were in the state of California and in the Gulf of California.
**Figure 4.** Variation among wolf packs in the proportion of telemetry locations within the primary zone and within the recovery area (Apache/Gila N.F.). These data include all telemetry locations of reintroduced Mexican wolves from 3 March 1998 to 3 March 2001.

**Figure 5.** Temporal trends in the proportion of telemetry locations (pooled across all packs) within the primary zone (Apache N.F.) and within the recovery area (Apache/Gila N.F.). These data include all telemetry locations of reintroduced Mexican wolves from 3 March 1998 to 3 March 2001.
Figure 6. Approximate area occupied by free-ranging Mexican wolf population in Arizona and New Mexico, 1998-2001.

Figure 7. Density of free-ranging Mexican wolf population in Arizona and New Mexico, 1998-2001.
**Figure 8.** Seasonal distribution of free-ranging Mexican wolf population in Arizona and New Mexico, 1998-2001.
Figure 9. Polygons reflecting the spatial extent of pack home ranges in relation to the primary zone (Apache N.F.) and recovery area (Apache/Gila N.F.). These data include all telemetry locations of reintroduced Mexican wolves from 03 March 1998 to 03 March 2001.
e. CONCLUSIONS

We conclude that some wolves have successfully established home ranges and possibly pack territories within the designated wolf recovery area. We caution, however, that frequent recaptures and re-releases confounded our analysis. These manipulations may also be interfering with pack formation and establishment and maintenance of home ranges. Lastly, individual wolves have shown some indication of dispersing outside the recovery area. This is to be expected and required if the regional population is to be viable.
6. HAVE REINTRODUCED WOLVES REPRODUCED SUCCESSFULLY IN THE WILD?

a. BACKGROUND
   i. Births versus recruitment
      (1) Compared with adults, pups have relatively low survival rates during the first year of life.
      (2) In a sense, pups do not really contribute to the viability of a population until they have survived a period of high mortality rate associated with being a pup.
      (3) Although the EIS refers to projected numbers of pups, the projections seem to treat pups as though they have been recruited into the adult population (i.e., with survival rates like adults).

b. DATA SUMMARY
   We used information recorded in the telemetry and events databases. Additional information on reproduction was garnered from discussions with the Field Team. Dense vegetation and the secretive nature of wolves precluded regular and accurate visuals of wolves. Consequently, the Interagency Field Team did not routinely observe wolves during spring and summer when pups are easiest to distinguish from adults. We assumed the presence of dens and rendezvous sites when movements became localized in April through July or when lactating females or pups were captured. Sometimes, ground checks confirmed potential denning and rendezvous areas.

c. METHODS
   We determined natality directly from field observations of dens, rendezvous sites (pup rearing and resting areas), and packs. We ascertained successful year-specific reproduction using changes in pack size from March to the following December. We assumed unsuccessful reproduction (i.e., no or failed reproduction) when a pack did not display focal activities in the summer. Annual recruitment was derived from winter pack sizes recorded in February.

d. RESULTS
   Births have taken place in the wild (Table 1). Births and recruitment rates, however are lower than projected in the EIS (Figures 10 and 11).
Table 1. Known births and recruitments of reintroduced Mexican wolves recorded from 1998-2001. Only 1 litter was conceived in the wild.

<table>
<thead>
<tr>
<th>PARENTS</th>
<th>ESTIMATED DATE OF BIRTH (M/D/Y)</th>
<th>CONCEIVED IN WILD?</th>
<th>WILD BIRTHS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>174 Male 166</td>
<td>35915</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>191 Male 208</td>
<td>5/1/99</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>482 Male 166</td>
<td>5/1/99</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>486 Male 131</td>
<td>5/1/00</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>191 Male 208</td>
<td>5/1/00</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>189 Male 190</td>
<td>4/15/00</td>
<td>No</td>
</tr>
</tbody>
</table>
Figure 10. Projected numbers of breeding pairs (in the EIS) and actual numbers of litters for reintroduced Mexican wolves, 1998-2001.

Figure 11. Actual and projected numbers of recruits for reintroduced Mexican wolves, 1998-2001.
e. CONCLUSIONS

The number of free-ranging Mexican wolves at the end of third year is similar to that projected in the EIS. Survival and recruitment rates, however are far too low to ensure population growth or persistence. Without dramatic improvement in these vital rates, the wolf population will fall short of predictions for upcoming years.
7. **IS WOLF MORTALITY SUBSTANTIALLY HIGHER THAN PROJECTED IN THE EIS?**

a. **BACKGROUND**

Researchers do not agree on the annual rate of mortality that causes a population decline in wolves. However, Keith (1983) and Fuller (1989) reviewed several wolf studies across North America and concluded that harvests exceeding 28-30% of fall populations resulted in declines. Fuller (1989) further concluded that populations would stabilize with an overall annual mortality rate of 35%. He felt, however, the effects of harvest could vary with time and population structure. Specifically, a population containing many pups could withstand much higher mortality.

Various researchers have suggested different rates of annual mortality they believe control growth of wolf populations. However, the annual rate of mortality that causes a population decline in wolves is unknown. Furthermore, many researchers consider only harvest (hunting or trapping) when they calculate mortality rates that cause wolf population declines. For instance, Mech (1970) concluded an annual harvest of 50% or more was necessary to control wolf populations based on pup-adult ratios but did not distinguish between harvest and natural mortality. Keith (1983) reviewed studies of 13 exploited populations and determined that harvests exceeding 30% of fall populations resulted in population declines. Similarly Fuller (1989) found annual rates of wolf increase vary in direct response to rates of mortality and where humans kill wolves, harvests exceeding 28% of autumn or early winter populations might result in a population decline. He concluded a population would stabilize with an overall rate of annual mortality of 0.35 or rate of human-caused mortality of 0.28. Consequently, the exact relationship between the annual rate of mortality from all human causes (harvest, collisions with cars and trains) and population limitation or decline in wolves is uncertain.

In areas where ungulate biomass is low, researchers have noted that starvation and intraspecific aggression are common. For instance, in southwestern Quebec, Messier (1985a) noted wolves with fewer prey available incurred more deaths from natural causes, namely starvation and intraspecific aggression. Similarly, Mech (1977a) noted occurrence of starvation and intraspecific aggression increased as prey availability declined in Minnesota. Disease cannot be linked with certainty to low availability of food but the relationship makes sense intuitively. A population of wolves lacking food should be more vulnerable to disease than one with more food available. Furthermore, food shortage leading to nutritional stress could combine with disease factors to increase the significance of otherwise innocuous or sub-lethal conditions (Brand et al. 1995).

In most studies, no disease-related mortality has been reported (VanBallenberghe et al. 1975, Mech 1977a, Fritts and Mech 1981, Messier 1985a, Potvin 1987, Ballard et al. 1989, Hayes et al. 1991, Meier et al. 1995, Pletscher et al. 1997). In other studies, from 2-21% of wolf mortality has been attributed to disease (Carbyn 1982, Peterson et al. 1984, Fuller 1989, Ballard et al. 1997). Ballard et al. (1997) concluded that occurrence of rabies was a significant factor in a decline of wolves from Alaska. In that study, rabies-caused mortality was 21%.

Quantifying the importance of food in limiting population growth based on cause of death alone is difficult. In the literature, results vary among studies. On Isle Royale, annual mortality from starvation and intraspecific strife (both related to low food availability) ranged from 18-57%
during a 20-year period (Peterson and Page 1988). In populations where some human-caused mortality occurs, and thus compensates for natural mortality (starvation, accidents, disease and intraspecific strife), about 8% of individuals greater than 6 months-of-age can be lost each year (Ballard et al. 1987, Fuller 1989). Some researchers have accepted this variability and decided any sign of starvation among adult wolves means food is limiting population growth (Fritts and Mech 1981, Ballard et al. 1997, P. Paquet, pers. comm.). This assumption is reasonable given adults typically are the last members of the population affected by food shortage (Eberhardt 1977) and as such, may be the most sensitive indicators of a shortage of food.


b. DATA SUMMARY
We used information recorded in the telemetry and events databases. Additional information, clarification of events, and interpretation of events was provided by the Interagency Field Team. All free-ranging Mexican wolves were radio-collared from time of release. Moreover, each radio-collared Mexican wolf was and continues to be relocated regularly and frequently via ground and aerial telemetry. Frequent monitoring reveals whether each wolf is alive or dead at the time of relocation.

c. METHODS
We were not able to address the question of annual mortality directly because removals and re-releases precluded calculating annual rates of mortality. Thus, we estimated survival rates for the Mexican wolf population and then compared these estimated values with the survival rates projected in the EIS. Survival rate is the chance (or probability) of surviving some specified time. Survival rates are typically expressed as values between zero and one. For example, if the annual survival rate of an individual is 0.82, we would say that individual has an 82% chance of surviving during the next year. Survival is a critical population process and estimating survival rates is an important part of measuring viability of populations. Management of protected wolf populations requires quantitative survival measurements to identify factors that drive population change. From the survival rate one can also understand the mortality rate. The mortality rate of an individual or population is one minus the survival rate.

Using the telemetry data we compiled a table showing the number of wolves that were alive each month, died each month, and recaptured each month. The table provided the foundation for formal analysis of survival rates. We estimated survival rates of radio-collared wolves using the Kaplan-Meier (K-M) product limit estimator (Kaplan EL and Meier 1958). We carried out this analysis using the programs MARK and Minitab (Version 12). Conceptually, the analysis uses the relationships between the number of wolves that die each month and the number monitored.
each month. Although estimating a rate of survival for each month is possible, the data show that annual survival rates do not vary substantially across longer periods. Thus, we estimated survival rates using an information-theoretic approach (Buhrnam and Anderson 1999) that determines the most appropriate time scale (e.g., monthly, seasonally, or annually).

From the perspective of a free-ranging population, returning a wolf to captivity (from now on, recapture event) is equivalent to a mortality event. Thus, we conducted 2 survival analyses. One analysis considered only true biological deaths, and the other treated biological deaths and recapture events as mortality events. In both analyses, we reincluded wolves from time of release until “mortality” or disappearance of the radio-signal occurred.

Sample sizes were too small to use Cox’s proportional hazards model and determine the influence of important covariates (such as age and sex) on survival. We did not calculate cause-specific mortality. Mortality was described, however, using percents. We assumed that the proximate cause of death was the ultimate cause of death. We were unable to assess the relative importance of other factors that may have been involved.

The starting date of the survival study was March 1998 and the end date was March 2001. For known deaths we estimated the date of mortality to the nearest day using evidence from the telemetry and events data bases. When information was unavailable, we deemed day of mortality the midpoint of the interval between the last day the wolf was known alive and the day it was discovered dead. The cause of mortality was often identified on site and when possible, confirmed by necropsy (Interagency Field Team pers. comm.)

d. RESULTS

Forty-seven (47) wolves were monitored from March 1998 (when Mexican wolves were first released) to March 2001. Twenty-three (23) wolves are currently being monitored. Four (4) wolves are unaccounted for. Twenty (20) wolves were recaptured following release. Nine (9) of these were re-released and are known to be alive. Two (2) wolves were re-released but contact was lost and their fate is unknown. One of the re-released wolves died. Eight (8) of the recaptured wolves were not re-released and some died in captivity. Seventeen (17) wolves are known to have died, 10 in the wild (Figure 12). Human caused mortality was the most common cause of death. Of the human related deaths, most were caused by gunshots (Figure 13). Wolves also died from distemper and parvovirus. Both these diseases are contracted or originally spread from domestic animals. Death by disease was higher than projected in the EIS.

When recaptures were included as mortalities, survival rates were lower than projected in the EIS (Figure 14). Excluding recaptures as mortalities resulted in survival rates exceeding the EIS projections in 1999 and 2000 (Figure 15). Survival rates from either method, however, were lower than for wolves in the Flathead region of Montana and British Columbia (Pletscher et al. 1997), lower than for wolves in the central Canadian Rocky Mountains, lower than a recovering wolf population in the Yukon (Hayes and Harestad 2000), and higher than an exploited population in Alaska (Ballard et al. 1987).
Figure 12. Causes of wolf mortality for Mexican wolves reintroduced to Arizona, 1998-2001.

Figure 13. Cause specific wolf mortality for Mexican wolves reintroduced to Arizona, 1998-2001.
Figure 14. Survival analysis of reintroduced Mexican wolf population assuming that recapture represents a mortality event. Analysis was conducted for the period 1998-2001.

Figure 15. Survival analysis of reintroduced Mexican wolf population assuming that recaptures do not represent a mortality event. Analysis was conducted for the period 1998-2001.
CONCLUSIONS

Frequent removals and re-releases of wolves confounded our analysis of rates and causes of mortality. However, if recaptured wolves were at high risk of being killed, then survival is much lower than projected in the EIS. Human-related deaths were the greatest source of mortality for reintroduced Mexican wolves. Shooting was the major source of death. Numerous other studies have reported human-caused deaths as the major cause of wolf mortality (Fuller and Keith 1980, Berg and Kuehn 1982, Boitani 1982, Carbyn 1982, Ballard et al. 1987, Fuller 1989, Mech 1989, Pletscher et al. 1997, and many others).
8. **IS POPULATION GROWTH SUBSTANTIALLY LOWER THAN PROJECTED IN THE EIS?**

a. **BACKGROUND**

Rates of increase in wild wolf populations have varied between 0.93 and 2.40 (Fuller and Keith 1980, Fritts and Mech 1981, Ballard *et al.* 1987, Hayes *et al.* 1991, Messier 1991, Pletscher *et al.* 1997). Several factors limit growth of wolf populations; those reported most commonly include ungulate biomass (Van Ballenberghe *et al.* 1975, Mech 1973, 1977a, 1977b, Fuller and Keith 1980, Packard and Mech 1980, Keith 1983, Messier 1985a, 1987, Peterson and Page 1988) and human-caused mortality (Van Ballenberghe 1981, Gasaway *et al.* 1983, Keith 1983, Peterson *et al.* 1984, Fuller 1989, Paquet *et al.* 1996, Noss *et al.* 1996). Keith calculated the maximum rate of increase for wolves ($r = 0.304$, $\lambda = 1.36$) (1983) based on the highest reproductive and survival rates reported from studies on wild wolves. He corroborated the results by comparing the estimate with data from wolves that colonized Isle Royale National Park, 1952-1959 ($r = 0.304$, $\lambda = 1.39$). These were likely maximum rates of increase because the population was initiated by few individuals with abundant food (Keith 1983). However, both rates are still much lower than a theoretical exponential rate of 0.833 ($\lambda = 2.30$) given maximum reproduction (Rausch 1967), a stable age distribution and no deaths.

Keith (1983) suggested the amount of food available and age structure of the population affect rates of growth of wolf populations. Van Ballenberghe (1981), Gasaway *et al.* (1983), Keith (1983), Peterson *et al.* (1984), Ballard *et al.* (1987), and Fuller (1989) found that wolf populations can be limited by harvest levels of 20-40%, but that the lower rate has a more significant effect in an area with low ungulate biomass (Gasaway *et al.* 1983). Another factor to consider is that effects of harvest vary with time and population structure (Peterson *et al.* 1984, Fuller 1989). If productivity is high, and consequently the ratio of pups to adults is high, the population can withstand a higher overall mortality because pups (non-producers) make up a disproportionate amount of the harvest (Fuller 1989). Furthermore, net immigration or emigration may mitigate the effects of harvest (Fuller 1989).

b. **DATA SUMMARY**

We assessed the density of the wolf population, size of established packs, and population growth using radiotelemetry data and direct observation by the Interagency Field Team. Most of these data are contained in the Monitoring and Events databases.

c. **METHODS**

We calculated density of wolves/1000 km$^2$ by determining intra-pack densities (home range size/number of wolves in pack) of radio-collared wolves and averaging these densities per year (Potvin 1987, Bjorge and Gunson 1989, Okarma *et al.* 1998). The size of packs was based on numbers of wolves observed during midwinter aerial locations (15 Jan-15 Feb). We estimated population growth using finite rates of increase ($\lambda$) based on the ratio of successive yearly estimates of density. Mean annual finite rate of increase was calculated by taking the antilogarithm of the mean exponential rate of increase ($r = \ln \lambda$) for the population (Fuller 1989).

The fundamental equation of population demography for a closed population is:
\[ N_t = N_{t-1} + B_t - D_t \]

where \( N_t \) = population size at time \( t \), \( B_t \) = number of recruits at time \( t \), \( D_t \) = number of deaths at time \( t \).

For a wild population, removals are similar to mortality and re-releases similar to recruitment. Therefore, the equation that best describes the reintroduced Mexican wolf population is:

\[ N_t = N_{t-1} + B_t - D_t + \delta_t - \beta_t \]

where \( \delta_t \) = (unpredictable) removals of ‘naughty’ wolves, \( \beta_t \) = subsequent re-releases of those ‘naughty’ wolves, \( \beta_t >> B_t \), \( \delta_t >> D_t \)

d. RESULTS

From available databases and discussions with the Interagency Field Team, we identified a number of events relevant to assessment of population dynamics (Table 2). Using this information, we calculated population growth rates (Figures 16, 17) and the varying number of free-ranging wolves over time (Figures 18 and 19). Growth rates and numbers of wolves were close to projections, although frequent re-releases and removals obscured comparisons. To provide context for interpreting these results, we also generated mean growth rates for other reintroduced and recovering wolf populations (Figures 20, 21, 22). To date, the growth rate of the reintroduced Mexican wolf population is comparable with similar reintroduction and recovery efforts.

Table 2. Population events recorded for reintroduced Mexican wolf population between 1998 and 2001.

<table>
<thead>
<tr>
<th>POPULATION EVENT</th>
<th>NUMBER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruits</td>
<td>3 - 5</td>
</tr>
<tr>
<td>Re-releases</td>
<td>21</td>
</tr>
<tr>
<td>Deaths</td>
<td>10 - 16</td>
</tr>
<tr>
<td>Removals</td>
<td>31</td>
</tr>
</tbody>
</table>
Figure 16. Projected and actual annual growth rates of free-ranging Mexican wolf population. Actual growth rate is strongly influenced by frequent intervention.
Figure 17. Projected and actual sizes of free-ranging Mexican wolf population, 1998-2001.
Figure 18. Number of free-ranging radiocollared Mexican wolves, 1998-2001. The difference between the max and min accounts for 4 wolves whose signals were lost, and in one case, a wolf that threw its collar.
Figure 19. Growth rates of other recovering wolf populations. Sources: <http://www.r6.fws.gov/wolf/annualrpt99/> and unpublished documents from JAV
Figure 20. Mean annual growth rate for other recovering populations.

Figure 21. Number of wolves over time in other recovering populations.
Assessing the average growth rate only tells part of the story. Fluctuations in growth rates are also critical. The more fluctuation the greater the extinction risk. In this case, to assess fluctuations, we need to examine the population trajectory on a different time scale.

Using data collected since March 1998, we calculated a 39% chance that the annual growth rate is < 0.0; a 43% chance the annual growth rate is \( \leq 0.10 \); and a 50% chance the annual growth rate \( \leq 0.20 \) (Figure 22). Using data collected since December 1998, we calculated a 23% chance that the annual growth rate is < 0.0; a 26% chance the annual growth rate is \( \leq 0.10 \); and a 29% chance annual growth rate \( \leq 0.20 \) (Figure 23).
*A monthly growth rate of 0.083 corresponds to an annual growth rate of 0.1. A monthly growth rate of 0.0166 corresponds to an annual growth rate of ~0.2.

**Figure 22.** Mean monthly growth rate ($r$) since March 1998. The expected value of $r$ is 0.02. The standard error is 0.07.*
Growth Rate (monthly)

Figure 23. Mean monthly growth rate ($r$) since December 1998 (when population went temporarily extinct). The expected value of $r$ is 0.06. The standard error is 0.08.
e. CONCLUSIONS

To date, intervention has dominated natural processes. So, determining if the growth rate is lower than predicted in the EIS is not possible. If the current rate of intervention continues, restoration of a population of 100 wolves would require 28 re-releases annually and 41 removals annually. Although the current population size is similar to that projected in the EIS, we suspect that population growth would have fallen far short of expectations without intervention. Clearly, managers must balance future introductions, recaptures, and re-releases with the need to establish and maintain natural population processes (Figure 24).

**Figure 24.** Because of frequent interventions the vital rates we derived (survival and population growth) are unlikely to reflect the population’s future viability. A balance between intervention and the effects of natural population processes is needed.
9. ARE NUMBERS AND VULNERABILITY OF PREY ADEQUATE TO SUPPORT WOLVES?

a. BACKGROUND

Without human disturbance, densities reflect the wolf’s dependency on ungulate prey species (Keith 1983). Wolf population dynamics are believed to be largely dictated by the per capita amount of prey and its vulnerability to predation, and the degree of human exploitation (Keith 1983; Fuller 1989). The effect of food on wolf demography is mediated by social factors, including pack formation, territorial behavior, exclusive breeding, deferred reproduction, intraspecific aggression, dispersal, and by primary prey shifts (Keith 1983).

Wolf populations are closely linked to population levels of their ungulate prey (Keith 1983, Messier 1985a, Fuller 1989). Maintaining viable, well-distributed wolf populations depends on maintaining an abundant, available, and stable ungulate population. Packard and Mech (1980) concluded that intrinsic social factors and the influence of food supply are interrelated in determining population levels of wolves. In situations where other factors reduce prey populations (e.g., winter weather), predation by wolves can inhibit the recovery of prey populations for long periods (Gasaway et al. 1983). In a multiprey system, the stability, or equilibrium, of ungulate prey and wolf populations seems to depend on a variety of factors, including the wolf predation rate, the number of ungulates killed by hunters, the ratio of ungulates to wolves, and the population growth rate of different ungulate species (Carbyn 1982, Huggard 1992, Paquet 1993, Paquet et al. 1996, Paquet 1989).

Changes in habitat composition and distribution can have a significant effect on prey densities and distributions, and therefore wolf spatial distribution. Wolf packs may react to changing conditions in varying ways, depending on the location of their territories in relation to other packs and prey distribution. If packs have lower prey densities within their territories, they may exploit territories more intensely.3 This may be achieved by 1) persevering in each attack, 2) using carcasses thoroughly, 3) feeding on alternative and possibly second-choice food resources such as beaver (*Castor canadensis*) (Messier and Crete 1985), and 4) patrolling their territory more intensely (Messier 1985). Messier, in his study area in southeastern Quebec, found daily distances of Low Prey packs were on average either greater (summer) or equal (winter) to daily distances of High Prey packs. The territory size, however, was approximately 35% smaller in the Low Prey area, supporting the fact that wolves were searching each unit area with greater intensity in both seasons.

Many studies emphasize the direct effects (e.g., prey mortality) wolves have on the population dynamics of their ungulate prey (Carbyn 1974, Mech and Kars 1977, Carbyn 1983, Gasaway et al. 1983, Messier 1994, Messier and Crete 1985, Peterson et al. 1984, Gunson 1983, Ballard et al. 1987, Boutin 1992, and others). However, predation can also profoundly affect the behaviour of prey, including use of habitat, time of activity, foraging mode, diet, mating systems,
and life histories (Sih et al. 1985). Accordingly, several studies describe the influence wolves have on movements, distribution, and habitat selection of caribou (Rangifer tarandus), moose, and white-tailed deer (Mech 1977, Stephens and Peterson 1987, Ballard et al. 1987, Nelson and Mech 1981, Messier and Barrette 1985, Messier 1994). Wolves can increase the rate at which they accrue resources by seeking out areas with dense concentrations of prey (Huggard 1991, Weaver 1994). Prey, in turn, can lower their expected mortality rate by preferentially residing in areas with few or no wolves. Several studies have suggested that ungulate prey seek out predator-free refugia to avoid predation by wolves (Mech 1977, Holt 1987, Paquet 1993). Wolf predation in the Superior National Forest of northern Minnesota was found to affect deer distributions within wolf territories (Mech 1977). Densities were greater along edges of territories where predation was thought to be less.

Unusually mild or severe winter weather can result in ungulate populations that are temporarily higher or lower than predicted habitat capability (which reflects long-term average maximum). Where predation is a factor, ungulates may exist at levels well below carrying capacity for relatively long periods. The interactions of ungulates and their predators (in our case wolves, coyotes, foxes, black bears, and cougars) may, under some circumstances, overshadow habitat capability as a controlling factor for ungulate populations. Ungulate populations may be more strongly influenced by the frequency and depth of population lows, than by habitat capability.

Ungulate biomass can affect rates of population increase and resulting densities of wolves. Building on work of Keith (1983), Fuller (1989) reviewed 25 studies of North American wolf and prey populations and found rates of increase of wolf populations are most affected by relative availability of ungulate biomass (directly influencing survival of pups <6 months old) and human-caused mortality. He concluded that regardless of prey type or stability of wolf populations, average wolf densities are clearly correlated with the biomass of ungulates available per wolf. Furthermore, he found the index of ungulate biomass per wolf is highest for heavily exploited (Ballard et al. 1987) or newly protected (Fritts and Mech 1981) wolf populations and lowest for unexploited wolf populations (Oosenbrug and Carbyn 1982, Mech 1986) or those where ungulates are heavily harvested (Kolenosky 1972).

b. DATA SUMMARY
We used information in the carcasses database to assess wolf use of prey species. Prey densities and the weights of prey were derived from Groebner et al. (1995).

c. METHODS
We estimated potential wolf numbers using regression equations that relate wolf numbers to ungulate biomass (Keith 1983, Fuller 1989). The equations were modified to reflect prey species available to wolves in Arizona and New Mexico. Accordingly, biomass was calculated by multiplying population densities of elk, white-tailed deer, and mule deer (O. hemionus) by average edible weights of elk, white-tailed deer, and mule deer. We used weights of 159 kg (350 lb.) for elk, 36 kg (80 lb.) for white-tailed deer, and 55 kg (122 lb.) for mule deer (Groebner et al.)

\[ Y = 0.041X \]
where \( Y \) = wolf numbers, \( X \) = prey biomass

\[ Y = 0.041X \]
where \( Y \) = wolf numbers, \( X \) = prey biomass
We used prey densities of 1.1 km² for elk, 0.9 km² for white-tailed deer, and 2.8 km² for mule deer (Groebner et al. 1995). Assuming that ungulate populations would decline slightly in the presence of wolf predation, prey densities were reduced 10% in our final calculations. We assumed prey were evenly distributed and equally available throughout the primary and secondary release sites. Bighorn Sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), javelina (*Tayassu tayacu*), and beaver (*Castor canadensis*) were not included in our analyses because no population data were available.

d. RESULTS

The Interagency Field Team recorded 55 probable wolf kills. Elk constituted 85%, mule deer 7%, and deer of unknown species about 4% of recorded kills. The predominance of elk in the diet was consistent among packs (Figure 25). Based on numbers of prey available and biomass available within the primary release site, elk were used disproportionately. Note, however, that observational bias may skew collection of kill data. Elk are easier to find because they are larger than deer and not consumed as rapidly. In addition, the seasonal movements of wolves and their prey can affect spatial overlap and thus availability. Lack of data and time prevented us from assessing this possibility.

Based on ungulate biomass, the Blue Range Wolf Recovery Area (6,854 mi² or 17,751 km²) can, in theory, support an estimated 468 wolves (range 292-821). The target recovery area of 12,950 km² (5,000 km²) could support between 212 and 599 wolves (Figure 26) (Table 3). We believe these estimates are high because they assume all prey are equal and will be consumed in proportion with availability. Given our experience with multiple prey systems elsewhere this is unlikely to occur. We therefore calculated wolf population estimates for individual prey species. Accordingly, elk in the Blue Range Wolf Recovery Area could support about 213 wolves, and the combined deer species about 255 wolves.
Figure 25. Prey (n = 55) probably killed by reintroduced Mexican wolves, 1998-2001.
Figure 26. Potential number of wolves that, in theory, could occupy target objective of 12,950 km² (5,000 mi²) within the Blue River Wolf Recovery Area. Estimates are based on prey biomass available to wolves and are maximum numbers. The individual contribution of ungulate prey species is shown for comparison with other studies.
Table 3. Potential wolf numbers (ranges) for recovery areas based on predicted population densities of ungulates 5 years post restoration of Mexican wolf population. We partitioned the table to show the contributions of different ungulate species.

<table>
<thead>
<tr>
<th>PREY SPECIES</th>
<th>Primary Zone (2,664 km²)</th>
<th>Recovery Objective* (12,950 km²)</th>
<th>BRWRA* Low (17,563 km²)</th>
<th>BRWRA* High (17,563 km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-tailed Deer</td>
<td>10-13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mule Deer</td>
<td>46-63</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-tailed and Mule Deer</td>
<td></td>
<td>118-323</td>
<td>162-245</td>
<td>293-443</td>
</tr>
<tr>
<td>Elk</td>
<td>50-67</td>
<td>94-276</td>
<td>129-195</td>
<td>250-378</td>
</tr>
<tr>
<td>All Prey</td>
<td>106-143</td>
<td>212-599</td>
<td>292-441</td>
<td>543-821</td>
</tr>
</tbody>
</table>

*For white-tailed and mule deer, we used an average biomass to derive wolf estimates.
e. CONCLUSIONS

Given the current ratio of wolves to ungulate prey, we conclude the reintroduced Mexican wolf population is not limited by food. Adequate prey are available to support and sustain a growing wolf population. Estimated wolf numbers derived from ungulate biomass were similar to numbers projected in the EIS. Because wolves depend primarily on ungulates for food, long-term survival of wolves in the study region depends primarily on protection of habitat for elk and deer.
10. **HAS THE LIVESTOCK DEPREDATION CONTROL PROGRAM BEEN EFFECTIVE?**

a. **BACKGROUND**
   Although an effective livestock depredation program is critical for wolf recovery, effective assessment of such a program requires more specific guidance and data than we were provided.

b. **DATA SUMMARY AND METHODS**
   Our analysis is based on interpreting records in the Events and Incidences databases.

c. **RESULTS**
   Forty-two (42) reports of possible wolf-livestock interactions were recorded between March 1998 and March 2001. Of these, the Interagency Field Team concluded that 5 events were accidents, 9 were non-wolf predators [e.g., bear (*Ursus americanus*), lion (*Felis concolor*), coyote (*C. latrans*)], 18 were wolf related, and 10 were probably wolf related. That is, 28 events involved wolves or probably involved wolves. These included uninjured livestock, injured livestock, and killed livestock (Table 4). The Interagency Field Team recorded 10 confirmed livestock-wolf interactions where no injury or death occurred. At a minimum, 55% (26) of all free-ranging wolves have interacted with livestock. Thirty-six percent (17) have interacted with livestock 3 or more times. Approximately 10% have interacted with livestock 5 or more times. Approximately three-quarters of the livestock injuries or deaths occurred on National Forests.

   The number of reported livestock-wolf interactions varied seasonally (Figure 27). The interactions reported annually since the first reintroduction of Mexican wolves were; 5 from March 1998 to March 1999, 17 from March 1999 to March 2000, and 6 from Mar 2000 to Mar 2001.

   Seventeen (17) reports of wolf interactions with cats or dogs were recorded between March 1998 and March 2001. These 17 reports included uninjured dogs, injured dogs, and killed dogs or cats. Of these, we concluded that; 13 interactions involved wolves; 1 interaction probably involved a wolf, and; 3 interactions cannot be classified using the data provided. The Interagency Field Team recorded 8 dog-wolf interactions where no injury or death occurred. Of the 13 interactions that definitely involved wolves, 5 resulted in the cat or dog being killed or injured (Table 5).

   The average response time for all reported domestic animal-wolf interactions was less than 24 hours. The longest response time was 3 days, which occurred once.
Table 4. Numbers of domestic animal injuries and deaths due to wolf depredation. The data are for confirmed, probable and unconfirmed wolf depredations.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>OUTCOME OF INTERACTION</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Injured</td>
</tr>
<tr>
<td>Cow</td>
<td>1</td>
</tr>
<tr>
<td>Calf</td>
<td>2</td>
</tr>
<tr>
<td>Bull</td>
<td>1</td>
</tr>
<tr>
<td>Mini Colt</td>
<td>0</td>
</tr>
<tr>
<td>Lamb</td>
<td>0</td>
</tr>
<tr>
<td>Dog</td>
<td>3</td>
</tr>
<tr>
<td>Cat</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>7</strong></td>
</tr>
</tbody>
</table>

Table 5. Ownership of property where domestic animal injuries and death due to wolves took place. The data are for confirmed, probable, and unconfirmed wolf depredations.

<table>
<thead>
<tr>
<th>OWNERSHIP</th>
<th>LIVESTOCK INJURIES OR DEATHS</th>
<th>CAT/DOG INJURIES OR DEATHS</th>
</tr>
</thead>
<tbody>
<tr>
<td>National Forest</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>Private</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Other or not recorded</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>
Figure 27. The number of livestock-wolf interactions fluctuated seasonally in the primary recovery zone.

d. CONCLUSIONS
Livestock are omnipresent in the Blue Wolf reintroduction area. Because of the extensive temporal and spatial distribution of livestock, interactions with wolves are unavoidable. From the information made available to us, we believe the Service has been responsive to wolf-livestock and wolf-domestic animal conflicts. An equivalent level of responsive will be necessary in the future. Similarly, livestock producers using public lands can make a substantive contribution to reducing conflicts with wolves through improved husbandry and better management of carcasses.
11. HAVE DOCUMENTED CASES OF THREATS TO HUMAN SAFETY OCCURRED?

Although no injuries or deaths have occurred, several wolf-human interactions have been reported. Consequently, evaluation of these incidences is largely qualitative based on our experiences with wolves in other parts of North America. We note that captive reared wolves released to the wild may behave differently than wild born wolves (Breitenemoser et al. in press).

a. DATA SUMMARY AND METHODS
Our analysis of this issue is based on interpreting records in the Events and Incidences database.

b. RESULTS
The Interagency Field Team reported eleven interactions between March 1998 and March 2001 (Table 6). On average, they reported one event every 3 months. However, the rate may be increasing (3 events from Mar 1998 to Mar 1999, 1 event from Mar 1999 to Mar 2000, 7 events from Mar 2000 to Mar 2001). If the rate is increasing, it is probably due to more wolves rather than an increased propensity for wolves to interact with humans. On average, one interaction was reported every 7 weeks from Mar 2000 to Mar 2001. Although data are too few to be certain, interactions do not seem to predominate in any particular time of the year.

Seven (of 11) interactions involved something that would be expected to attract wolves (e.g., dogs, deer carcass, livestock). Specifically, 5 (of these 7) involved dogs. One (of 11) interaction was instigated by the people involved (event #10). In 2 (of 11) events, the people involved felt as though their lives were threatened. In 4 (of the 11) events, an official response (i.e., from reintroduction personnel) occurred within 24 hours. In the other 7 events, no response date or time is reported. In 9 (of the 11) events, response involved an inspection of the site.

In 2 events (# 1 and #7), the people involved reported being fearful for their safety. However, experience suggests that because the people of event #7 responded appropriately, they were probably never in danger. In event #1, the wolf was shot. Event #8 is similar to cases in Ontario, British Columbia, and Alaska where wolves have injured people. In these all these cases, the people responded inappropriately to curious wolves or wolves attracted to food.

Twelve (12) different wolves have been involved with human interactions. Approximately 25% of all the wolves that have been released into the wild have been involved in a reported wolf-human interaction. Eight (of these 12) wolves were involved in only a single event. One (of these 12) wolves (i.e., 590) was involved in 4 events. All these events took place in August and September of 2000. Since then, wolf 590 has not been involved in any human interactions. Three (of the 12) wolves (i.e., 587, 509, 511) were involved in 3 events. All 3 events included wolf 590.

The ‘immediate’ fate of the 12 wolves was: 1 shot, 2 brought into captivity, 1 brought into an acclimation pen, and in 8 cases no attempt was made to capture the wolf. The ‘ultimate’ fate of the 12 wolves was: 2 shot, 3 permanently brought into captivity, 6 either are still free-ranging or died of natural causes, and for 1 wolf (i.e., #298, the potential data entry error) no data were available.

<table>
<thead>
<tr>
<th></th>
<th>DATE</th>
<th>WOLVES INVOLVED</th>
<th>MEMO</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>April 28, 1998</td>
<td>156</td>
<td>Wolf 156 was shot by a camper who feared for his family's safety when the wolf came into their camp and attacked their dog.</td>
</tr>
<tr>
<td>2</td>
<td>May 8, 1998</td>
<td>494</td>
<td>494 became a nuisance frequenting the town of Alpine from 5/8/98 through 5/28/98 and was permanently removed from the wild.</td>
</tr>
<tr>
<td>3</td>
<td>January 6, 1999</td>
<td>166, 482</td>
<td>Campbell Blue pair jerked down a deer carcass hanging in some archery hunter's camp.</td>
</tr>
<tr>
<td>4</td>
<td>January 5, 2000</td>
<td>522</td>
<td>Female 522 hanging around hunters camp interacting with dogs. Trapped and put in acclimation pen to hold through hunting season.</td>
</tr>
<tr>
<td>5</td>
<td>April 14, 2000</td>
<td>166, 518</td>
<td>Dean Warren reported very aggressive encounter with Campbell Blue pair with the female, 518 bumping his horse and passing under it. Wolves also attacked one of his dogs. They followed him to cabin and he held up in it until the wolves left.</td>
</tr>
</tbody>
</table>
Don and his cocker spaniel were out in the middle of the meadow behind his trailer when 4 wolves (most likely Francisco) came tearing out of the woods towards them. Don fired 1 hot in front of the wolves but they kept coming ("one with a look of fierce determination"). He fired a second shot as they got closer and they reared away. He was very upset at the situation and felt that they were a danger to both people and animals/pets. Later that week, people camped nearby observed several wolves and pups resting in the shade under and around Don’s trailer. At the time, he was inside watching golf with his dog, unaware that the wolves were outside. He was irrate when he learned of the incident, stating that this was not the behavior of wild animals and concerned about what would have happened had he or his dog come out of the trailer.

Scott observed Francisco (and Cienega) on multiple occasions during his time camping at Double Cienega. Sometimes they came right through cmp < 5 ft of him taking pictures, although the pups seemed more skittish, other times farther away within the campground or out in the meadow. He also saw them once farther up Double Cienega and "the shaggy one" (yearling male 590) laid down w/in 10 ft and just looked at him while he took pictures.

Yearling male 590 hanging around Double Cienega Campground for the majority of the day.
5-6 people camped in Double Ciénega from about 8/21-8/30/00. Throughout the week they interacted with Francisco. On multiple occasions they howled the pack in, chased them on ATVs, left food out, and shot blunt arrows at them. The wolves also chased their horses, mules, and the people in the ATVs.

They were informed that this behavior was not acceptable, and we explained that what they were doing may possibly have negative effects on the wolves behavior. On 8/30/00, while speaking with the hunters, N. Sanchez observed the wolves chasing the mules. He then hazed the wolves by running at them and throwing rocks. They ignored him. We first spoke with the group on about 8/23/00. We informed them about the Mexican Wolf Recovery Project, the presence of wolves in the area, and proper behavior with respect to the wolves (ie. Do not leave out food; keep an eye on mules/ horses; if you see the wolves, yell and throw rocks at them.) We also told them to let us know if they had any interactions with the wolves.

At about 0440 Cole went out the front door on the porch and observed an animal in the driveway. At first he thought it was a German Shepard, then by the color and size he realized it was a wolf. He shewed it away and it headed west down the road. He tried to follow it in his truck but lost track of it. When he got back to the house it was by the back door eating out of the dog dish. He shewed it away again and it ran behind the house between the animal pens and the barn. He checked the dog dish and it was empty. He was not sure if there had been food in it or not.

Stark and Grant responded to the call made by Ms. Leona Brown (the landowners sister). We looked at the area where the report was taken and observed large canid tracks in the driveway and yard. (track size=5x3 1/2", in sand and gravel). No other tracks were found in area. Stark and Armistead returned on 10/2 at about 0500.

c. CONCLUSIONS
Wolf-human interactions have been reported consistently and regularly since the beginning of the program. Approximately 25% of the individuals in the free-ranging population have been involved with wolf-human interactions. As the wolf population grows, the Program should be prepared for steadily increasing frequencies of wolf-human interactions. Over time, the frequency of wolf-human interactions (per wolf) may decline with wild-born wolves that are less tolerant of humans. Because wolves can pass information between generations, the attraction to humans may take some time to extinguish. In the Republic of Georgia, for example, captive-born wolves were intensively trained to kill wild prey and to avoid humans before their reintroduction. This release procedure was considered successful after the third generation of wild-born wolves still showed the same behavior as their hand raised parents (J. Badrize pers. comm.).

The Program has responded well to wolf-human interactions, although documentation and data recording have been poor. For example, in the databases USFWS provided us no response dates or times were recorded for 7 events. It is critical that the Interagency Field Team keep comprehensive notes on wolf-human interactions. The Program should continue its practice of responding to all wolf-human interactions with immediate on site inspections and investigations. The Interagency Field Team appears to have made responsible decisions regarding the recapture of wolves involved in human interactions.
12. OVERALL CONCLUSIONS AND RECOMMENDATIONS

a. PREFACE

On 25 April we convened a meeting in Globe, Arizona to present our draft report to the Mexican Wolf Interagency Management Advisory Group (IMAG). We purposefully presented a draft to provide the IMAG a chance to make substantive contributions to our review. Many comments we received during the meeting clarified issues, thus materially improving our review. During the week of 30 April the draft report was, without our knowledge released to the media. During the following weeks several newspaper stories presented the findings of our draft review as final determinations. Moreover, on 12 May the Arizona Game and Fish Commission received a briefing about the reintroduction from representatives from the Arizona Game and Fish Department who also presented our draft findings as final determinations. Draft reports are by definition works in progress. Any discrepancy between the conclusions and recommendations presented in the draft report and those presented here are a result of that simple fact.

Our conclusions and recommendations are based on our analysis of the data. We believe the long term objective is to protect the wolf population and meet human needs by reducing the potential for one to seriously encroach upon the other. Current circumstances demand that wolves be conserved in a human dominated landscape. This requires a systematic and rigorous approach to wolf recovery that integrates the social and economic aspirations of humans with the ecological necessities of wolves.

b. CONCLUSIONS

The ultimate factor determining population viability for wolves is human attitude. Thus, an active and fully enabled Recovery Program comprising private interests, non governmental conservation organizations, local, state, federal, and tribal agencies is essential to ensure success of any restoration. The biology, politics, and sociology of wolf reintroduction in the Blue River Wolf Recovery Area are too complex for recovery to be successful without a fully engaged and participatory Program. Fortunately, the Service has a successful history of reintroducing and effectively managing recovered wolf populations in other parts of the country (Refsnider 2000). Based on this success and the first 3 years of the Mexican wolf reintroduction, we think that expecting a similar outcome in the Blue River Wolf Recovery Area is reasonable.

Overall we are satisfied with the progress of the reintroduction project since its inception in 1998. During May 2001, the Service reported that at least 28 wolves were free-ranging. Most of these animals are in social groups and the Service reports up to 5 litters have been produced in the wild this spring. Monitoring of reintroduced wolves has revealed that captive-born Mexican wolves can adjust to life in the wild by primarily preying on elk. This fact combined with the likely presence of several litters in the wild bodes well for the future. We believe the likelihood is high that continued application of the Service’s current practices will result in the restoration of a self-sustaining population of Mexican wolves in the Blue Range Wolf Recovery Area. We believe, however, the Program should continue with some adjustments and modifications.

Not surprisingly, our review revealed room for improvement. Restoration of any wildlife population is fraught with uncertainty and work elsewhere shows that many projects are unsuccessful because of a failure to accommodate new information (Breitenmoser et al. in press).
Several factors currently hinder recovery of a self-sustaining and viable wolf population. Those that predominate are:
1. The small areal extent of the primary recovery zone, which greatly hinders the vigor of the reintroduction phase of the reestablishment project
2. The Service’s insistence that wolves only inhabit the small Blue Range Recovery area, which is at odds with the naturally extensive movements that characterize gray wolves and current thinking regarding the viability of large carnivore populations (Noss et al. 1996).
3. The Service’s embrace of a target population of 100 wolves (EIS, page 2) when such a population is not viable over the long term (Shaffer 1987, IUCN 1994, Noss et al. 1996, Breitenmoser et al. in press).

RECOMMENDATIONS
The architects of the Mexican wolf reintroduction program properly accounted for the inevitable uncertainty and difficulty of the project by establishing adaptive management as the overarching operational paradigm. Consequently, our recommendations are largely the inevitable result of the reintroduction project’s maturation. In this regard, we predict that the next review will also identify changes that can be made for improving the program.

If the Service adopts the recommendations presented below then the effectiveness of the reintroduction project and prospects for success will improve. Proper adoption of our recommendations will require a long-term and diligent effort by the Service. For many of the recommendations to be effective, biologists involved in the daily matters of the reintroduction effort must embrace them as standard operating procedures.

The current reintroduction project will greatly influence the future of the Mexican wolf recovery program since additional reintroduction projects will be required to remove *Canis lupus baileyi* from the list of endangered and threatened wildlife. Accordingly, we used our review to develop a few recommendations that consider Mexican wolf recovery overall. We also decided to consider programmatic issues that are germane to reintroduction, and issues the Service did not provide data for such as injuries resulting from capture. All of the recommendations below relate directly to the successful restoration of Mexican wolves the BRWRC. We did not elaborate on several biological issues, identified in our recommendations as important, because the reintroduction process is in too early a stage to have accumulated sufficient data.

### Biological and Technical Aspects

**WE RECOMMEND THAT THE SERVICE:**

- Continue to develop appropriate opportunities to release (and re-release) wolves for at least 2 years to ensure the restoration of a self-sustaining population.

- Begin developing population estimation techniques that are not based exclusively on telemetric monitoring. As the wolf population grows it will become increasingly difficult to maintain telemetric contact with all known or suspected packs. Consequently, the Service needs to
develop non-telemetrically-based methodology (e.g., track station surveys, genetic sampling of
hair or fecal material) for assessing the distribution and size of the wolf population.

**Develop data collection forms and data collection and management procedures similar to
those used by the red wolf restoration program in North Carolina.**

**Require biologist to promptly and carefully enter field data into a computer program for
storage and analysis.** The Service should require biologists to record data on a per wolf and per
day basis. Data checking should be improved to eliminate data entry errors. In this regard,
picklists and auto filling fields can simplify data entry and improve accuracy. Lastly, the Service
should require that data files be proofed at least once before they conduct analyses. We remind
field biologist working on the project that generally 1 hour of productive time in the field requires
2 hours in the office for data management and initial analyses.

**Make all data available for research and peer review.**

**Carefully consider using a modified #3 soft-catch trap for capturing Mexican wolves rather
than the McBride #7.** We are concerned that the #7 might cause unacceptably frequent and
serious foot injuries. The Service might find that a modified #3 soft-catch trap is more appropriate
for capturing wolves that have a high probability of being re-released or that are fairly small (e.g.,
smallish adults or pups). Modified soft-catch traps have been used to capture hundreds of red
wolves that are similar in size to Mexican wolves and larger gray wolves (Quebec) with no
serious foot injuries (M. Phillips unpublished data, P. Paquet unpublished data). However, careful
consideration of all aspects of capturing wolves with leghold traps will lead to a proper decision
about the use of a modified trap for capturing Mexican wolves.

**Encourage research that will help to inform future Program evaluations and adjustments.**
The research we suggest is beyond the scope of the current Mexican wolf program because of
resource limitations (personnel and fiscal) and the need to focus on the central mission of
reintroducing wolves. However, research partnerships with universities and other organizations
should be developed. Increasing the capacity of the Mexican wolf recovery Program, should be a
principle charge of the Recovery Team. The following areas are of contemporary conservation
and academic interest and should be research priorities:

1. Population modeling (PVA and metapopulation model) and sensitivity analysis of short-
and long-term demography and distribution
2. Assessment of new threats to population including new guild structure, disease, and human
activity.
3. Habitat viability analyses of the release area and projected population range (environment,
resources, carrying capacity, spatial characteristics, etc.)
4. Development of guidelines for decision-making in conflict situations
5. Reassessment of policies for intervention in the release phase
6. Assessment of monitoring programs
7. Evaluation and design of long-term management program, including
a. Evaluation design of long-term monitoring program
   1. demography and population range
   2. genetic surveillance
   3. health surveillance
   4. long-term adaptation of individuals and population to ecosystem
   5. effects on ecosystem (predation, displacement)

7. The interaction of Mexican wolves with other carnivores in the reintroduction area. Reintroduction or recolonization of wolves influences the behavior, abundance, and distribution of other carnivore species. For example, wolf recovery in the Rocky Mountains has resulted in interference and exploitation competition among wolves, bears, coyotes, and cougars, causing changes in the composition and structure of the carnivore guild.

Develop a contemporary definition of a biologically successful wolf reintroduction and the criteria needed to measure success. The latter includes methods and time scales. Specific issues that need to be considered are:

1. How many wolves and how many breeding pairs will result in a demographically and genetically viable population?
2. How do metapopulation dynamics affect the viability of Mexican wolves?
3. How broad a geographic area would such a population inhabit?
4. What affect will a viable population have on elk, deer, cattle, etc.?
5. What target population size will lead to long-term demographic viability?
6. What target population size will lead to long-term genetic viability?

We propose the application of the IUCN Red List Categories (IUCN 1994) to assess success and failure at 5 and 10 years following completion of the release phase (Table 7). The classification is based on an assessment using 5 criteria; population reduction, area of occurrence and occupancy, 2 criteria for population density, and a quantitative analysis of the extinction probability. If the population is assessed as “critically endangered” after 10 years the project should be considered a failure because there is a very high risk of extinction in the wild in the future. The minimum standard for success should be vulnerable or better. Vulnerable populations still face a high risk of extinction in the medium-term future and require ongoing management.

Table 7. Biological criteria for measuring project success of Mexican wolf reintroduction at about 5 and 10 years following completion of reintroduction phase. If the evaluation falls between failure and success, the viability of the population should be classified as uncertain. These guidelines follow the Red List Categories (IUCN 1994: www.iucn.org/themes/ssc/redlists/ssc-rl-c.htm)

<table>
<thead>
<tr>
<th>CRITERIA</th>
<th>FAILURE</th>
<th>SUCCESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population reduction of x%, projected or suspected within the next 10 years.</td>
<td>&gt; 80%</td>
<td>&lt; 20%</td>
</tr>
</tbody>
</table>
Extent of occurrence estimated to be $x$ km² or area of occupancy estimated to be $y$ km², and estimates indicating 2 of the following: (1) severely fragmented or known to exist in only one location; (2) projected decline or extreme fluctuations in extent of occurrence, area of occupancy, habitat area or quality, number of locations or subpopulations, or number of mature individuals; (3) continuous, observed, inferred or projected decline in area, extent or quality of habitat.

- $x < 100$  
- $y < 10$

Population estimated to number $x$ mature individuals and projected continuous decline in number of mature individuals, and population severely fragmented or all individuals in a single population

- $x < 250$

Population estimated to number $x$ mature individuals.

- $x = 50$

Probability of extinction is $x$ within $y$ years or $z$ generations, whichever is longer.

- $x \geq 50\%$
- $y = 10$, $z = 3$
- $x < 20\%$
- $y = 20$, $z = 5$

**Valuational and Organizational Aspects**

*We recommend that the Service:*

**Modify the recovery team by inviting an appropriate individual other than the recovery coordinator to serve as the team leader.** While ultimate responsibility for Mexican wolf recovery would still reside with the recovery coordinator, enlisting another individual to serve as team leader would increase the capacity of the recovery program. Other recover program use this administrative structure and it works well (e.g., the California condor recovery program).

**Instruct the modified recovery team to revise by June 2002 the 1982 recovery plan.** A revision of the recovery plan is long overdue for several reasons. First, the current plan does not contain any standards for removing *C. l. baileyi* from the endangered species list. Second, since the plan was approved great advances have been made in the science of conservation biology; such advances would greatly instruct revision of the recovery plan. Finally, due to work with red wolves in the southeast, gray wolves in the Great Lakes states and the northern Rockies, and Mexican wolves in the Blue River Wolf Recovery Area we have a much greater understanding of wolf reintroductions and management; such understanding would greatly inform revision of the Mexican wolf recovery plan.
Immediately engage the services of the modified recovery team. The challenges of wolf restoration are many and varied. Meeting such challenges requires a restoration effort that is itself diverse and capable. The current reintroduction project and Mexican wolf recovery in general would benefit substantially from the efforts of a fully engaged recovery team.

Immediately modify the final rule (Parsons 1998) and develop the authority to conduct initial releases into the Gila National Forest. Several releases conducted during the first 3 years of the reintroduction project resulted in wolves settling much of the primary recovery zone in the Blue River Wolf Recovery Area. As work elsewhere (Phillips unpublished data) has revealed, wolves should not be released in areas that support resident animals. Over time, it will become harder for the Service to find suitable release sites in the primary recovery zone. The Service can best address this problem by obtaining the authority to conduct initial release in the secondary recovery zone, most notably the Gila National Forest. This recommendation was first made to the Service by a panel of experts (including Phillips) enlisted by the Service to review the reintroduction program in January 1999. Despite the Service’s approval of the recommendation, they have taken no implementation action. This is by far the most important and simplest change the Service can make to the existing reintroduction project. The Gila National Forest is approximately 75% of the 4.4 million acre Blue River Wolf Recovery Area. The Gila Forest includes about 700,000 acres that are roadless and free of livestock. Several high-quality release sites are available in the area. Using them is the best way for improving the cost-effectiveness and certainty of the reintroduction project. Accordingly, we strongly recommend that the Service immediately take whatever action is necessary to conduct initial releases of captive-born (and wild-born if appropriate) Mexican wolves to the Gila National Forest.

Immediately modify the final rule to allow wolves that are not management problems to establish territories outside the Blue River Wolf Recovery Area. For specific language and instruction for this modification we strongly recommend that the Mexican wolf recovery program review the final rule promulgated for the gray wolf recovery in the northern Rockies (Bangs 1994). During the first 3 years of the reintroduction the Service recaptured some Mexican wolves simply because they left the Blue River Wolf Recovery Area. As the wolf population grows, more animals will disperse from the Blue River Wolf Recovery Area. Retrieving animals because they wander outside the primary recovery area is inappropriate because it is:

1. inconsistent with the Service’s approach to recover wolves in the southeast, Great Lakes states, and the northern Rockies;
2. will lead to serious logistical and credibility problems as the wolf population grows and more wolves disperse from the area; and
3. needlessly excludes habitat that could substantially contribute to recovery of *Canis lupus baileyi*.

Before the current Mexican wolf reintroduction project was initiated, the red wolf recovery program adopted a similar approach (Henry 1995) with dire consequences (Phillips and Smith 1998). Extensive tracts of public land and some private land outside the Blue River Wolf Recovery Area are suitable for wolves. Consequently, we strongly recommend that the Service develop the appropriate flexibility to allow wolves to occupy lands outside the Blue River Wolf
Recovery Area. We believe that obtaining the requisite flexibility will require that the Service modify the final rule currently governing the reintroduction project.

We recognize that the statements above as they relate to private land may cause controversy so we offer the following remarks. Allowing Mexican wolves to inhabit suitable tracts of private land (e.g., large holdings) in the absence of problems, would bring the reintroduction project into compliance with Service-led efforts to recover wolves elsewhere. Allowing wolves to inhabit private property in the absence of a problem should not be construed to mean that the Service would begin to actively target private lands as wolf habitat that needs to be settled. Quite the contrary, and note that nowhere is the Service effecting management of private land to promote wolf conservation. However, throughout the U.S (except in the Blue River Wolf Recovery Area) if a wolf wanders onto private property and does not cause a definable problem, and its mere presence is not a definable problem, then the Service is not required to remove the animal even if the landowner demands such action.

Such an approach to wolf recovery is consistent with the determination in the United States that the public owns wildlife, rather than private landowners. Within limits, landowners can manage their property in a way that promotes or hinders the welfare of wildlife. However, through laws enforced by state and federal officials, citizens decide under what circumstances wildlife can be captured and moved or killed from public and private land. Such decisions are not the prerogatives of the landowner, regardless of whether the animal(s) in question are naturally occurring or present because of a reintroduction program.

In sharp contrast with the Service’s approach elsewhere, the Mexican wolf project developed a rule that requires wolves to be removed from public and private land outside the Blue River Wolf Recovery Area, even in the absence of a problem (Parsons 1998). Such regulations are inappropriate for at least 2 reasons: 1) they are nearly impossible to effectively carry out as the wolf population grows because of the difficulties of managing an ever-increasing number of wide-ranging dispersing animals, and 2) they establish a precedent that could be effectively used to argue for the removal of other endangered species inhabiting certain tracts of public or private land.

Certainly local opposition to the Mexican wolf reintroduction program affected the development of such a rule. Indeed, the recovery program coordinator assumed from personal knowledge of local politics and sentiments that a more restrictive rule would have significantly hindered and possibly caused the termination of the project (D. R. Parsons personal communication 1996). Maybe this was a valid assumption. Opinion polls, however, suggest widespread and persistent local support for wolf recovery in the southwest (Duda and Young 1995, Pate et al. 1996, Meadows 2001). Regardless, noting that wolf recovery elsewhere has faced substantial opposition is instructive, but the Service did not promulgate similarly onerous rules (e.g., see Bangs 1994, Henry 1995). And to date, recovery efforts elsewhere have been quite successful (Refsnider 2000).

Resist any opportunity to reintroduce Mexican wolves in the White Sands Wolf Recovery Area (WSWRA). Two independent assessments suggest that the WSWRA could support only 20 to 30 wolves (Bednarz 1989, Green-Hammond 1994); such a population is not viable (Shaffer 1987). The inability of the WSWRA to support a viable population of wolves is due to the area’s relative smallness (about 10,311 km² or 4,028 mi²) and its distance from other suitable habitat.
For example, the WSWRA is about 100 km (62 miles) from the extreme eastern edge of the BRWRA. While wolves can easily traverse such a distance, the “dispersal area” comprises very poor wolf habitat, supports the town of Truth or Consequences, New Mexico in its core, and is bisected by the heavily traveled federal Interstate 25. Accordingly, the USFWS should not expend resources on reintroducing wolves to the WSRWA.

Provide biologists with opportunities to visit other wolf projects to gain training with capturing and handling free-ranging and captive wolves.

Station the field coordinator in the Blue River Wolf Recovery Area (e.g., in Glenwood or Silver City, New Mexico or Alpine, Arizona) and insist that this person be intimately involved with all aspects of fieldwork (wolf management; public relations; data collection, management, analysis, report preparation; etc.). We think it would be a serious mistake to station the field coordinator in the Regional Office in Albuquerque. Such a decision would add a level of complexity that is entirely unwarranted.

Put forth a concerted effort to develop realistic expectations for the project. Restoration is an imprecise process that is by definition “heavy-handed”. The Service needs to constantly remind the public and the media of this fact. It is certain that the Service will have to overcome great challenges in the future. Such challenges will mean that intervention will be required, that wolves will disappear, and that some animals will die. But just as certainly, meeting the challenges will ensure the restoration of a self-sustaining population of Mexican wolves in the Blue River Wolf Recovery Area.

Initiate programs to educate people about wolf behavior. In most events involving humans, wolves are interested in dogs or food (e.g., carcasses, dog food, etc.). Members of the program expected to respond to wolf-human interactions should be well educated on the nature and variety of reports from Algonquin provincial park, Alaska, and British Columbia. The Program should contact other western communities and agencies that have dealt with large carnivore-human interactions (e.g., mountain lions, bears, wolves). The Program should also actively warn people that dogs, deer/elk carcasses, and livestock carcasses may attract wolves. Although the danger is not the same, hunters should be advised to behave as though they are in grizzly bear country.

Require livestock operators on public land to take some responsibility for carcass management/disposal to reduce the likelihood that wolves become habituated to feeding on livestock. Currently livestock grazing is permitted on about 66% of the Blue River Wolf Recovery Area. At least 3 packs were removed from the wild because they scavenged on dead livestock left on national forest lands. Such scavenging may predispose wolves to eventually prey on livestock. Accordingly, reducing the wolves’ access to carcasses will greatly facilitate coexistence between ranchers and wolves in this portion of the recovery area carcasses.

While some predation on livestock is inevitable, reasonable means of reducing the frequency of occurrence will enhance wolf recovery so that is respectful of the needs and concerns of livestock producers. Consequently, livestock producers using public land in occupied Mexican
wolf range should be required to exercise reasonable diligence in finding livestock that have died to either dispose of the carcass or enable the Service to do so. Such diligence will probably reduce predation on livestock, which in turn will improve the cost-effectiveness and certainty of the reintroduction project.

When writing or lecturing about the project, the Service should emphasize a community approach to understanding the wolf reintroduction project and its effect on other species and ecological processes. Conservation policy is shifting away from the preservation of single species toward preservation and management of interactive networks and large-scale ecosystems on which species depend. It is extremely important that the Service view the wolf reintroduction program in this context.
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Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates

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Abstract

Population size is a major determinant of extinction risk. However, controversy remains as to how large populations need to be to ensure persistence. It is generally believed that minimum viable population sizes (MVPs) would be highly specific, depending on the environmental and life history characteristics of the species. We used population viability analysis to estimate MVPs for 102 species. We define a minimum viable population size as one with a 99% probability of persistence for 40 generations. The models are comprehensive and include age-structure, catastrophes, demographic stochasticity, environmental stochasticity, and inbreeding depression. The mean and median estimates of MVP were 7316 and 5816 adults, respectively. This is slightly larger than, but in general agreement with, previous estimates of MVP. MVPs did not differ significantly among major taxa, or with latitude or trophic level, but were negatively correlated with population growth rate and positively correlated with the length of the study used to parameterize the model. A doubling of study duration increased the estimated MVP by approximately 67%. The increase in extinction risk is associated with greater temporal variation in population size for models built from longer data sets. Short-term studies consistently underestimate the true variances for demographic parameters in populations. Thus, the lack of long-term studies for endangered species leads to widespread underestimation of extinction risk. The results of our simulations suggest that conservation programs, for wild populations, need to be designed to conserve habitat capable of supporting approximately 7000 adult vertebrates in order to ensure long-term persistence.

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Keywords: Demographic stochasticity; Endangered species; Extinction; Minimum viable population size; Population variability; Population viability analysis

1. Introduction

The Earth is currently suffering a catastrophic loss of biodiversity (Lawton and May, 1995). A primary goal of conservation biology is to arrest this loss. Population size has been shown to be the major determinant of persistence in populations of a variety of animal species (Brown, 1971; Jones and Diamond, 1976; Toft and Schoener, 1983; Diamond et al., 1987; Newmark, 1987; Pimm et al., 1988, 1993; Richman et al., 1988; Soule et al. 1988; Berger, 1990; Kindvall and Ahlén, 1992; Schoener and Spiller, 1992; Rosenzweig, 1995; Foufopoulos and Ives, 1999). As the catastrophic loss of biodiversity continues unabated, guidelines for how extinction risk is related to population size should be a high priority in conservation biology (Shaffer et al., 2000).

Population viability analysis (PVA) provides a quantitative means for predicting the probability of extinction and for prioritizing conservation needs (Shaffer, 1981; Gilpin and Soule 1986; Beissinger and Westphal, 1998). PVA can take into account the combined impacts of stochastic factors (demographic, environmental and genetic stochasticity) and deterministic factors (e.g.
habitat loss, over exploitation) (Miller and Lacy, 1999; Beissinger and McCullough, 2002). Individual-based stochastic models of population dynamics typically use population-specific life history information to forecast future population sizes using computer simulation (Miller and Lacy, 1999; Sjögren-Gulve and Ebenhard, 2000; Beissinger and McCullough, 2002).

A number of scientists have pointed out the limitations of PVA (Beissinger and Westphal, 1998; Coulson et al., 2001). However, despite criticism, the use of PVA models in conservation continues to grow and no attractive alternatives have arisen (Mann and Plummer, 1999; Beissinger and McCullough 2002; Brook et al., 2002). Consequently, it is extremely important that variables affecting the predictive power of PVA be identified, so that there can be improvement in this important conservation tool.

A minimum viable population size (MVP) can be defined as the smallest size required for a population or species to have a predetermined probability of persistence for a given length of time (Shaffer, 1981). During the last decade, the concept of a generally applicable minimum viable population size has fallen into disfavor. This lack of interest in the concept of a minimum viable population size seems to be due to two major causes. (1) The perception that there is a great deal of taxonomic and environmental specificity involved in population dynamics, and (2) a greater emphasis on ecosystem and landscape conservation (e.g. Christensen 1997).

Reed et al. (2002) suggest that PVA should never be used to estimate minimum viable population sizes. Yet, they provide no reasoning for this statement. Any estimate of extinction risk is a de facto estimate of minimum viable population size. Because the resources available to conservation programs are finite and because political and administrative decisions are frequently made without the time for case-specific evaluations, general yet scientifically defensible estimates of minimum population sizes and habitat areas are essential (Shaffer et al., 2000). With this information, time, money and habitat areas can be rationally and efficiently allocated (Lacy, 1992). We suggest that using PVA to estimate MVPs can have great heuristic value and lead to scientifically defensible generalizations concerning viable populations.

We developed, or found in the literature, population viability models for 102 vertebrate species based on actual life history data. This approach allows us to estimate MVPs for a wide range of vertebrate species with a high level of replication. It also allows us to include most of the variables believed to be important to population persistence, using the best demographic and life history data available for wild populations. Further, PVA has been shown to provide reasonable predictions of extinction risk for well-studied species (Brook et al., 2000; McCarthy and Broome 2000; McCarthy et al., 2000; but see Lindenmayer et al., 2001; McCarthy et al., 2001).

It is not feasible to estimate MVPs from field studies for a wide variety of species within a reasonable time. The only realistic way to obtain MVPs for a large number of species and develop general guidelines is to use PVA, as originally envisaged by Shaffer (1981). The aims of our study were to: (1) Use PVA to estimate MVPs for 102 vertebrate populations, allowing us to make recommendations based on the characteristics of this distribution. (2) Search for explanatory variables causing the variation in MVPs using a large number of case studies. This allows for the specification of MVPs for different groups of species or circumstances. (3) Use the data from this study, and a review of pre-existing data, to address the arguments, presented above, against a widely applicable MVP. We use these 102 PVA models to test for the underlying phenomena causing variation in minimum viable population sizes across demographic, ecological, study, and taxonomic parameters and groupings.

2. Methods

2.1. Definition of minimum viable population size

All MVP estimates in this data set are for a 99% probability of persistence for 40 generations. We estimated minimum viable population sizes using three different criteria. (1) The primary variable manipulated in this study is the mean carrying capacity required for a 99% probability of persistence for 40 generations (MVPK). This was determined by setting the initial population size (Ni) equal to the carrying capacity (K) and varying these until the threshold risk of extinction is reached, as detailed later. (2) Output from the population viability analysis software used (VORTEX; Miller and Lacy, 1999) allows the calculation of the number of adults expected in a population of size Ni with N set equal to K, assuming a stable age distribution. Since the practical imperative is usually to define a minimum habitat area suitable for establishment of breeding territories, hunting grounds, etc., we will focus on this minimum viable adult population size (MVPA). This is a particularly relevant measure, as most conservation organizations couch population size in terms of the number of sexually mature individuals. (3) Output on heterozygosity can be used to calculate the effective population size (Ne) for any given K. This is the minimum viable effective population size MVPNe. This measure is relevant as a comparison with predictions of minimum viable population size based on genetic theory.

The three measures of MVP all correlate very strongly with each other (r > 0.93 in all comparisons) and the choice of measure does not qualitatively change the conclusions reached in any of the analyses.
2.2. *PVA models*

VORTEX version 8.01 (Miller and Lacy, 1999) was used to model the 102 populations examined in this study. VORTEX is an individual-based, age-structured population simulation model that can include carrying capacity, demographic stochasticity (in mortality and breeding structure), environmental stochasticity, catastrophes, density-(in)dependent reproductive rates, inbreeding depression, and allows a range of user defined functions to replace fixed parameter terms (Miller and Lacy, 1999). VORTEX has been extensively applied to endangered species conservation by the Conservation Breeding Specialist Group of the World Conservation Union and others (Seal et al., 1998).

2.3. Vortex inputs and outputs

Most model inputs were gathered directly from the species-specific studies. Age-specific birth and death rates and their variance, mean age at first breeding, mean litter size and its variance, and proportion breeding and its variance, were all calculated from the available demographic information. If no data on maximum age were available, it was estimated from the shape of the mortality curve.

The frequency and magnitude of catastrophes was estimated from the species-specific study, from data available on the Global Population Dynamics Database (NERC Centre for Population Biology, 1999), or estimated from Reed et al. (in press).

Inbreeding depression is the one variable where a default value was used. A conservative figure of five lethal equivalents, per diploid genome, for juvenile survival was used. The actual number of lethal equivalents for juvenile mortality may be higher (Jiménez et al., 1994; Crnokrak and Roff, 1999; Keller et al., 2002) and certainly inbreeding depression in natural populations affects adult survival and fecundity as well as juvenile survival (Keller, 1998; Cheptou et al., 2000; Meagher et al., 2000; Keller et al., 2002). The model allowed for the purging of the genetic load via selection against deleterious recessive alleles. The evidence for genetic effects on fitness and persistence in wild populations now seems irrefutable (Vrijenhoek, 1994; Saccheri et al., 1998; Westermeier et al., 1998; Crnokrak and Roff 1999; Madsen et al., 1999; Hedrick and Kalinowski, 2000; Richards, 2000; Nieminen et al., 2001; Reed and Frankham, in press).

Density-dependence as a form of regulation for population size is very common (Woiwood and Hanski, 1992; Godfray and Hassell, 1992; Holyoak, 1993; Turchin, 1995; Lunde et al., 2002). It is thought by many to greatly influence the probability of population persistence (e.g. Den Boer, 1968; Hanski et al., 1996; Dennis et al., 1998). However, whether density-dependence in reproductive and mortality rates increases or decreases the probability of extinction depends on the shape of the density-dependent function. All populations modeled had at least one form of density dependence, in that population size could not exceed a ceiling size ($K$). Where density-dependent rates of mortality or fecundity for a specific species had been measured, the species-specific density-dependent function was used. For species where evidence of strong density-dependence was available, but no details of the form provided, a logistic model of density-dependence was used. There is no consensus about the prevalent form of density dependence in real populations, however, ceiling and logistic models of density-dependence differ little in their extinction rates when all else is equal (Foley, 1997).

Many of the parameters analyzed are outputs of the model (population growth rate, generation length) or are calculated from model outputs (CVN). Thus, no information from the literature was required for these parameters. Rather, they are the result of the demographic and life history data entered into the model.

2.4. Estimating minimum viable population size

To estimate MVP$_K$, a series of runs of each PVA model was performed using different values of $K$, until the estimates encompassed the threshold extinction probabilities of population survival for the required definition of MVP. Extinction risk at various $K$ values were plotted and MVP interpolated from the regression line. Subsequently, runs around this predicted value are done to refine the MVP estimate ($\pm0.5\%$). One thousand replicate simulations are used to provide adequate precision (Harris et al., 1987; Burgman et al., 1993).

2.5. Choice of species

The 102 vertebrates modeled for this study include two amphibians, 28 birds, one fish, 53 mammals, and 18 reptiles. Populations with strong negative growth rates were not included in this data set. Even populations in excess of 100,000 will not be viable if strong deterministic (anthropogenic) factors and habitat destruction are the forces driving the population to extinction. For these cases, the cause of decline must be identified and ameliorated before a useful estimate of MVP can be made (Caughley, 1994). No other filter was applied. The populations represent a wide range of habitats, ecologies, and geographic locations. The species modeled, their estimated MVP, and other pertinent information are listed in the Appendix.

2.6. Methodological assumptions

There are two fundamental assumptions associated with our approach. (1) No habitat loss (since we are
concerned with the minimum habitat area to be maintained over a given time frame. (2) Individual populations are discrete and isolated (not distributed in a source-sink or metapopulation configuration).

2.7. Factors influencing MVP

Backwards stepwise regression and factor analysis were performed to identify the key variables responsible for variation among species in MVP. We used two measures of population fitness and growth, two measures of population variability and two measures of study duration (Table 1). The relationships between coefficient of variation in population size (CVN) and both MVP and duration of study (in generations) were assessed using linear regressions with natural log transformed data.

In the test for a causal link between study duration and extinction risk, a paired t-test was used to determine whether a random sequential one-third sample of the data reduced MVP compared to that for the full data set within each of 10 species.

Analysis of variance was used to test whether MVP differs among major taxonomic groups (birds, mammals, and poikilotherms) and trophic levels (carnivores, omnivores, and herbivores). Linear regression was used to test whether there was an effect of latitude on MVP.

2.8. Adjusting for bias

There is a strong and highly significant relationship between the length of the study (in generations) used to parameterize the population viability model and the estimated minimum viable population size ($r^2 = 0.467$, $P < 0.0001$) (Fig. 1). This relationship is the result of an increase in the temporal variation in population size in models created from longer data sets. Because of this increasing variance with increasing study length, uncorrected estimates of minimum viable population size would obviously be underestimates (i.e. the longer data sets provide the better parameter estimates). Therefore, all 102 minimum viable population size estimates were corrected, using the following formula:

$$\ln \text{MVP}_C = \ln \text{MVP}_A + 0.75423 \times \ln(40/\text{SLG})$$

where MVP$_C$ is the minimum viable adult population size corrected to 40 generations worth of data for each species, MVP$_A$ is the minimum viable adult population size as estimated from the available data regardless of study length, and SLG is the study length in years divided by the species’ generation length in years. This is similar to using residuals from the linear regression, and provides estimates of MVP for all species under the assumption that 40 generations of data were available for each. This correction makes the variance in MVP$_C$ due to variance in study length equal to zero.

MVP values were transformed using natural logarithms to normalize data prior to statistical analyses. $F$ tests were carried out to determine whether major taxa, global latitude, or trophic level affected MVP.

### 3. Results

#### 3.1. Effect of study duration

We performed backwards stepwise multiple regression and factor analysis to examine underlying causes of variation among minimum viable population sizes. Both analyses produced very similar results. Thus, only the results of the multiple regression are shown (Table 1).

To our surprise, study duration had a major impact on minimum viable population size (Table 1, Fig. 1). Critically, shorter studies caused a systematic underestimation of extinction risk, rather than simply a less precise estimation, as often assumed. Further, the relationship was significant only when study duration was measured relative to the generation length of the organism.

A doubling of study duration increased minimum viable population size by approximately 67%, based on the regression equation. Study duration explained 47% of the variation in MVP among species. Further, study duration was the most important variable predicting differences in MVP when multiple regression was used to test two measures of population fitness and growth, two measures of population variability and two measures of study duration (Table 1). The only other variable explaining a significant proportion of the variance in MVP was the rate of population growth per generation ($\ln R_0$).

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### Table 1

| Test of predictors of minimum viable population size using stepwise multiple regression*
<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Variable</td>
<td>$F$</td>
<td>$P$-value</td>
</tr>
<tr>
<td>Study duration (generations)</td>
<td>20.58</td>
<td>$&lt;0.0001$</td>
</tr>
<tr>
<td>Population growth rate ($\ln R_0$)</td>
<td>9.68</td>
<td>0.0025</td>
</tr>
<tr>
<td>Standard deviation of $r$</td>
<td>1.09</td>
<td>0.2992</td>
</tr>
<tr>
<td>Study duration (years)</td>
<td>0.92</td>
<td>0.3410</td>
</tr>
<tr>
<td>Coefficient of variation of $r$</td>
<td>0.87</td>
<td>0.3536</td>
</tr>
<tr>
<td>Intrinsic rate of increase ($r$)</td>
<td>0.22</td>
<td>0.6378</td>
</tr>
<tr>
<td>Adjusted $R^2 = 0.630$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Study duration (generations) | 96.11 | $<0.0001$ |
| Population growth rate ($\ln R_0$) | 53.00  | $<0.0001$ |
| Adjusted $R^2 = 0.639$ |

* The top panel shows significance levels for individual variables, and the total variance explained when all six of the original variables are included in the model. The bottom panel shows the results of the multiple regression model when only the two significant variables are included.
As greater temporal variability in population size is positively correlated with extinction risk (Vucetich et al., 2000), we hypothesized that the relationship between study duration and predicted extinction risk was a result of an increase in CVN with length of time the population was studied. Thus, MVP (extinction risk) and length of the study used to parameterize the model should both be strongly related to variability in population size. These predictions were confirmed. CVN was strongly correlated with MVP, explaining 65% of the variation in MVP among species \((r^2 = 0.649, P < 0.0001)\). The relationship between study duration and CVN was also positive and highly significant \((r^2 = 0.340, P < 0.0001)\).

If study duration causes the differences in predicted extinction risk, then the effect should also be found within species. This was evaluated by comparing predicted extinction risk for ten species, based either on the use of the full data set, or a random sequential one-third subset. Minimum viable population size estimates were significantly greater for the total data set than for the data sub-set \((t = 3.58, \text{d.f.} = 9, P < 0.005)\).

3.2. Minimum viable population sizes

The distribution of MVPc is presented in Fig. 2. Means and medians for the three measures of MVP are presented in Table 2. The mean for MVPc is 7316 and the median is 5816. All MVP distributions are positively skewed. MVPc is the most relevant measure in conservation terms and the median and mean provide our estimate that a minimum habitat area capable of supporting approximately 7000 sexually mature adults is required to maintain long-term minimum viable populations of vertebrates in the wild.

Estimates of minimum viable population size are very scale dependent. Based on a subset \((n = 38)\) of the 102 species used in this study, approximately 5800 adult animals are needed for a 95% chance of persistence over 40 generations, 4700 for 90% persistence, and 550 for a 50% chance of persistence.

3.3. Variables affecting MVP

There were no significant differences in minimum viable population size, among the 102 species modeled, due to global latitude \((F = 0.006, P = 0.455)\), taxonomic grouping \((F = 0.053, P = 0.949)\), or trophic level \((F_{2.97} = 0.479, P = 0.621)\). The statistical power of these tests was sufficient to detect a 7% or greater difference among groups with at least a 87% probability (Zar, 1999).

Table 2

<table>
<thead>
<tr>
<th>Mean (with standard error) and median minimum viable population sizes for the 102 vertebrate species modeleda</th>
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</thead>
<tbody>
<tr>
<td>Mean</td>
</tr>
<tr>
<td>MVPc</td>
</tr>
<tr>
<td>MVPk</td>
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<tr>
<td>MVPNe</td>
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</table>

a MVPc is the carrying capacity (model ceiling), providing a 99% probability of persistence for 40 generations, stated as a number of adults. MVPk represents the carrying capacity in number of total individuals. MVPNe the minimum viable effective population size. The estimates are corrected for the length of study as explained in the methods section.
Allelse being equal, minimum viable population sizes should be larger for more variable populations. Indeed, in these 102 models, minimum viable population size is closely correlated with temporal variability in population size. There were also no significant differences in population variability among mammalian orders on a per generation scale ($F_{4.72} = 0.967$, $P = 0.431$) or between carnivores and herbivores ($F_{1.75} = 0.257$, $P = 0.614$) in our analysis of the data collected by Sinclair (1996).

Linear regression shows MVP to be significantly and negatively related to the population growth rate per generation ($ln R_0$) ($r^2 = 0.351$, $P < 0.001$) (Fig. 3). The regression formula predicts an MVP$_C$ of 13,455 when the growth rate is 0 ($R_0 = 1.0$), 2221 when the growth rate is 1 ($R_0 = 2.72$), and 6006 when the growth rate is the mean value ($R_0 = 1.565$) for the 102 vertebrate species modeled in this study.
the growth rate is 0 \( (R_0 = 1.0) \), 2221 when the growth rate is 1 \( (R_0 = 2.72) \), and 6006 when the growth rate is the mean value \( (R_0 = 1.565) \) for the 102 vertebrate species modeled in this study.

4. Discussion

The major findings of this investigation are: (1) Estimated MVPs were strongly influenced by the duration of the study, relative to the generation length of the organism, used to parameterize the model. Larger MVPs are predicted from longer studies because those models produce greater temporal variation in population size. (2) MVPs did not differ among major taxa, or with latitude or trophic level. (3) MVPs were significantly and substantially affected by the population growth rate, being larger with smaller growth rates. (4) The mean and median estimated MVP was 7316 and 5816, respectively. Each of these findings and their conservation implications are elaborated on later.

4.1. Factors influencing MVP estimates

The predicted MVP increased with increasing length of the study used to parameterize the model. This relationship was only statistically significant when study duration was measured relative to the generation length of the organism. Thus, shorter studies caused a systematic underestimation of extinction risk, rather than simply a less precise estimation, as often assumed (Boyce, 1992; Ludwig, 1999; Coulson et al., 2001). Besides underestimating the risk of extinction, the study-duration effect compromises the use of PVA in determining relative risk among different species and prioritizing management decisions unless explicitly accounted for.

Both study duration and MVP were significantly correlated with the temporal variability of population size, measured as the coefficient of variation in population size \( (CV_N) \). Increases in the length of the study used to parameterize the model, relative to the generation length of the organism, increases the amount of temporal variability in population size produced by the model, therefore increasing the MVP necessary to maintain a given level of extinction risk.

The explanation for why shorter studies consistently underestimate extinction risk is that fluctuations in population size through time are positively autocorrelated and the range of fluctuations increases over time (Halley, 1996; Morales, 1999). Thus, random samples from any continuous time period will underestimate the true variance. While it has been shown previously that variation in population size increases over time for census data (Pimm and Redfearn, 1988; Inchausti and Halley, 2001) and that under some conditions this can lead to underestimates of extinction risk (Ripa and Lundberg, 1996; Johst and Wissel, 1997; Morales, 1999), this is the first time that it has been demonstrated that extinction risk estimated from individually estimated demographic parameters increases with study duration. Further, we provide the first estimate of the magnitude of the effect. PVA models built from short-term studies will systematically underestimate extinction risk. Interestingly, Thomas et al. (2002) have found that a short-term (four generation) study of the metapopulation dynamics of a butterfly greatly underestimated the 30-generation colonization and extinction rates within the metapopulation. Thus, the underestimation of population variability with short-term data sets seems to exist at the demographic, population, and metapopulation levels.

How long do populations have to be studied to allow the possibility of accurate predictions of extinction risk? The relationship between \( CV_N \) and the study duration was determined using a wide variety of non-linear functions. Yet, the best fitting relationship between study duration and \( CV_N \) was linear. Thus, the variance in population size is still increasing across the range of study durations examined (up to 43 generations) in this study. Similarly, temporal variability in population size had not reached an asymptote for the majority of the 544 data sets studied by Inchausti and Halley (2001). Greater than 12 generations of data are required to produce minimum viable population sizes that are in broad agreement with theoretical and empirically based approximations (Soulé, 1987; Thomas, 1990; Reed and Bryant, 2000).

The median generation length of the 102 vertebrates modeled in this study was greater than 5 years. Thus, many decades or even centuries of research would be required to encompass most of the variation in demographic parameters. Since most ecological studies are of very short duration, typically two or three years (Tilman, 1989; Baskin, 1997), the underestimation of extinction risk will be ubiquitous.

It has been suggested that PVA models routinely overestimate extinction risk due to the inclusion of error variance (Beissinger and Westphal, 1998). Every attempt should be made to remove error variance from the estimates of demographic parameters, however, three circumstantial lines of evidence suggest that the study length is the stronger effect. (1) As mentioned earlier, the study length required to produce minimum viable population sizes in accordance with theoretical and empirical evidence is quite large. Yet, small studies with greater error variance do not produce MVPs in accordance with theory. (2) Population variability and population growth rate explain > 75% of the variation in MVP. (3) Brook et al. (2000) found that PVA predicted without bias quasi-extinction events in 20 well-studied species. This would not be expected if error
variance wildly exaggerated extinction risk. Two other recent studies have also shown broad agreement between the predictions of PVA models, created from long-term datasets, and the actual population dynamics of the population modeled (McCarthy and Broome, 2000; McCarthy and Lindenmayer, 2000).

How can the systematic underestimation of extinction risk be avoided? It is not feasible to delay decisions while adequate data are collected for each species. The alternative to PVA is to rely on human intuition, but this is notoriously inaccurate (Zeckhauser and Viscusi, 1990). One remedy is to use default values for stochastic parameters derived from data on well-studied species. Default values are used already, especially in VORTEX (Miller and Lacy, 1999), but their origin is unclear and they are not sourced to published analyses of long-term data sets.

In addition to study length, differences in MVPs based on population growth rate exist. As would be expected, populations with larger growth rates (ln $R_0$) required smaller numbers of adults to avoid extinction than did populations with lower growth rates. Because the differences in MVP are not due to broad-scale environmental differences or taxonomy, it is likely that the differential growth rates reflect habitat quality and the extent of anthropogenic interference. The actual population size required for long-term persistence may range from 2000 in pristine habitat to $>13,000$ in substantially degraded habitats. This implies that the amount of habitat required to maintain minimum viable population sizes, can be reduced through habitat restoration and by increasing population fitness through immigration into inbred populations (Westermeier et al., 1998).

### 4.2. Minimum viable population size

We estimate that in order to ensure long-term persistence of vertebrate populations, sufficient habitat must be conserved to allow for approximately 7000 breeding age adults. How do our estimates, using detailed PVAs on 102 species, compare with the small amount of empirical data available? Pimm et al. (1988) provide population sizes and median extinction times for multiple populations of 62 species of birds. We divided median extinction time by generation length and regressed this against population size. The regression suggests that approximately 125 breeding pairs would be required for a 50% probability of persistence over 40 generations. Similarly, Berger (1990) gathered data on extinction times for more than 102 populations of bighorn sheep. Linear regression of population size against time until extinction suggests that 775 animals are needed for a 50% probability of persistence for 40 generations. These two numbers are in rough agreement with our estimate of 550 adults for a 50% probability of persistence for 40 generations.

Extinction records from national parks in the western USA (Newmark, 1987; Soulé, 1987) shed some light on what is likely to constitute a minimum viable population size. Of 69 populations of lagomorphs (rabbits and hares), the 9 populations (13%) that went extinct had median population sizes of 3276. The parks were established about 75 years prior to the study and, therefore, would represent 40–50 generations for a lagomorph. Thus, 3000 animals do not appear to be sufficient to ward off extinction during these time frames.

Table 3 illustrates how our estimates, using PVA, compare with estimates of minimum viable population size derived using other methods, such as genetic theory or simple models of population variability. Probably the first attempt to arrive at a generalized minimum viable population size was by Franklin (1980). His estimate of an effective population size of 500 was based on an expected equilibrium between the loss of quantitative genetic variation due to drift and its replenishment by mutation. An effective population size of 500 is approximately 4500 adults (Frankham, 1995). Reed and Bryant (2000) monitored fitness and adaptability in laboratory populations of the housefly and estimated that $>2000$ individuals would likely be necessary for
long-term persistence in wild populations. Schultz and Lynch (1997) and Whitlock (2000) have used mathematical models, incorporating the decline in fitness due to the fixation of deleterious alleles and the restoration of fitness through beneficial mutations, to estimate minimum viable population sizes. Both studies suggest that an effective population size of greater than 200 \((N \sim 2000)\) is needed to maintain equilibrium fitness. Although this approach holds promise, the genetic parameters used in the model are known with very little precision. Thomas (1990), using data on the fluctuations in population size of small vertebrates and some invertebrates, concluded that a minimum viable population size of 5500 is needed to avoid an unacceptable risk of extinction.

4.3. Homogeneity of population dynamics

In the introduction, we presented two reasons that are often cited as failings of the general minimum viable population size concept. These were: (1) The perception that there is a great deal of taxonomic and environmental specificity involved in population dynamics. (2) A retreat from ‘single species’ conservation to ecosystem and landscape conservation. We will address both of these later.

The second objection can be dealt with briefly. The goal of basing conservation efforts at ecosystem and landscape scales is a laudable one. However, regardless of whether we manage conservation efforts on the basis of conserving ecosystems, landscapes, or ‘hotspots’ of biodiversity, those conservation units must contain viable populations of any species we seek to have remain extant. Conservation efforts directed at carefully selected, charismatic, land-intensive species probably provide the best and most pragmatic means to protect, not only that particular population but, the ecosystem and other species falling under its ‘umbrella’ (Foose et al., 1995).

The first objection is more contentious. It has long been believed that there is no single value for population size that may be applied to all populations to ensure persistence (Gilpin and Soulé, 1986; IUCN 1994). However, recent evidence calls this into question. In this study, no differences in MVP were found due to taxon, trophic level, or global latitude. Likewise, studies examining temporal variability of population sizes, which is expected to correlate strongly with extinction risk, have found little evidence for large-scale patterns. The variability in population size for 123 vertebrate species was remarkably similar regardless of taxonomy or trophic level (Inchausti and Halley, 2001). Temporal variation in the population size of herbivores is similar regardless of body mass, taxonomic group, or ecological habitat (Gaillard et al., 2000). An analysis of data, originally presented in Sinclair (1996), also fails to show differences in population variability, among mammals, due to taxonomic grouping or trophic level. The applicability of default values is strengthened by this growing body of evidence demonstrating homogeneity in population variability among environments and taxonomic groups.

Much of the perceived variation in previous estimates of minimum viable population size is due to differences in the temporal scale being measured (e.g. 50 years, 200 years, 10 generations), the extinction risk assumed (e.g. 1, 10, 50%), or what is actually being considered a population (e.g. number of adults, effective population size). When generation length is controlled for and the units of measure made the same, much of the variation in estimates of minimum viable population size disappear.

With the possible exception of Amazonia, the Russian Far East, and Canada, continuous blocks of land capable of supporting populations of 7000 large vertebrates, especially carnivores, is not available. Thus, the need to coordinate networks of smaller populations to ensure viable populations through the use of corridors, or managed immigration, should be a high priority.

Our estimate for MVP is designed to provide broad guidelines for species conservation planning. Population viability analysis is an inexact science, the variance among species estimates was large, and some of the variance around our estimated MVPs is unexplained. A number of upward and downward biases in estimating extinction risk exist (Brook, 2000). Many of our models unavoidably incorporated sampling error, so our MVP estimates may be too large. However, since we use a population ceiling, conservative estimates of inbreeding depression, and do not model Allee effects, we may underestimate MVP (Lacy, 1993, 2000; Lindenmayer et al., 1995). In short, we can provide no ‘magic number’ that will ensure persistence.

However, population viability analysis provides a holistic method for estimating MVPs and is the method that most capably brings all the factors considered important to population persistence under one umbrella. Thus, our goal in writing this paper is to stimulate a quantitative assessment of MVP approaches to conservation planning and to add to the body of literature that suggests that we should be thinking in terms of several thousands—not hundreds—of individuals in our goal to maintain viable populations of vertebrates.

Acknowledgements

This work was supported by an Australian Research Council grant. We thank A. Beattie, M. Boyce, T. Coulson, S. Ellner, M. Gillings, I. Hanksi, R. Lacy, L. Lim, D. Ludwig, M. McCarthy, H. Possingham, S. Pimm, M. Shaffer, and M. Soulé for helpful comments on this manuscript.
### Appendix

<table>
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<th>MVPc</th>
<th>ln R0</th>
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A complete set of references for the building of the models, or for any single species, can be obtained by e-mailing the corresponding author.
References


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A Model Analysis of Effects of Wolf Predation on Prevalence of Chronic Wasting Disease in Elk Populations of Rocky Mountain National Park

N. Thompson Hobbs
4/12/2006

Background
Increasing mortality rates in diseased populations can retard disease transmission and reduce disease prevalence (Barlow 1996, Lafferty and Holt 2003, Packer et al. 2003, Ostfeld and Holt 2004). Increasing mortality slows transmission via two mechanisms. First, it reduces the average lifetime of infected individuals. Reduced lifespan, in turn, can compress the time interval when animals are infectious, thereby reducing the number of infections produced per infected individual. The effect of reduced intervals of infectivity is amplified by reductions in population density that occur as mortality increases, reductions that cause declines in the number of contacts between infected and susceptible individuals. Both of these mechanisms retard the transmission of disease. If these mechanisms cause the number of new infections produced per infected individual to fall below one, then the disease will be eradicated from the population.

Any elevation in mortality rate has the potential to cause these effects, however, reductions in transmission rates and disease prevalence can be particularly large if mortality rates are elevated in the infected portion of the population to a greater extent than in the susceptible portion. This explains why diseases that cause rapid death fail to persist. However, other, non-disease agents of selective mortality can exert the same, beneficial effect. For example, if predators prey selectively on diseased individuals, it is reasonable to expect that they might reduce disease prevalence much more rapidly than would occur if mortality were non-selective.

Here, I use a simple mathematical model to evaluate the potential for selective predation by wolves to reduce or eradicate chronic wasting disease in populations of elk in Rocky Mountain National Park.

Model Structure
Miller et al. (2004) showed that CWD can be transmitted to susceptible animals from residues of excreta from infected animals and their carcasses. Using data from two epidemics of CWD in a captive population of mule deer, Miller et al. (submitted) found that models of indirect transmission of CWD from excreta had almost 7 times more support in data than more traditional models of direct, animal to animal transmission. The best approximating model in their studies used three linked differential equations representing the number of infected and susceptible animals and the mass of infectious material in the environment:
\[
\begin{align*}
\frac{dS}{dt} &= a(I + S) - S(\gamma E + m), \\
\frac{dI}{dt} &= \gamma SE - I(m + \mu), \\
\frac{dE}{dt} &= \varepsilon I - \tau E,
\end{align*}
\]

where

\[S = \text{number of susceptible animals},\]
\[I = \text{number of infected animals},\]
\[E = \text{the mass of infectious material in the environment},\]
\[a = \text{the per capita birth rate},\]
\[m = \text{the per capita death rate from causes other than CWD},\]
\[\gamma = \text{the indirect transmission coefficient},\]
\[\mu = \text{the per capita death rate from CWD},\]
\[\varepsilon = \text{the per capita rate of excretion of infectious material by infected animals},\]
\[\tau = \text{the mass specific rate of loss of infectious material from the environment}.
\]

This model is based on two assumptions, that the instantaneous per capita rate of infection was directly proportionate to the mass of infectious material in the environment, i.e., \( \frac{dI}{dtS} = \gamma E \), and that the rate of uptake of infectious material by elk has negligible effects on the pool size.

I modified this model to include density dependent effects on recruitment into the population and to include predation by wolves:

\[
\begin{align*}
\frac{dS}{dt} &= a(S + I) \left(1 - \frac{S + I}{K_a}\right) - S(\gamma E + m) - d_s, \\
\frac{dI}{dt} &= \gamma SE - I(m + \mu) - d_i, \\
\frac{dE}{dt} &= \varepsilon I - \tau E,
\end{align*}
\]

where \(K_a\) is the population density where recruitment = 0 and \(d_s\) is the number of susceptible elk killed by wolves per unit time and \(d_i\) is the number of infected elk killed by wolves. The total number of elk killed by wolves was calculated using a type III functional response (Coughenour 2002) assuming that wolves preyed exclusively on elk. Thus, the total kill rate \(d\) was calculated as

\[
d = \frac{WF_{max} (S + I)^2}{w_0^2 + (S + I)^2}
\]
where $W$ is the number of wolves, $F_{\text{max}}$ is the maximum annual kill rate, and $w_0$ is the density of elk at the maximum rate of increase in the kill rate, that is, the inflection point in the functional response.

The total kill rate ($d$) was partitioned into infected animals killed ($d_i$) and susceptible animals killed ($d_s$) as

$$d_i = p(1-c_i)d$$
$$d_s = (1-p)(1-c_s)d$$

(4)

where $c_i$ represents the extent to which wolf predation is compensatory with natural mortality and disease mortality in infected animals and $c_s$ represents the extent to which wolf predation is compensatory with natural mortality in susceptible animals. The values of the $cs$ range from 0 to 1. When they are equal to 0, then wolf mortality is completely additive. When they are equal to 1, then kills by wolves are completely compensatory and do not add to other sources of mortality.

The $p$ term in equation 4 represents the proportion of the total kill that is infected. It is calculated as

$$p = \frac{vI}{vI + S}$$

(5)

where $v$ is the relative vulnerability of infected animals relative to susceptible ones. Relative vulnerability is a multiplier giving the number of infected animals in the total kill per susceptible animal assuming equal abundance of infected and susceptible. Thus, a value of $v = 2$ means that if susceptible and infected animals were equally abundant, wolves would kill twice as many infected animals as susceptible ones. A value of $v = 1$ indicates no vulnerability of infected animals and increasing values of $v$ above 1 indicate increasing vulnerability.

The number of wolves ($W$) is treated as a constant in the model under the assumption that management action, both culling and introductions, would be used to maintain a constant pack size.

**Estimates of Model Parameters**

Parameters for population dynamics in the absence of disease ($a, m, K_a$) were estimated from a time series of data on elk abundance using maximum likelihood techniques (Fig. 1) (Table 1). Estimates of parameters governing disease transmission have not been estimated for elk. In the absence of these estimates we modified parameter values for deer obtained by Miller et al. (in preparation). It appears that CWD transmission in elk populations occurs substantially more slowly than in deer (Miller et al. 1998, Miller and Wild 2004). Thus, as a first approximation, we estimated transmission rates ($\gamma$) in elk as an order of magnitude less rapid than those for deer and excretion rates ($e$) as $1/2$ the value for deer. Model experiments were conducted to examine sensitivity of predictions to variation in these approximations. The turnover rate of infectious material in the environment was estimated from Miller et al. (submitted) and compensation terms for susceptible animals ($c_s$) as well as parameters of functional response ($F_{\text{max}}, w_0$) were obtained from Coughenour (2002). The values of vulnerabilities ($v$) and compensation...
for infected animals \((c_i)\) were not estimated, but instead were varied across a range of plausible values in model experiments.

Table 1. Estimates of model parameters.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Units</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>maximum per capita rate of recruitment</td>
<td>yr(^{-1})</td>
<td>0.188</td>
</tr>
<tr>
<td>m</td>
<td>per capita natural mortality rate</td>
<td>yr(^{-1})</td>
<td>0.041</td>
</tr>
<tr>
<td>(\mu)</td>
<td>per capita mortality rate from CWD</td>
<td>yr(^{-1})</td>
<td>0.57</td>
</tr>
<tr>
<td>(\gamma)</td>
<td>transmission rate</td>
<td>mass(^{-1}) yr(^{-1})</td>
<td>0.0789</td>
</tr>
<tr>
<td>(\varepsilon)</td>
<td>excretion rate</td>
<td>mass yr(^{-1})</td>
<td>0.055</td>
</tr>
<tr>
<td>(\tau)</td>
<td>turnover rate of infectious material</td>
<td>yr(^{-1})</td>
<td>2.55</td>
</tr>
<tr>
<td>Ka</td>
<td>population number where recruitment is 0</td>
<td>number</td>
<td>1287</td>
</tr>
<tr>
<td>S0</td>
<td>initial number of susceptibles</td>
<td>number</td>
<td>300</td>
</tr>
<tr>
<td>E0</td>
<td>initial mass of infected material</td>
<td>number</td>
<td>0</td>
</tr>
<tr>
<td>I0</td>
<td>initial number of infecteds</td>
<td>number</td>
<td>10</td>
</tr>
<tr>
<td>W</td>
<td>number of wolves</td>
<td>number</td>
<td>20</td>
</tr>
<tr>
<td>Fmax</td>
<td>maximum kill rate</td>
<td>yr(^{-1})</td>
<td>25</td>
</tr>
<tr>
<td>wo</td>
<td>inflection point of functional response</td>
<td>number</td>
<td>968</td>
</tr>
<tr>
<td>(c_i)</td>
<td>Compensation between predation and natural mortality</td>
<td>unitless</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Model Experiments

Dynamics of infected and susceptible pools were estimated using numerical methods (4\(^{th}\) order Runge-Kutta). I ran the model without disease, with disease and without wolves, and with disease and with wolves. To add wolves to the simulation, I allowed the model to run for 49 years with disease and without wolves. Fourteen wolves were introduced at year 50. The number of years required to eradicate the diseases was recorded for 7 levels of vulnerability \((v = 1, 1.5, 2.0, 2.5, 3, 3.5, 4)\) and four levels of compensation \((c_i = 0, .25, .50, .75)\). In addition, we varied excretion rate of infectious material and the transmission rate as .1, .3 and .5 \(\times\) values observed for deer while holding vulnerability constant at 2 and compensation constant at .5.

Results

In the absence of disease the model predicted that the elk population would reach an ecological carrying capacity of 1044 animals over about 35 years (Figure 1). Adding disease in year 1 produced oscillatory dynamics typical of epidemics (Figure 2 A, B). Adding wolves in year 50 caused relatively rapid decline in the prevalence of CWD, leading to eradication 19 years after introduction (Figure 3 A, B). The time required to eradicate the disease was sensitive to assumptions on vulnerability of infected animals and compensation between predation and mortality due to disease and natural causes (Figure 4). Increasing vulnerability of infected animals accelerated the rate of eradication but did not influence the number of susceptible elk at steady state, which was approximately 240 animals, regardless of vulnerability.
Figure 1. Model fit to data on elk population size in Rocky Mountain National Park assuming no influence of disease on population dynamics.

Figure 2. Model output for population sizes (A) and disease prevalence (B) assuming no wolves.

Figure 3. Model predictions of population sizes (A), prevalence (B), and number of animals killed by wolves following introduction of 14 wolves in year 50 (arrow). These simulations assume that CWD infected elk are twice as vulnerable to wolf predation than susceptible animals are. Simulations also assume that compensation between wolf predation and CWD mortality = .50 and between predation and natural mortality = .30.
Figure 4. Model experiment varying relative vulnerability (x-axis) of infected elk to predation by wolves and level of compensation between predation and mortality from CWD (series). Relative vulnerability is a multiplier giving the number of infected animals in the total kill per susceptible animal assuming equal abundance of infected and susceptible. Thus, a value of $v = 2$ means that if susceptible and infected animals were equally abundant, wolves were kill twice as many infected animals as susceptible ones. A value of $v = 1$ indicates no vulnerability of infected animals and increasing values of $v$ above 1 indicate increasing vulnerability. Compensation estimates the extent to which predation mortality fails to add to other sources. When compensation = 0, predation mortality is entirely additive.

Predictions of time to eradication were sensitive to assumptions on values for excretion rate and transmission rate (Figure 5), varying by more than 10 fold over a relatively narrow range of parameter values.

Time to eradication declined as the population size of wolves increased (Figure 6). For any given wolf population size, times to eradication increased with increases in the extent of compensation between predation and disease mortality. When compensation between disease mortality and predation mortality was high (i.e., .75), there was a threshold population size of wolves somewhere between 10 and 15 animals where eradication of CWD was infeasible (causing the truncation of the .75 compensation curve in Figure 6). When the wolf population size dropped below this threshold, predation simply pushed the prevalence of the disease to a new, lower steady state in the elk population. Near this threshold, time to eradication declined dramatically with increasing numbers of wolves. However, when the wolf population size exceeded 20, further increases in numbers of wolves had much less dramatic effects on time to eradication (Figure 6).
Figure 5. Sensitivity of predicted time to eradication to assumptions on rate of transmission of CWD (x-axis) and rate of excretion of infectious material (series). In theses simulations, I held constant parameter values for relative vulnerability of infected animals ($\nu = 2$) and compensation of predation mortality for disease mortality ($c_i = .5$). Areas of the graph that lack points indicate combinations of parameters for which eradication was infeasible during 150 year simulations.

Figure 6. Sensitivity of predicted time to eradication to assumptions on the number of wolves maintained in the population (x-axis) and the extent of compensation between predation and disease mortality (series). These simulations assumed that vulnerability of infected elk to wolf predation was twice as great as vulnerability of susceptible elk and that the transmission rate was
Discussion
Results from simulations suggest that predation by wolves has the potential to eliminate CWD from an infected elk population. Although the time required to achieve this result depends in a fundamental way on assumptions about prey vulnerability, the nature of compensation among different sources of mortality, as well as parameters regulating disease transmission, it appears that eradication within two or three decades would be feasible by maintaining a constant population of approximately 20 wolves.

This result must be tempered with the very important caveat that the elk population is closed to infection from outside sources. If infection is continually reintroduced, then eradication may not be feasible. However, model results suggest that even of open populations, wolf predation will substantially reduce prevalence. Moreover, the model does not represent a potentially large benefit of predation, the removal of carcasses as sources of infection. Although I did not have any way to estimate parameters for transmission from carcasses, such transmission is known to occur in mule deer.

Selective predation does not allow a larger population of susceptible animals relative to the non-selective case because wolves are assumed to consume more susceptible animals as infected ones become rare.

Model experiments reveal that uncertainties in estimates of values of parameters for transmission and excretion rates cause substantial uncertainty in estimates of time required to eradicate CWD from elk populations. Thus, the quantitative result from the simulations described here is not strong—we cannot specify with confidence how long it might take for predators to eliminate CWD from an elk population. Moreover, there are combinations of parameters for which eradication is infeasible. In particular, if transmission and excretion rates are high, it appears unlikely that predation by wolves will cause eradication within any reasonable period of time.

These results suggest that predation by wolves could have potent effects on disease prevalence under certain conditions. Although non-selective predation, as might occur with culling for example, may also be effective in eradicating the disease in a closed population, our results suggest that natural predation could substantially reduce the time required to eliminate the disease.
Literature Cited
EIGHTY-SEVENTH ANNUAL MEETING
AMERICAN SOCIETY OF MAMMALOGISTS

UNIVERSITY OF NEW MEXICO
ALBUQUERQUE, NEW MEXICO

Organizing Committee and Local Committee Chairs: Joe Cook (Organizing Committee Chair and MSB Accreditation), Jon Dunnum (Organizing Committee Chair, Social Events), Bill Gannon (Organizing Committee Chair, Program Committee, Daycare, Cookbook), Terry Yates (Organizing Committee Chair, Board Meeting, Media and Corporate Sponsorship), Jerry Dragoo (Registration, Website), Cathy Osborn (Event Coordination), Heather Paulsen (Event Accounting), Veronica Armijo (Group Photo), Natalie Dawson (Signage), Mike Friggens (Transportation and Parking), Dave Hafner (Kirkland Fun Run), Larisa Harding (Poster Presentations), Christine Hice (Vendors), Andrew Hope (Oral Session Audio-Visual Committee), Christy McCain (Auction), Bob Parmenter (Field Trips and Spouse Events), Cheryl Parmenter (Packets, Help Desk), Paul Polechla (Breakfast with a Scientist), Gabor Rac (Technical Review Committee for Presentations), Felisa Smith (ASM Committee Meetings); Local Committee: Tierney Adamson, Scott Altenbach, Mike Bogan, Jim Brown, Dolly Crawford, Don Duszynski, Andrew Edelman, Blair Wolf, Rick Winslow, David Schmidly, Ian Murray, Yadeeh Escobedo, Alan Pierce, Jim Findley, Jose Frances, Patti Geggick, Jason Malaney, Steve MacDonald, Anson Koehler, Elizabeth Racz, Aaron Roberts, Mike Richards, Angela England, Cindy Mathisen, Jason Thomas, Jim Stuart, Cindy Ramotnik, Ben Schaff, Elisha Song, Scarlett Swanson, Fernando Torres, Ernie Valdez, Christa Weise, Nancy Yates, Scott Knapp, Vani Aren, Bob Dickerman, Larry Layne, Jewels Bennett.

Members were notified by e-mail of on-line access to the Program before the meeting and abstracts for papers presented were provided on CD to members attending the meeting. Abridged minutes of the directors’ and members’ meetings follow.

ABRIDGED MINUTES OF MEETINGS OF THE
BOARD OF DIRECTORS

Meetings were held between 0859 and 1741 on 6 June 2007 and between 1238 and 1450 on 9 June 2007. The meetings were attended by 33 and 26 Officers and Directors and 18 and 12 invited guests, respectively. The minutes of the last meeting were read and approved. Reports were read, accepted, or otherwise acted upon from the President, the Recording Secretary, the Secretary-Treasurer, the Trustees, Publications, Ombudsman, Animal Care and Use, Historian/Archives, Checklist, Conservation, Conservation Awards, Coordination, Development, Education and Graduate Students, Grants-in-Aid, Grinnell Award, Honoraria, Honorary Membership, Human Diversity, Informatics, International Relations, Jackson Award, Latin American Fellowship, Legislation and Regulations, Mammal Images Library, Marine Mammals, Membership, Merriam Award, Nomenclature, Planning and Finance, Program, Public Education, Public Relations, Resolutions, and Systematic Collections standing committees; the ad hoc AIBS-ASM Graduate Student Public Policy Internship Committee, and from the ASM representatives to other organizations.

Actions of interest to the membership were: announcement by the Secretary-Treasurer that we have 3,205 members (including 2,307 Annual, 666 Life, 62 Patron, 158 Emeritus, and 12 Honorary Members) and that subscriptions to the Journal of Mammalogy totaled 846; recommendation of 405 new nominees for membership, and termination of 346 individuals; announcement that there were 16 members who reinstated membership, 21 resignations, 5 deaths, 8 persons completing Life Membership payments and two completing Patron Membership payments; notification that as of 31 December 2006 the operating account of the Society had a balance of $70,250.43, notification that the Future Mammalogists Fund increased by $6,029.50, the Latin American Student Field Mammalogy Fund took in $10,470.00, the ASM General Contribution Fund received $21,407.29; the Oliver Pearson Fund received $275.00 in donations, and the ASM Century Fund received $1000 in donations; acceptance with thanks for the report of the Secretary-Treasurer; and nomination of Ronald Van Den Bussche to another three-year term as Trustee; notice from the Trustees that the value of the Society’s net reserve principle was $3,417,301.00 as of 31 December 2006; notice from the Trustees that the value of the Society’s Pooled Income Fund was $65,474.00 as of 31 December 2006; election of Don Wilson to another three-year term as Trustee of the Pooled Income Fund; acceptance with thanks of the Trustees’ report; extension of enthusiastic thanks to outgoing Journal of Mammalogy Associate Editors Craig Frank and Douglas Kelt; the reconfirmation of Ed Heske, as Journal Editor; and appointment of Fritz Geiser and Christian Voigt as Associate Editors.

The following budget for general expenses in 2008 was adopted: $34,110 for committees; $2,000 honorarium for the Secretary-Treasurer and $1,500 for support of this office; $60,100 editorial honoraria, editorial expenses (including transfer of the Journal Editor’s office), and commissioned articles; $12,000 for A.M. & M. Services; $8,200 for on-line member services; $68,000 Grants-in-Aid; $6,900 for Student Honoraria; $7,500 for Latin American Field Mammalogy Award; $19,000
for ASM Graduate Fellowship; $7,000 for the Oliver P. Pearson Award; $850 for Conservation Awards; $300 for the Grinnell Award; $150 for the Jackson Award, and $60 for the Merriam Award; $250 AAZN dues; $125 AIBS dues and $6,500 contribution to support the AIBS public policy office; $100 NSCA dues; $550 IUCN dues; $500 SCAW dues and $1,500 to send a representative to the SCAW/OLAW meeting; $1,000 for sending a representative to the AAAS meeting; $1,000 indemnity/liability insurance, $3,000 for audit/tax preparation and $100 for bank fees; $3,000 President’s contingency fund, transfer of $152,745 from the Reserve Fund brought the estimated expenses and income both to $345,395.00.

**Abridged Minutes of the Annual Meeting of Members**

The first session was called to order at 1040 and was recessed at 1157 on 8 June 2007 and the second was called to order at 1030 and adjourned at 1213 on 9 June 2007.

Minutes of the preceding meeting were approved as published in abridged form in the *Journal of Mammalogy* and as approved by the Directors and Officers. Abridged minutes of the first Board meeting were read. Reports were presented in oral and/or written form from the President for the Executive Committee, the Secretary-Treasurer, the Recording Secretary, the Trustees, standing committees, ad hoc committees and ASM representatives to other organizations.

Actions of interest to members were: acceptance of 405 new members, reinstatement of 16 members, and dropping of 346 members delinquent in dues payment; election of Vice-President, Recording Secretary, and seven Directors, including one Student Director (new officers and directors listed on page iv of this issue); election by acclamation of Jerry Choate (Fort Hays State University) and Richard Thorington (National Museum of Natural History, Smithsonian Institution) to Honorary Membership; notification that the 2008 annual meetings are scheduled from 21–25 June at South Dakota State University, Brookings, South Dakota, and decision to hold the 2009 meetings at the University of Alaska, scheduled from 24–28 June 2009; announcement at the Banquet that Grants-in-Aid had been awarded to: Jacob Esselstyn (University of Kansas)—B. Elizabeth Horner Award; Louise Allen (Boston University), Erin Atkin (Humboldt State University), Ken Berger (University of Idaho), Kristin Bondo (University of Regina), Rachel Bricklin (Eastern Michigan University), Carson Brown (Angelo State University), Joseph Busch (Purdue University), Sarah Courbis (Portland State University), Brandi Coyner (Oklahoma State University), Andrew Flies (Michigan State University), Colin Garroway (Trent University), Meeghan Gray (University of Nevada, Reno), Laura Hajduk (Southern Illinois University), John Hanson (Texas Tech University), Christopher Himes (University of Washington), Frances Johnson (San Diego State University), Sarah Johnson (George Mason University), Nick Kerhoulas (Humboldt State University), Evan Kingsley (Harvard University), Brian Kot (University of California, Los Angeles), Sara Krause (University of California, Davis), Jennifer Lewis (Florida International University), Peggy Macqueen, (The University of Queensland), Nora Magyara (University of Lethbridge), Sean Maher (University of Kansas), Gregg Marcello (Miami University), Rosa Moscarella (Michigan State University), Mariana Muñoz-Romo (Boston University), Amanda Murray (Utah State University), Bret Pasch (University of Florida), Jose Santos (University of California, Berkeley), Brent Sewall (University of California, Davis), Elise Apple Snider (Florida State University), Daniel Thornton (University of Florida), Wenfei Tong (Harvard University), Jack Tseng (University of Southern California), Amy Turmelle (University of Tennessee), Paul Velazco (University of Illinois at Chicago & The Field Museum), Elizabeth Watson (University of Illinois), Corey Welch (University of Washington), Julie Woodruff (University of California, Berkeley), Dou-Shuan Yang (University of Washington), Adrian Young (University of California, San Diego). The recipient of the ASM Fellowship in Mammalogy, Justin Boyles (Indiana State University) and the nominee for the Albert R. and Alma Shadle Fellowship in Mammalogy, Paul Velazco (The University of Illinois at Chicago) were announced at the banquet.

The Anna M. Jackson Award went to Karen Mabry (University of California, Davis), the A. Brazier Howell Award went to Ana Paula Cutrera (Universidad Nacional de Mar Del Plata), and the Elmer C. Birney Award went to Jackie Metheny (University of North Carolina, Greensboro). The ASM Undergraduate Awards were presented to: Vagan Mushchyan (University of Central Oklahoma), Samuel Skalak (Christopher Newport University), and Ali Raza (City University of New York); presentation at the annual banquet of the Latin American Student Field Research Awards to Jesús Fernández (Louisiana State University), Noé de la Sancha (Texas Tech University), Ignacio Benitez Moreno (Pontificia Universidade Católica do Rio Grande do Sul), María Arbarca Medina (Instituto Venezolano de Investigacion Cientifica), and María Clara Arteaga (Universidad Nacional Autónoma de México); the Oliver P. Pearson Award to Eduardo Secchi (Fundacao Universidade Federal do Rio Grande in Brazil), the Joseph Grinnell Award for Excellence in Education in Mammalogy to Peter Weigl (Wake Forest University), the Hartley H. T. Jackson Award to Barbara Blake (Bennett College, Emeritus), the C. Hart Merriam Award to Robert Hoffmann (National Museum of Natural History, Smithsonian Institution), and the Aldo Leopold Award to Rodrigo A. Medellín (Universidad Nacional Autónoma de México). The William T. Hornaday Award was not presented this year.

The following resolutions were adopted:

**Economic Growth and Mammalian Species**

WHEREAS, humans are mammals, and, like all mammalian species, human populations and rates of resource consumption are limited by the availability of natural capital and energy flows; and,
WHEREAS, humans compete with other mammalian and non-mammalian species for energy and other resources (Pianka 1974); and,

WHEREAS, because of the tremendous growth of the human population and breadth of the human niche, which has expanded via new technology (Kingdon 2003), human resource use contributes substantially to global climate change (e.g., Ehrlich and Goulder 2006; IPCC 2007), and threatens the ecological balance of the Earth and the survival of other mammalian and non-mammalian species (Czech et al. 2000; The Wildlife Society 2003); and,

WHEREAS, economic growth is tightly linked to technological progress, and vice versa (Jones 1998; Daly and Farley 2003), and both require increased use of energy and material resources, subject to the first and second laws of thermodynamics (Jevons 1906; Georgescu-Roegen 1971; Denison 1974); and,

WHEREAS, economic growth reaches an optimal point beyond which social and economic welfare diminish (Daly 1997) and ecosystems, ecological processes, and biodiversity of Earth can no longer be sustained (Daly and Farley 2003); and,

WHEREAS, numerous indications exist that the global economy and the economies of many nations have grown beyond the optimal size (Daly 1997); and,

WHEREAS, imminent peaks in global oil production (Deffeyes 2001), unsustainable consumption of other non-renewable and renewable resources, and additional human impacts on water, fisheries, soils, and other natural resources indicate that many national economies, and possibly the global economy, are now beyond sustainable size (Hails 2006); and,

WHEREAS, the optimal size of an economy should be approximated and pursued via public policy with democratic participation, assuming citizens are well-informed about the tradeoffs between economic growth and other aspects of human welfare (Daly 1997), including but not limited to conservation of mammals and other taxa (Czech and Daly 2004); and,

WHEREAS, economic growth has been a primary goal of local, state, provincial, and national governments, often with little input from scientists and citizens (Fodor 1998; Collins 2000);

THEREFORE BE IT RESOLVED THAT the American Society of Mammalogists, meeting at its 87th Annual Meeting at the University of New Mexico, Albuquerque, New Mexico, 6–10 June 2007, recognizes that: 1) there is a fundamental conflict between economic growth and the conservation of ecosystems, mammalian populations, and species; 2) a steady-state economy is a viable, sustainable alternative to a growing economy and is an appropriate goal, especially for wealthier nations, including the United States, and for the conservation of mammals and other taxa; 3) increasing per capita consumption remains an appropriate goal in developing nations for the sake of attaining basic health and happiness; 4) the goals, policies, and activities of international banks and trade organizations should be adjusted to reconcile the establishment of steady-state economies in wealthier nations with the need for increasing per capita consumption in developing nations; 5) the long-term sustainability of steady-state economies requires their establishment in wealthier nations quickly enough to avoid the breaching of ecological capacity during supply shocks, such as droughts and energy shortages, and to avoid severe economic and social disruptions associated with exceeding ecological capacity; and 6) while establishing steady-state economies, wealthier nations, including the United States, should assist other nations in moving from the goal of economic growth to the global goal of steady-state economies.

LITERATURE CITED
WHEREAS, since its inception, the American Society of Mammalogists has opposed those predator-control programs that are not based on sound scientific research; and,

WHEREAS, the U.S. Endangered Species Act mandates formal recovery plans for all listed taxa using the best available science; and,

WHEREAS, the Mexican gray wolf (Canis lupus baileyi) has been listed as federally endangered since 1976 with a formal recovery plan initiated in 1982 that mandates its reintroduction to the wild (Parsons 1998); and,

WHEREAS, the Mexican gray wolf is one of the most imperiled mammals in North America because of the concerted predator-control program formerly conducted by the U.S. Fish and Wildlife Service and its predecessor agency, the Bureau of Biological Survey (Robinson 2005); and,

WHEREAS, the Mexican gray wolf is native to Mexico and the adjoining borderlands in the United States (Nelson and Goldman 1929; Young and Goldman 1944; Nowak 1995); and,

WHEREAS, the last Mexican gray wolves in the wild—5 individual animals—were captured between 1977 and 1980 for a captive-breeding program, leaving none left in the wild for almost 2 decades (Parsons 1996); and,

WHEREAS, the Mexican Wolf Recovery Plan adopted in 1982 (USFWS 1982) called for reintroduction to achieve 2 viable populations in the wild, as a first step toward eventual recovery, but did not specify demographic criteria that would constitute recovery; and,

WHEREAS, Mexican gray wolves were reintroduced to the wild beginning in 1998, and the environmental impact statement (USFWS 1996) projected growth of the population to 102 wolves, including 18 breeding pairs, by the end of the 9th year; and,

WHEREAS, at the end of the 9th year (2006) U.S. Fish and Wildlife Service reported only 59 wolves, including 7 breeding pairs, in the wild (Mexican Wolf Interagency Field Team 2007); and,

WHEREAS, grazing policies of the U.S. Forest Service result in continued conflicts between a federally subsidized livestock industry and a federally endangered taxon; and,

WHEREAS, the rationale for predator control of Mexican gray wolves differs from that of other endangered taxa, including wolves elsewhere, because it confines wolves to an arbitrary area and creates conflicts with livestock; and,

WHEREAS, U.S. Fish and Wildlife Service Standard Operating Procedure 13 mandates the killing or permanent removal of any wolf involved in 3 livestock depredations in 1 year even though 95% of the Blue Range Wolf Recovery Area is public land, most of which is grazed by livestock (USFWS 1996); and,

WHEREAS, to ensure success of Mexican gray wolf reintroduction and achievement of population goals, the 2001 independent scientific panel (Paquet et al. 2001) recommended a rule change allowing wolves to roam freely and requiring removal of livestock carcasses so as not to attract wolves; and,

WHEREAS, the U.S. Fish and Wildlife Service did not implement the primary recommendations of the Paquet Report and instead has announced a rule-change process that likely will continue to limit movements of Mexican gray wolves and exacerbate conflicts with livestock owners using public lands (Mexican Wolf Blue Range Adaptive Management Oversight Committee and Interagency Field Team 2005); and,

WHEREAS, the impending rule-change process is premised on limiting the number of wolves at 125 animals, and preventing wolves from becoming established in new areas where wolves may be allowed to roam (Mexican Wolf Blue Range Adaptive Management Oversight Committee and Interagency Field Team 2005; and Povilitis et al. 2006);

THEREFORE BE IT RESOLVED that the American Society of Mammalogists, meeting at the 87th Annual Meeting at the University of New Mexico, Albuquerque, New Mexico, 6–10 June 2007, calls upon the U.S. Forest Service to revise its land management policies to allow recovery of this federally endangered taxon, and for the U.S. Fish and Wildlife Service to: 1) expedite a revision of the 25-year-old Mexican Wolf Recovery Plan, prior to finalizing a rule change, to develop a recovery goal and identify new recovery areas; 2) suspend all predator control directed at Mexican gray wolves at least until the interim 100-wolf goal of the current reintroduction program December 2007
has been achieved; 3) protect wolves from the consequences of scavenging on livestock carcasses; 4) ensure the recovery and sustainability of populations of Mexican gray wolves; and 5) allow wolves to roam freely throughout the Southwest.

LITERATURE CITED


CONSERVATION OF JAGUARS IN NORTH AMERICA

WHEREAS, The American Society of Mammalogists is concerned with the future of mammals worldwide in increasingly threatened habitats, and strongly supports mammalian conservation and responsible use based on sound scientific research; and,

WHEREAS, in historical times, jaguars (Panthera onca) have been documented throughout the southern tier of the United States, from the west to the east coasts, and as far north as Monterey Bay, the Grand Canyon, and the southern Great Plains; and,

WHEREAS, jaguars have been recorded in a wide variety of ecosystems and habitats in the United States, including coniferous forests up to about 3,000 m in elevation, grasslands, and deserts; and,

WHEREAS, the range of the jaguar in the United States was reduced to Arizona and New Mexico by the mid-20th century resulting from loss of habitat and human activities (Leopold 1959; Hall 1981; Brown and Lopez 2001); and,

WHEREAS, continuing persecution, including federal predator control, resulted in the extirpation of jaguars from the southwestern United States, with the last female jaguar in the United States killed on the Mogollon Rim in Arizona in 1963 (Brown and Lopez 2001); and,

WHEREAS, jaguars continue to decline throughout significant portions of their remaining range in the Republic of Mexico, Central America, and South America (Nowell and Jackson 1996); and,

WHEREAS, habitats for jaguars in the United States, including Arizona and New Mexico, are vital to the long-term resilience and survival of the species (Channell et al. 2000), especially in response to ongoing climate change; and,

WHEREAS, ecosystems in the United States in which jaguars formerly occurred are not intact without the sustained presence of jaguars (Ray et al. 2005); and,

WHEREAS, jaguars continue to recolonize parts of southern Arizona and New Mexico by dispersing from northern Mexico (Arizona Game and Fish Department and New Mexico Department of Game and Fish 2007a), and this dispersal across the international border is essential for viability of the species in the United States; and,

WHEREAS, the jaguar was listed as an endangered species under the Endangered Species Conservation Act of 1969, but inadvertently was not afforded protection in the United States under the Endangered Species Act of 1973 until 1997; and,

WHEREAS, recovery plans authorized under the Endangered Species Act of 1973 provide a framework for vital conservation actions unique to each endangered taxon; and,

WHEREAS, effectiveness of critical habitat designation under the Endangered Species Act of 1973 results in progress toward recovery of listed taxa (Taylor et al. 2005); and,
WHEREAS, despite the requirements of the Endangered Species Act and an urgent conservation imperative, the U.S. Fish and Wildlife Service has not developed a jaguar recovery plan or designated jaguar critical habitat; and,

WHEREAS, the Jaguar Conservation Team, an interagency group, has identified and mapped large areas of New Mexico and Arizona that might be suitable for jaguar recovery (Robinson et al. 2006; Van Pelt 2006); and,

WHEREAS, the Jaguar Conservation Team has not specified recovery criteria or management actions for jaguars, and formally opposes potential mechanisms for recovery that are specified in the Endangered Species Act of 1973 (Arizona Game and Fish Department and New Mexico Department of Game and Fish 2007b),

THEREFORE BE IT RESOLVED that the American Society of Mammalogists, meeting at its 87th Annual Meeting at the University of New Mexico, Albuquerque, New Mexico, 6–10 June 2007, calls upon the U.S. Fish and Wildlife Service to develop a recovery plan, designate critical habitat for jaguars, and address issues related to dispersal of jaguars across the international border.

LITERATURE CITED


ARIZONA GAME AND FISH DEPARTMENT AND NEW MEXICO DEPARTMENT OF GAME AND FISH. 2007b. Memorandum of Understanding between the Arizona Game and Fish Department and the New Mexico Department of Game and Fish for jaguar conservation. AGFD, Phoenix, Arizona.


HOST RESOLUTION AMERICAN SOCIETY OF MAMMALOGISTS ANNUAL MEETING

WHEREAS, the 87th annual meeting of the American Society of Mammalogists was held at the University of New Mexico, Albuquerque, New Mexico, 6–10 June 2007; and,

WHEREAS, Mammalogists reminisced about the meeting 20 years ago and were reminded that the University’s official color was adobe; and,

WHEREAS, the University of the New Mexico experiment testing the Findley hypothesis “that if you want a job done right, hire a mammalogist,” is in place with David Schmidly as President and Terry Yates as Vice-President for Research and Economic Development, but will their experimental algorithm detect inbreeding depression; and,

WHEREAS, Terry Yates had to abandon his limo-based Margarita pouring service for picking up mammalogists at the airport to adapt to his new administrative position; and,

WHEREAS, Terry Yates gave us a lesson on Economics 101: How to make fortunes investing other people’s money, advancing a new hypothesis that the best way to protect old people’s retirement funds (including those of your parent’s) is to donate them to the ASM’s Pooled Fund, attend the annual ASM meetings, enjoy the free beer, and be assured that ASM Trustees will be wise investors; and,

WHEREAS, rumor has it that President David Schmidly has recently purchased a home in Brookings, South Dakota and is looking for property in Fairbanks, Alaska; and,

WHEREAS, the phone number given by Bill Gannon for all emergencies was Dial-A-Prayer; and,

WHEREAS, shuttles could not be provided on Monday, June 11th—maybe that’s why mammalogists were provided with personalized shipping labels; and,

WHEREAS, Betty Horner would have enjoyed being carded for a glass of wine; and,

WHEREAS, we wonder if all of the hot air generated at the ASM Board meeting on Wednesday was the genesis of continental wind storms that delayed and cancelled flights as far away as Denver; and,

WHEREAS, Interstate 25 served as a test of a border wall to prevent free dispersal of mammals between Embassy Suites
and campus (it worked for Mexican gray wolves and jaguars, but failed to prevent the movement of mammalogists); and,

WHEREAS, the 2 mile trip to the starting line for the “Run for Research” was longer than the actual event; and,

WHEREAS, Karen Mabry taught us that there is no place like home when Peromyscus choose a new dispersal site; and,

WHEREAS, Jackie Methany taught us that big brown bats are not picky about the genetics of those they sleep with; and,

WHEREAS, Ana Cutrera taught us that MHC selection in Ctenomys is an underground activity; and,

WHEREAS, Ryan W. Norris revisited the geological age of the last ancestor of Rattus and Mus, and concluded that fossils and molecular data are significantly linked; and,

WHEREAS, Sergio Solari taught us that even a short-tailed opossum merits respect and the cover of Nature; and,

WHEREAS, we were relieved to find out that the term “Dome on the Range” referred to the construction of the Sternberg Museum and not to the characteristics of the cranial pelage of the Grinnell Award winner; and,

WHEREAS, David McDonald provided new definitions of “to badger” which include grooming for parasites, long range dispersals for males and females, group sex, litters with multiple paternities and bum-kissing; and,

WHEREAS, the tight corridor for the poster sessions and group photo promoted the first opportunity for mammalogists to try out the European badger greeting by bum-kissing; and,

WHEREAS, mammalogists were treated to a scatological lesson in bathroom stalls in the dormitories with the newly published Bristol Stool Chart designed for field studies; and,

WHEREAS the Human Diversity Committee had a difficult time getting mammalogists to complete their questionnaires, they resorted to a mark-recapture protocol using multi-colored wristbands in an experimental setting which would attract a maximum number of mammalogists (a bar with free beer and wine), Men-in-Black bouncers ensured a truly closed population, and many attendees were found to be trap-happy; and,

WHEREAS, President Bob Timm demonstrated his taxonomic skills by synonymizing the positions of Recording Secretary and Treasurer without following the law of priority; and,

WHEREAS, former journal editor Barbara Blake indicated that she was going to remain silent so as to not be included in this year’s host resolution; and,

WHEREAS, Barbara Blake, in withdrawal from all her editorial duties over the last 15 years, created errors in typing a list of nominees at the members meeting thereby requiring the use of one of our 4 new Associate Editor positions as an Associate Editor for Nominations; and,

WHEREAS, the Latin word for bag is “scrotum” and this year’s host has provided attendees with the most capacious meeting bags ever provided to meeting attendees of ASM meetings; this year’s meetings shall be recognized as the year of “scrotum maximum”; and,

WHEREAS, David Schmidly, who is well-known for using a chainsaw to separate the head from the body of a pygmy sperm whale, declared that despite the spacious capacity of this year’s registration bag, it was insufficient to carry all of his field gear; and,

WHEREAS, the Ombudsperson Dick Thorington proved that you can be squirrelly and still be recognized with the highest award from this society; and,

WHEREAS, Jerry Choate was awarded Honorary Membership, although his Grinnell address was a big fish story; and,

WHEREAS, the Local Committee made sure that we enjoyed wonderful weather, plenty of food and drink, and stimulating scientific talks and discussions; and,

WHEREAS, the bands Nosotros, Syd Masters and the Swing Riders, and Mariachi Tenampa provided outstanding musical entertainment at our social events; and,

WHEREAS, Jerry Dragoo and his partner Gwen provided a new activity, dancing with the stars; and,

WHEREAS, the Local Committee provided an impressive insight into local culture in each meeting event;

THEREFORE BE IT RESOLVED that the American Society of Mammalogists, meeting at its 87th Annual Meeting at the University of New Mexico, Albuquerque, New Mexico, 6–10 June 2007, provides our heartfelt thanks to Terry Yates, Joe Cook, David Schmidly, Jerry Dragoo, Jon Dunnum, Bill Gannon, Felisa Smith, Kathy Osborn, Heather Paulson and the rest of the Local Committee for all of their hard work and dedication in hosting a tremendously successful and rewarding scientific meeting.
Minimum viable population size: A meta-analysis of 30 years of published estimates

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\section{ABSTRACT}

We present the first meta-analysis of a key measure in conservation biology: minimum viable population (MVP) size. Our analysis is based on studies published since the early 1970s, and covers 141 sources and 212 species (after filtering 529 sources and 2202 species). By implementing a unique standardization procedure to make reported MVPs comparable, we were able to derive a cross-species frequency distribution of MVP with a median of 4169 individuals (95\% CI = 3577–5129). This standardized database provides a reference set of MVPs from which conservation practitioners can generalize the range expected for particular species (or surrogate taxa) of concern when demographic information is lacking. We provide a synthesis of MVP-related research over the past 30 years, and test for ‘rules of thumb’ relating MVP to extinction vulnerability using well-known threat correlates such as body mass and range decline. We find little support for any plausible ecological and life history predictors of MVP, even though correlates explain >50\% of the variation in IUCN threat status. We conclude that a species’ or population’s MVP is context-specific, and there are no simple short-cuts to its derivation. However, our findings are consistent with biological theory and MVPs derived from abundance time series in that the MVP for most species will exceed a few thousand individuals.

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\section{1. Introduction}

Conservation practitioners are challenged to make informed choices about the allocation of finite resources to mitigate the current extinction crisis (Ceballos and Ehrlich, 2002; Thomas et al., 2004), while being cognizant of the complex ecological (Shaffer, 1985) and socio-political (Woodroffe et al., 2005) systems in which such decisions are embedded. Accelerating habitat and species losses have mandated consideration of this problem in terms of the number of individuals required for persistence within a specified timeframe (Shaffer, 1981; Shaffer, 1987) because small and range-restricted populations are highly vulnerable to extinction (Terborgh and Winter, 1980; Gilpin and Soulé, 1986; Schoener and Spiller, 1987). The concept of a ‘minimum viable population’ (MVP; Shaffer, 1981; Lacava and Hughes, 1984) has been used extensively in species recovery and conservation management programs (Clark et al., 2002), and is relevant to the IUCN’s Red List (www.iucnredlist.org) criteria concerning small and range-restricted populations. However, the biological and utilitarian value of MVP to species conservation has remained controversial (Shaffer, 1987; Caughley, 1994; Reed et al., 1998).
Past reviews of the concept (Samson, 1983; Glipin and Soulé, 1986; Ewens, 1990) and its application (Sjögren-Gulve and Ebenhard, 2000; Bulte, 2001; Stinchcombe et al., 2002) have been theoretical, qualitative or cursory, with the primary literature tending to focus on inherent problems of estimation (Reed et al., 1998; Brook et al., 2000) rather than utility per se. Despite both debate on the real-world applicability of the concept (Caughley, 1994; Reed et al., 1998) and its sustained popularity (Bulte, 2001; Reed et al., 2003; Tear et al., 2005; Brook et al., 2006), there has been no broad-scale quantitative assessment of the MVP literature. This is perhaps due in part to the difficulty of standardization (e.g., definition of risk and timeframe, alternative model structures) across studies.

Individual case studies of MVP for any given species cannot reveal: (a) the form and variance of the cross-species distribution of MVP, and whether these agree with theoretical predictions, or match with genetic, demographic or environmental rules of thumb for MVP; (b) the existence (or absence) of taxonomic or life history patterns in MVP; and (c) generalizations useful for conservation management. Here we provide the first quantitative meta-analysis of published MVP estimates, to determine the ensemble properties of MVP and whether useful generalizations emerge.

2. Methods

2.1. Dataset

We conducted an exhaustive meta-analysis of the MVP-relevant literature. All MVP data were obtained from published articles, book chapters and scientific reports. Primary literature was identified through ISI’s Web of Science (www.isinet.com) and Elsevier’s Science Direct (www.sciencedirect.com) databases. The online search engines Google (www.scholar.google.com) and Yahoo (www.yahoo.com) were used to identify, and where possible source, scientific reports and other grey literature. Search terms such as “minimum & viable” and “extinction” were used, among others. Monographs and book chapters were sourced through university library databases. A cross-check of the reference list of each article permitted further collation, especially for sources published prior to 1992. Each article was reviewed for MVP estimates, and where population viability analysis (PVA) methods were used, populations were considered ‘viable’ only where >80% of the initial population survived for ≥20 years (Shaffer, 1981). If the initial population was considered unviable but a target MVP estimate provided, the latter was used. Where MVP was not specified explicitly, we required at least the risk of extinction for a defined timeframe and initial population size to be reported. Data from baseline PVA models were selected and hypothetical scenarios ignored. MVP estimates derived through genetic analyses or population censuses were also included. A database was collated and structured according to taxonomic group. Attributes such as species IUCN Red listing (IUCN, 2006) were later assigned, and the completed database is available online as Supplementary Material (Table S1).

2.2. Controlling for differences in the modelling technique used to derive MVP

Data were collated for 287 MVP estimates, initially by collecting all parameters that some or all of the models used to derive MVP. These were (1) probability of persistence, (2) duration of persistence in years, (3) duration of persistence in generations, (4) model type or method used to derive MVP estimate, (5) sex ratio at birth, (6) adult sex ratio, (7) form of density dependence, (8) carrying capacity, (9) Allee effect (present/absent), (10) inbreeding depression considered, (11) probability of catastrophe, (12) birth to adult survival, (13) adult survival, (14) per cent of female population breeding, (15) fecundity, (16) age at parturition, (17) longevity, (18) density and (19) dispersal ability. In many cases, data for the above parameters were omitted or not given by the authors.

Using logic and previous hypotheses based on extinction theory (Akcakaya, 1998; Brook et al., 2006), we reduced the initial 19 model attributes to six predictors which we hypothesized would be relatively independent and explain much of the methodological variation in MVP among studies: (1) Model used [MOD]: a categorical index of method or model used to derive MVP. This was restricted to: (a) individual-based simulation, (b) matrix/cohort-based simulation (including time series methods), (c) empirical census or (d) genetic analysis; (2) Persistence probability [PER]: a continuous variable of the probability of population persistence over a given time period. If not used, and where the population was stated as viable, the probability was assumed to be 100%; (3) Duration [DUR]: a continuous variable being the period of time over which a population was deemed viable, expressed as a continuous variable in generations (3–1200). When generation length of the species was not provided, we assumed it to be equal to the age at primiparity. Where a MVP was estimated from a census or genetic analysis, or where the time frame of viability was not stated explicitly (n = 13), viability was assumed to be 100 years and the number of generations estimated on this basis; (4) Density dependence [DEN]: a categorical factor classified as: (a) density-independent, (b) ceiling-type density dependence or (c) functional-type density dependence. The differentiation between categories (b) and (c) was necessary to account for their opposite effect on MVP – ceiling density dependence increases extinction risk, whereas non-Allee functional density dependence (negative feedback) decreases extinction risk, relative to density-independent models (Ginzburg et al., 1990); (5) Inbreeding depression [INB]: a categorical factor indicating whether the loss of genetic variation in the population was modelled or not. This was most commonly, although not universally, applied as 3.14 diploid lethal equivalents on juvenile survival; and (6) Catastrophes [CAT]: a categorical factor indicating whether random catastrophe outside the normal distribution of environmental stochasticity was included or not.

2.3. Ecological extinction predictors

Following previous work (Brook et al., 2006), we reduced a set of postulated ecological, life history and anthropological extinction correlates to a set of eight composite predictors. Where these correlates were not given in the sourced litera-
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ture, data were derived from online databases or published papers on that species (see Appendix S1, Supplementary Material). Predictors used were: (1) Body weight [BWT]: an allometric scaling covariate (mass in g). Body mass data for the mostly herbaceous plants were estimated using a benchmark wet-weight for a similar-sized species, and forestry timber data used to estimate mass for large Monocotyledons; (2) Generation length [GNL]: taken as age at sexual maturity and estimated in months; (3) Fecundity [FEC]: a continuous variable representing the mean number of young produced per female per year. This included the average number of eggs laid/young born, but did not account for the probability of survival to adulthood (such as in birds and herptiles). Multiple broods within a year were taken into consideration to calculate a total yearly output of offspring; (4) Social grouping [SOC]: a categorical index of mating systems. These were (a) colonial (i.e., large breeding colonies and spawning sites), (b) polygamous or gregarious, (c) monogamous and (d) solitary (i.e., a brief period of copulation only or asexual/hermaphroditic breeding, and plants); (5) Dispersal [DSP]: the migratory or dispersive capability of a species, where dispersal and migration are used interchangeably, and categorized broadly as (a) migratory or (b) constrained. A species was considered constrained if it remained within a 20-km radius of its place of birth/hatching; (6) Range [RAN]: the geographic distribution scored as either (a) geographic range spanning more than one major biome (Smith and Smith, 2003), or (b) the species was primarily restricted to a single biome; (7) Human impact [HMP]: a categorical index of the (a) beneficial or (b) generally adverse influence of people. Species considered to benefit from humans were domesticated animals, harvested crops and commensals, for example; and (8) Population trend [TRE]: a categorical index of (a) stable or increasing population or (b) a population in general decline. TRE was assumed to account for deterministic population decline.

2.4. Statistical analyses

For all analyses we reduced the population dataset from 287 populations to 212 unique species to avoid potential problems of pseudo-replication caused by multiple representations (different populations) of the same species. Two a priori model sets (Burnham and Anderson, 2002) were constructed to examine the amount of variation explained in MVP (Table 1): (a) six models encompassing a selection of the model characteristics used to derive MVP, and (b) eleven models encompassing a selection of ecological, life history and anthropogenic threat terms.

To gauge the relative importance of each derived variable for predicted MVP, we fitted a series of generalized linear mixed-effects models (GLMM) to log(MVP) in the R Language (R Development Core Team, 2004), using the lmer function (in the lme4 library). MVP was assumed on a priori grounds to be log-normally distributed (Brook et al., 2006). The random effects error structure of GLMM was used to correct for non-independence of species due to potential shared evolutionary life history traits (Felsenstein, 1985) by decomposing the variance across species by hierarchical Linnaean taxonomy (Class) (following Blackburn and Duncan, 2001). Class was selected as the taxonomic random term in preference to Order because of sample size limitations: many Orders were represented by a single species only. The importance of considering taxonomy in the GLMM was assessed also by repeating the analyses using a series of generalized linear models (GLM) with the same ecological and life history correlates. Asymptotic indices of information loss were used to assign relative strengths of evidence to the different competing models (Burnham and Anderson, 2002), with both Akaike’s Information Criterion corrected for small sample sizes (AICc) and Bayesian Information Criterion (BIC) weights used as an objective means of model comparison (Burnham and Anderson, 2002). AICc identifies tapering effects where n, per term, exceed approximately 20 data, whereas BIC only identifies main effects (Link and Barker, 2006). Full model results are shown in Table 1.

Because MVP estimates taken from the literature vary due to the particular methods employed in each case, it was necessary to standardize estimates (MVP,a) to a consistent model structure. To do this we used the best-ranked GLMM based on BIC (Table 1) for the model characteristics set (the model including persistence probability, duration of persistence, inbreeding depression and catastrophes, and a phylogenetic correction, setting persistence probability (PER) to 99%, the number of generations (GNL) over which MVP was estimated to 40, and set the β coefficients for the factors to have inbreeding depression (INB) and catastrophes (CAT) included. The standardizing equation was therefore:

\[
\log_{10}(\text{MVP}_{\text{std}}) = \log_{10}(\text{MVP}_{\text{org}}) + \beta_{\text{PER}} \cdot \log_{10}\left(\frac{0.99}{\text{PER}}\right) + \beta_{\text{GNL}} \cdot \log_{10}\left(\frac{40}{\text{GNL}}\right) + \beta_{\text{INB}} + \beta_{\text{CAT}}
\]

where \(\beta_{\text{PER}} = 22.5618\), \(\beta_{\text{GNL}} = 0.4365\), \(\beta_{\text{INB}} = 1.2306\), \(\beta_{\text{CAT}} = 0.4258\). The distributions of the original versus standardized MVP estimates are shown in Fig. 1. For each species, the

Fig. 1 – Comparison of original versus standardized minimum viable population sizes. Relative frequencies of the 212 MVP species estimates (log scale) for the original, uncorrected values, taken directly from the literature (solid line, Supplementary Notes) and the same values after standardization for differing structure of the MVP-generating method/model (dotted line).
respective coefficients were set to zero when its original MVP-generating model matched the defined standardization criterion. Although the per cent deviance explained in MVP by the highest BIC-ranked model was only ~6%, standardization was still required to avoid potentially spurious relationships in the analysis of MVP and ecological correlates.

We tested the ecological predictors by fitting GLMM to log-

\( \log_{10} \text{MVP} \) with Class set as a random effect for phylogenetic control, and then fitted GLM without random effects to examine the importance of including phylogenetic control in the models. To provide an independent check of the biological authenticity of the derived ecological predictors with respect to a measure of extinction proneness, we constructed analogous models using the IUCN Red Listing (IUCN, 2006) of species (17 models). Of the 212 species represented in the meta-analysis, 92 were Red-Listed (anything other than ‘Least Concern’).

3. Results

We sourced 529 relevant articles published between January 1974 and December 2005, describing up to 2202 species and a minimum of 1444. The exact count of distinct species could not be determined because one large study (Fagan et al., 2001) did not report which species were examined. Excluding a recent study on MVP which fitted a set of simple phenomenological models to 1198 abundance time series (Brook et al., 2006), 141 articles met the selection criteria and listed 287 MVP estimates for 212 species. A gradual increase in MVP-related publications over the past 30 years was matched by a concomitant rise in the number of species studied (Fig. 2). The establishment of public-access online databases (e.g., IUCN Red list and Global Population Dynamics Database [GPDD], www.cpntsl.bio.ic.ac.uk/gpdd/) and subsequent multi-species analyses (Fagan et al., 2001; Reed et al., 2003; Brook et al., 2006) in recent years were responsible for large increases in the number of species evaluated (Fig. 2).

A bias toward large-bodied species in extinction-related research was evident. Ultimately, we found that the frequency distribution of species studied was skewed towards heavier species, with 53.8% of all species and 85.3% of mammals exceeding 1000 g (Fig. 3). By contrast, only 31% of 4049 extant mammals listed in a large database of body masses (Smith et al., 2003) are >1000 g. Moreover, vertebrates accounted for 47% of all species studied, despite this taxon representing only a few percent of named species (IUCN, 2006), and of the 92 species in the meta-analysis that were IUCN Red-Listed, 62.0% were mammals. Surprisingly, the Red Listing of species included in all MVP-related studies showed an over-representation of non-threatened species (Fig. S1, Supplementary Material), likely due to larger studies (Brook et al., 2006) being based on abundance time series collected for purposes not directly related to conservation, such as monitoring and harvesting.

The reported MVP values were not comparable in a quantitative meta-analysis because of differences in the specified risk definitions and structure of the generating models. We therefore collated relevant model type and structure data for each species and fitted a set of GLMM and used AICc, and BIC to select the most parsimonious model(s) for standardizing MVP (see Section 2). The most parsimonious model relating MVP to ‘generating-model structure’ was, according to AICc, the one that included all model characteristics; however only 7.5% of the deviance was explained by the saturated model after controlling for phylogeny (Table 1). An analysis on a reduced dataset, using Class/Order as a nested random effect, yielded an equivalent result. It has been shown that with sufficient sample sizes, the Kullback-Leibler prior used to justify AICc weighting favours more complex models (Link and

![Fig. 2 – Publication trends for minimum viable population size (MVP), 1974–2005. The cumulative number of species in studies related to population viability and extinction (log₁₀ scale, solid line), and a 5-year moving-average of the number MVP-related peer-reviewed and unpublished literature sources (dotted line). A large increase in species studied since 2001 marked the advent of freely-accessible online population databases.](image)

![Fig. 3 – Relative frequency distribution of body weight (log₁₀ scale in g). All species (open bars) and mammals (solid bars) with estimates of minimum viable population size are shown, with the relative distribution of body weights for all extant mammals for which data are available (Smith et al., 2003) (dotted line) for comparison.](image)
Barker, 2006), so we also considered model ranking according to the dimension-consistent BIC weights to identify the main drivers of structural variation in MVP (i.e., ignoring tapering effects). The latter metric signalled that only four of the six correlates considered (probability of persistence, duration, inbreeding and catastrophe – see Section 2) explained an important component (6.3%) of the deviance in MVP (Table 1). Thus, using the best BIC-supported model's coefficients, we standardized MVPs (MVP$_{std}$) to a 99% persistence probability, and time frame of 40 generations (a previously used time frame – Brook et al., 2006).

Median MVP$_{std}$ was 4169 individuals (3577–5129, 95% CI), compared to the median reported uncorrected MVP of 3299 individuals. This is similar to the recommended effective population size of 4500 individuals based on genetic data (Frankham, 1995), and the median MVP of 5816 reported for vertebrates (Reed et al., 2003). The frequency distribution of the standardized published MVP estimates (Fig. 4) was more symmetrical and peaked at a higher MVP than the model-averaged distribution of MVPs derived from an independent time series analysis (Brook et al., 2006). This result contradicts the view that estimates of population viability derived from scalar models may be overly precautionary (Dunham et al., 2006), probably because Brook et al. (2006) considered functional density dependence, whereas Dunham et al. (2006) only used a population ceiling function.

4. Discussion

Deciding how much habitat is needed to achieve conservation goals requires robust rules of thumb because in many situations there are insufficient data to develop a species-specific population viability analysis (Shaffer et al., 2002). So, can we provide any generalities from this meta-analysis of MVP? Models relating ecological attributes predicted a priori to

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<th>Table 2 – Summary of median (and bootstrapped 95% confidence bounds) minimum viable population sizes from all available literature (n = number of species; standardized = MVP$<em>{std}$; original = MVP$</em>{orig}$)</th>
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a Reptiles and amphibians.
b Mosses, ferns, dicotyledons, monocotyledons and gymnosperms.
c Molluscs and crustaceans.
correlate with extinction risk failed to explain much of the variation in MVP; the saturated correlates model accounted for 20.6% of the explained deviance after taking phylogeny into account as a random effect (Table 1). The most parsimonious GLMM, according to BIC, failed to find evidence for any main effects. Yet these predictors explained 54% of the deviance in whether or not a species was IUCN Red-Listed. This contrast between the predictability of MVP versus IUCN status has been described in previous work (Brook et al., 2006), using MVP estimated from an independent source (time series data), and effectively highlights two different paradigms (Caughley, 1994). Ecological predictors of threatened status indicate a species’ sensitivity to the largely systematic drivers of extinction (Cardillo, 2003), confirmed here by the support for IUCN listing. MVP represents, on the other hand, the small population paradigm (Caughley, 1994); that is, a population already reduced in size and subject to a host of population-specific threats (many stochastic) which cannot be accounted for in broad species comparisons such as ours.

MVP is thus an appropriate measure of the viability of populations that have declined deterministically (or catastrophically) to a small size, but subsequently ‘stabilized’ (though they continue to fluctuate stochastically). As such, context-specific factors such as variability of the local environment are more relevant for determining MVP than the broad-scale extinction drivers that cause endangerment. MVP size and regional or global extinction risk are thus unrelated (Brook et al., 2006). Note that the majority of vertebrates considered threatened by IUCN are listed under Criterion A, which relates threat to rate and magnitude of population size or range decline (IUCN, 2006). The assessment of vulnerability of IUCN is complementary, but essentially unrelated, to that derived from MVP.

Despite the lack of predictability of MVP based on plausible (and measurable) correlates of extinction risk, we can draw some broad generalizations from the meta-analysis. MVP-related studies have gradually increased over the past three decades, with no apparent decline in the concept’s use, and with a trend toward multi-species analyses (Fig. 2). Depending on the strength of density dependence, MVP follows either a weakly right-skewed or symmetrical distribution (Fig. 4), with the highest probability density in the range of a few thousand, rather than hundreds, or tens of thousands of individuals, comparable to the findings of Brook et al. (2006) and Reed et al. (2003). While there was some broad taxonomic variation, the true magnitude of any differences is uncertain because some taxa have been poorly sampled to date (fish and invertebrates – Table 2).

A major product of this collation and standardization of published MVPs, especially when coupled with a previous phenomenological analysis (Brook et al., 2006), is a database of MVPs and species attributes that span a broad range of biomes, body sizes, life histories and threat status. This resource (Table S1, provided as a searchable spreadsheet table in the Supplementary Material) can be used by conservation practitioners as a preliminary guide to the MVP range expected for particular species or surrogate taxa of concern, or indeed to derive a target MVP for data-deficient species (we recommend the upper 95% confidence limit of MVP for the taxon in question, excluding poorly sampled taxa such as insects, fish and marine invertebrates). Moreover, these results provide important baseline data for testing future research hypotheses regarding population size and extinction risk, particularly with the now-evident shift toward the Bayesian paradigm within ecology and the concomitant need for robust informative prior information (Clark and Gelfand, 2006). We also support a disciplinary shift away from charismatic species (as highlighted by the lack of data available for fishes, insects and marine invertebrates) and focus of expertise and resources on IUCN-listed species and hotspots of latent extinction risk (Cardillo et al., 2006).

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2007.06.011.

References


Indirect Effects and Traditional Trophic Cascades: A Test Involving Wolves, Coyotes, and Pronghorn

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Abstract. The traditional trophic cascades model is based on consumer–resource interactions at each link in a food chain. However, trophic-level interactions, such as mesocarnivore release resulting from intraguild predation, may also be important mediators of cascades. From September 2001 to August 2004, we used spatial and seasonal heterogeneity in wolf distribution and abundance in the southern Greater Yellowstone Ecosystem to evaluate whether mesopredator release of coyotes (Canis latrans), resulting from the extirpation of wolves (Canis lupus), accounts for high rates of coyote predation on pronghorn (Antilocapra americana) fawns observed in some areas. Results of this ecological perturbation in wolf densities, coyote densities, and pronghorn neonatal survival at wolf-free and wolf-abundant sites support the existence of a species-level trophic cascade. That wolves precipitated a trophic cascade was evidenced by fawn survival rates that were four-fold higher at sites used by wolves. A negative correlation between coyote and wolf densities supports the hypothesis that interspecific interactions between the two species facilitated the difference in fawn survival. Whereas densities of resident coyotes were similar between wolf-free and wolf-abundant sites, the abundance of transient coyotes was significantly lower in areas used by wolves. Thus, differential effects of wolves on solitary coyotes may be an important mechanism by which wolves limit coyote densities. Our results support the hypothesis that mesopredator release of coyotes contributes to high rates of coyote predation on pronghorn fawns, and demonstrate the importance of alternative food web pathways in structuring the dynamics of terrestrial systems.

Key words: Antilocapra americana; Canis latrans; Canis lupus; carnivore competition; mesopredator release hypothesis; predator–prey; Program MARK.

INTRODUCTION

Large carnivores can shape the structure and function of ecological communities (Ray et al. 2005), yet few ecosystems still harbor apex predators (Schaller 1996). Most species are declining globally due to habitat loss, fragmentation, disease, and human persecution (Weber and Rabinowitz 1996, Woodroffe and Ginsberg 1998, Woodroffe 2001), the latter often as a result of conflicts over livestock (Johnson et al. 2001, Ogada et al. 2003, Berger 2006). In addition to threatening the survival of these species, the loss of large carnivores carries broader implications for the maintenance of biodiversity as a result of indirect effects at lower trophic levels (Crooks and Soulé 1999, Henke and Bryant 1999). For instance, in the absence of grizzly bears (Ursus arctos) and wolves (Canis lupus) in the southern Greater Yellowstone Ecosystem (GYE), moose (Alces alces) numbers expanded, resulting in a reduction in both willow communities and the attendant diversity of neotropical songbirds (Berger et al. 2001). Similarly, the extirpation of vertebrate predators led to a 10- to 100-fold increase in herbivore densities and a concomitant decrease in the number of seedlings and saplings of canopy trees on islands in Venezuela (Terborgh et al. 2001).

Trophic cascades have been defined as predation-related effects that result in inverse patterns of abundance or biomass across multiple trophic levels in a food web (Micheli et al. 2001). Although the classic cascade is based on a three-tiered system consisting of predators, herbivores, and plants (Hairston et al. 1960), cascades can involve more than three trophic levels and apply to any multilink linear food web interaction (Polis et al. 2000). In systems with top-down control, the pattern of biomass that emerges depends on the number of trophic levels (Fig. 1). In even-numbered food chains with four or more trophic levels, herbivores can expand and overgraze plant communities because mesocarnivores are held in check by apex carnivores (Fig. 1; Oksanen et al. 1981, Fretwell 1987). The loss of primary
carnivores from a four-tiered food chain shifts the trophic structure to a three-tiered system in which populations of secondary carnivores can increase (Fig. 1). This process, termed mesopredator release (Soule et al. 1988), affects the persistence of both ground- and scrub-nesting birds through increased nest predation by striped skunks (Mephitis mephitis), raccoons (Procyon lotor), and grey foxes (Urocyon cinereoargenteus; Rogers and Caro 1998, Crooks and Soule 1999).

Efforts to experimentally test predictions of the mesopredator release hypothesis using large carnivores have been hampered by an absence of appropriate baselines against which to measure changes, a lack of spatial and temporal controls, and logistical and ethical difficulties associated with large-scale manipulations of terrestrial communities (Polis et al. 2000, Steneck 2005). As a consequence, natural experiments involving the recolonization or recolonization of large carnivores to systems where they have been absent offer important opportunities to evaluate the effects of apex predators (Gittleman and Gompper 2001).

The recolonization of wolves to Grand Teton National Park (GTNP), Wyoming, USA, is a case in point. Wolves were extirpated from northwestern Wyoming by the 1930s and were absent for nearly 70 years until their reintroduction to Yellowstone National Park (YNP) in 1995 (Smith et al. 2003). During late 1997, dispersing wolves from YNP recolonized GTNP (U.S. Fish and Wildlife Service, unpublished data). In the absence of wolves, coyotes (Canis latrans) were the dominant canid predator throughout the GYE. However, wolves and coyotes play different trophic roles in the system, as evidenced by size differences in their prey. Whereas wolves regularly take adult moose, elk (Cervus elaphus), and bison (Bison bison), coyotes prey disproportionately on small mammals and neonatal ungulates (Paquet 1992, Arjo et al. 2002).

To date, research on trophic cascades involving large carnivores has focused on cascades precipitated by direct predator–prey interactions (McLaren and Peterson 1994, Estes et al. 1998, Berger et al. 2001, Ripple et al. 2001, Terborgh et al. 2001, Fortin et al. 2005). Here we investigated potential direct and indirect effects of recolonizing wolves on pronghorn (Antilocapra americana) neonatal survival, as mediated by changes in the distribution and abundance of a mesocarnivore, coyotes, a major predator of neonate pronghorn (Fig. 1). Wolves exert top-down effects on coyotes through both interference competition (Peterson 1995a, Berger and Gese 2007), and intraguild predation (Polis and Holt 1992, an extreme form of interference competition in which the intraguild prey is consumed (M. Hebblewhite, personal communications). In the absence of wolves, coyote populations may therefore expand and threaten the persistence of pronghorn populations by limiting fawn recruitment. Following the mesopredator release hypothesis, we tested three primary predictions: (1) survival of pronghorn fawns is positively associated with wolf density, (2) survival of pronghorn fawns is negatively associated with coyote density, and (3) an inverse relationship characterizes coyote and wolf densities.

**METHODS**

*Study area and field sites*

The study took place in Grand Teton National Park (GTNP), Wyoming, USA, and on the adjacent Bridger

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**Fig. 1.** Hypothesized relationships among trophic levels and changing trophic structure in Grand Teton National Park, Wyoming, USA. The weights of the arrows indicate the relative strengths of the effects. Relative abundance of organisms at each trophic level is indicated by the size of the circles. Mesocarnivore release in coyotes is thought to have occurred between the 1930s and 1999 as a consequence of the extirpation of wolves in northwestern Wyoming.
Teton National Forest (BTNF), from September 2001 to August 2004 (Fig. 2). The Park is bordered to the southeast by the National Elk Refuge (NER), a 100-km$^2$ area established in 1912 to provide secure winter habitat for elk (Smith et al. 2004). Elevation ranges from 1900 m to >4000 m. Within this broad array of protected lands, we selected three sites to exploit spatial and temporal variation in wolf distribution and abundance. The Elk Ranch site (ER) was used extensively by wolves when denning and pup rearing occurred (May–September) and periodically throughout the winter (November–April), whereas the Gros Ventre site (GV) was used by wolves only during winter (Fig. 2). In contrast, the Antelope Flats (AF) site was not used by wolves during either season. All sites are characterized by shrub-steppe habitat dominated by big sagebrush (*Artemesia tridentata*), low sagebrush (*A. arbuscula*), Antelope bitterbrush (*Purshia tridentata*), and associated understory grasses of the genera *Stipa*, *Bromus*, and *Poa*. The Antelope Flats and Elk Ranch sites are periodically used for livestock grazing; consequently, some native vegetation at both sites has been replaced with smooth brome (*Bromus inermis* Leyss).

**Handling and monitoring of coyotes**

We monitored the movements of coyotes captured at the Elk Ranch and Antelope Flats sites. No coyotes were captured at the Gros Ventre site because restrictions on access during winter precluded recovery of coyote carcasses during the period when mortality due to wolf predation was most likely to occur (Peterson 1995a). We captured coyotes with padded foothold traps or with a net-gun fired from a helicopter (Gese et al. 1987). Coyotes were equipped with VHF collars with eight-hour mortality sensors (Advanced Telemetry Systems, Isanti, Minnesota, USA). Point and sequential locations obtained by ground and aerial telemetry were used to monitor survival and develop coyote home ranges (Gese et al. 1990). For ground locations, ≥3 compass bearings with intersecting angles between 20°
and 160° were used (White and Garrott 1990). Locations were estimated using the program Locate II (Pacer, Truro, Novia Scotia, Canada), and home ranges by the fixed-kernel density method (Worton 1989) with the “adehabitat” package (Calenge 2006) in program R (R Development Core Team 2006). To estimate home ranges, we used an ad hoc smoothing parameter \( h_{adj} \) designed to prevent over- or under-smoothing. This method involves choosing the smallest increment of the reference bandwidth \( h_{ref} \) that results in a contiguous 95% kernel home range polygon that contains no lacuna (i.e., \( h_{adj} = 0.9 \times h_{ref}, 0.8 \times h_{ref}, \text{etc.}; J. G. Kie, unpublished data) \).

### Estimation of coyote densities

We classified all coyotes as either residents or transients. Resident coyotes actively defended well-defined territories, whereas transients were not associated with a particular pack or territory. Densities of resident coyotes were assessed using a combination of spring (pre-whelping) pack sizes of known (i.e., radio-collared) individuals and indices of coyote abundance based on scat deposition surveys. Scat transects were located along ~7.5 km of unimproved road at each site. Transects were initially cleared of all scats and then walked once/week for three weeks each spring and fall (Gese 2001). For known individuals, we determined pack sizes based on aerial and ground-based observations of animals displaying affiliative behaviors such as traveling, hunting, and resting together, or territorial maintenance (Camenzind 1978). For 2003 and 2004, we calculated resident coyote densities at the Elk Ranch and Antelope Flats sites by dividing the number of adult (>1 year) coyotes in each pack by the size of the pack’s home range using the 95% probability contour. Estimates for all packs at a site were then averaged to determine a site-specific mean and variance. We estimated transient coyote densities at the Elk Ranch and Antelope Flats sites based on the ratio of radio-collared transients to total radio-collared coyotes in 2003. We used 2003 as the baseline because we conducted extensive helicopter captures of coyotes that year and had the largest number of collars (n = 26) deployed. Densities of resident and transient coyotes were combined to produce estimates of total coyote density for both sites. Because we had radio collars on coyotes in too few packs to estimate numbers directly for 2002, we estimated coyote densities at the Elk Ranch and Antelope Flats sites based on the following relationship between coyote densities at both sites in 2003 and 2004 and assessments of relative abundance determined by scat deposition surveys (regression through the origin, \( r^2 = 0.912, P = 0.011 \)):

\[
\text{Coyote density} = 1.644 \times \text{scat deposition index.} \quad (1)
\]

For 2003 and 2004, coyote densities at the Gros Ventre site were estimated using Eq. 1. No estimate of coyote density was available for the Gros Ventre site in 2002 because we did not conduct scat deposition surveys there until the spring of 2003.

### Estimation of wolf densities

Capture and collaring of wolves was handled by the U.S. Fish and Wildlife Service. Radio-tracking of wolves followed the same procedures as for coyotes. Seasonal wolf densities were based on known pack sizes for the summer (May–September) and winter (November–April) periods (U.S. Fish and Wildlife Service, unpublished data). These periods corresponded to seasonal shifts in centers of activity between the wolf pack’s den site in GTNP and the state-run elk feed grounds in the BTNF. Summer density estimates were based on the number of adults in the pack, whereas winter estimates were based on the number of adults and pups. Pups were included in the latter estimates because their presence would increase competition at kills and, thus, might make wolves less tolerant of coyotes at carcasses. To calculate seasonal wolf densities, we divided the number of wolves in the pack each season by the size of the pack’s seasonal home range. Seasonal home ranges for wolves were estimated using the same procedures as for coyotes.

### Capture and monitoring of neonate pronghorn

We monitored the survival of pronghorn fawns captured at the Antelope Flats site during June 2002–2004, and at the Gros Ventre and Elk Ranch sites during June 2003–2004. All fawns were equipped with expandable, breakaway VHF radio-collars with four-hour mortality sensors (mass ~60 g; Advanced Telemetry Systems, Isanti, Minnesota, USA), weighed using a canvas sling hung from a spring scale, and aged based on observation of birth or the degree of desiccation of the umbilicus (Byers and Moodie 1990). Fawns were monitored daily for the first 60 days of life, and then weekly until the fall migration.

### Statistical analysis

We evaluated the relationships between coyote density and pronghorn fawn survival, wolf density and fawn survival, and coyote density and wolf density using correlation analysis. We used correlation analysis rather than simple linear regression or multivariate regression because for each bivariate comparison, values of the independent variable were subject to measurement error; thus, we did not meet the assumptions of regression analysis (Gotelli and Ellison 2004). Furthermore, the hypothesized relationship between wolf density and fawn survival was indirect and mediated by changes in coyote density; thus, we expected that the relationship between wolf density and fawn survival would be confounded by the coyote variable in a multivariate analysis (Cohen et al. 2003). Although correlation analysis uses a slightly different line-fitting algorithm that minimizes both the vertical and horizontal (i.e., \( x \) and \( y \)) distance of each point from the regression line,
the correlation coefficient is identical to that produced by linear regression (Gotelli and Ellison 2004).

We estimated survival of pronghorn fawns for the first 60 days of life using a known fate model in Program MARK (White and Burnham 1999). The analysis was based on individual encounter histories, with a single encounter for each cohort that indicated whether the fawn survived or died during the 60-day period. We evaluated 37 models to assess the effects of individual covariates (gender and birthweight) and group covariates (coyote density, summer wolf density, and winter wolf density) on fawn survival. For fawns that were not newborns at capture, we calculated mass at birth based on the following relationship (modified from Byers 1997) as follows:

\[
\text{birthweight} = \text{weight at capture} - 0.2446(\text{age in days})
\]

The global model considered was \( \hat{S} + g + m + c + sw + ww \), where \( \hat{S} \) was estimated survival probability, \( g \) was gender, \( m \) was birthweight, \( c \) was coyote density, \( sw \) was summer wolf density, and \( ww \) was winter wolf density. We also tested models that included dummy variables for site (s), wolf-free site (wf), and year (y) to examine possible differences in fawn survival among sites and years that were not captured by the group covariates. We used Akaike’s Information Criterion adjusted for small sample sizes (AICc) and Akaike weights to rank models (Burnham and Anderson 2002). Using the top-ranked (i.e., minimum AICc) model from the initial analyses, we fit one additional model to assess whether an irruption in white-tailed jackrabbits (\( Lepus townsendii \)) at the Gros Ventre site might account for an observed increase in fawn survival in 2004.

**RESULTS**

**Coyote captures**

We radio-collared 38 coyotes at the Elk Ranch and Antelope Flats sites. The percentage of coyotes classified as residents and transients was 51% (\( n = 18 \)) and 49% (\( n = 17 \)), respectively. In three cases, the animal died too soon after capture for its status to be determined. In addition to the three coyotes of unknown status, seven coyotes were censored from all analyses because they dispersed to areas outside our field sites.

**Coyote and wolf densities**

Total coyote densities were highest at the Antelope Flats site in 2003 (0.479 ± 0.065 coyotes/km\(^2\)) and lowest at the Elk Ranch site in 2004 (0.215 ± 0.002 coyotes/km\(^2\); Fig. 3). Densities of resident coyotes at the Antelope Flats site (\( \bar{X} = 0.251 \pm 0.025 \)) were similar to those at the Elk Ranch site (\( \bar{X} = 0.232 \pm 0.029 \), Student’s \( t \) test, \( P = 0.687 \)), whereas transient densities were significantly lower at Elk Ranch (\( \bar{X} = 0.188 \pm 0.019 \) vs. \( \bar{X} = 0.039 \pm 0.005 \), Student’s \( t \) test, \( P < 0.001 \); Fig. 4). With respect to wolves, densities were highest at the Elk Ranch site during the winter of 2003 (0.061 wolves/km\(^2\)), and lowest at the Elk Ranch site during the summer of 2003 (0.015 wolves/km\(^2\); Fig. 5). Wolves made only rare visits to the Antelope Flats site; thus, wolf density at this site was effectively zero for all years.

**Pronghorn neonatal survival**

We included 108 marked individuals (19 in 2002, 44 in 2003, and 45 in 2004) in the analysis of fawn survival, distributed by site as follows: ER = 27, GV = 30, and AF = 51. On the basis of minimum AICc, the best model of fawn survival contained parameters for gender, birthweight, and coyote density (Table 1). However, the top-ranked model had just 13.7% of the Akaike weights (Table 1), indicating there was considerable uncertainty as to which of the highly ranked candidate models was
actually the best predictor of fawn survival (Burnham and Anderson 2002). Coyote density appeared in all nine of the top-ranked models, with a cumulative Akaike weight of 62.4% (Table 1). Thus, the overall importance of this single variable likely contributed to model-selection uncertainty, as a model that included only coyote density was nearly as good ($D_{AIC}^c = 1.311$) at predicting fawn survival as one that also included both gender and birthweight (Table 1). Models that included variables for coyote and wolf densities outperformed comparable models that suggested that fawn survival differed among the sites independent of coyote and wolf densities (Table 1).

Model-averaged survival estimates (Burnham and Anderson 2002) during the first 60 days of life ranged from a low of $\hat{S} = 0.049$ at the Antelope Flats site in 2003, to a high of $\hat{S} = 0.440$ at the Elk Ranch site in 2004 (Table 2). Based on the parameter estimates from the top-ranked model, fawn survival was negatively correlated with coyote density ($\beta = -12.313 \pm 3.875$, Wald test, $P = 0.002$) and positively correlated with birthweight ($\beta = 0.413 \pm 0.263$, Wald test, $P = 0.116$). Survival of male fawns was lower than for females ($\beta = -0.496 \pm 0.266$, Wald test, $P = 0.062$). Based on the results of correlation analysis, fawn survival was negatively correlated with coyote density ($r = -0.882$, $P = 0.009$; Fig. 6a) and positively correlated with winter wolf density ($r = 0.791$, $P = 0.034$; Fig. 6b), and the relationship between coyote and winter wolf densities was negative ($r = -0.740$, $P = 0.036$; Fig. 6c). Summer

![Fig. 5. Seasonal wolf densities at two sites in northwestern Wyoming, 2002–2004. The Antelope Flats site is not shown because wolves did not use the site.](image)

### Table 1. Model selection results for survival ($S$) of pronghorn fawns during the first 60 days of life at three study sites in northwestern Wyoming, USA, 2002–2004.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>Akaike weight</th>
<th>Model likelihood</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_{g+m+c}$</td>
<td>4</td>
<td>107.003</td>
<td>0.000</td>
<td>0.137</td>
<td>1.000</td>
<td>98.611</td>
</tr>
<tr>
<td>$S_{g+c}$</td>
<td>3</td>
<td>107.357</td>
<td>0.353</td>
<td>0.115</td>
<td>0.838</td>
<td>101.124</td>
</tr>
<tr>
<td>$S_g$</td>
<td>2</td>
<td>108.314</td>
<td>1.311</td>
<td>0.071</td>
<td>0.519</td>
<td>104.198</td>
</tr>
<tr>
<td>$S_{g+m}$</td>
<td>3</td>
<td>108.566</td>
<td>1.563</td>
<td>0.063</td>
<td>0.458</td>
<td>102.333</td>
</tr>
<tr>
<td>$S_{g+m+c+j}$</td>
<td>5</td>
<td>108.804</td>
<td>1.800</td>
<td>0.056</td>
<td>0.407</td>
<td>98.209</td>
</tr>
<tr>
<td>$S_{g+m+c+sw}$</td>
<td>5</td>
<td>109.014</td>
<td>2.011</td>
<td>0.050</td>
<td>0.366</td>
<td>98.420</td>
</tr>
<tr>
<td>$S_{g+m+c+ww}$</td>
<td>5</td>
<td>109.122</td>
<td>2.119</td>
<td>0.048</td>
<td>0.347</td>
<td>98.528</td>
</tr>
<tr>
<td>$S_{g+c+sw}$</td>
<td>4</td>
<td>109.282</td>
<td>2.278</td>
<td>0.044</td>
<td>0.320</td>
<td>100.889</td>
</tr>
<tr>
<td>$S_{g+c+ww}$</td>
<td>4</td>
<td>109.431</td>
<td>2.428</td>
<td>0.041</td>
<td>0.297</td>
<td>101.039</td>
</tr>
<tr>
<td>$S_{g+c+sw}$</td>
<td>5</td>
<td>109.729</td>
<td>2.725</td>
<td>0.035</td>
<td>0.256</td>
<td>101.336</td>
</tr>
<tr>
<td>$S_{g+c+ww}$</td>
<td>5</td>
<td>109.772</td>
<td>2.769</td>
<td>0.034</td>
<td>0.250</td>
<td>103.539</td>
</tr>
<tr>
<td>$S_{g+m}$</td>
<td>3</td>
<td>109.829</td>
<td>2.826</td>
<td>0.033</td>
<td>0.243</td>
<td>105.714</td>
</tr>
<tr>
<td>$S_{g+sw}$</td>
<td>3</td>
<td>109.873</td>
<td>2.870</td>
<td>0.033</td>
<td>0.238</td>
<td>103.640</td>
</tr>
<tr>
<td>$S_{g+ww}$</td>
<td>3</td>
<td>110.364</td>
<td>3.360</td>
<td>0.026</td>
<td>0.186</td>
<td>104.131</td>
</tr>
<tr>
<td>$S_{g+m+c+ww+sw}$</td>
<td>6</td>
<td>110.590</td>
<td>3.587</td>
<td>0.023</td>
<td>0.166</td>
<td>97.750</td>
</tr>
<tr>
<td>$S_{g+m+c+sw+WW}$</td>
<td>6</td>
<td>110.728</td>
<td>3.725</td>
<td>0.021</td>
<td>0.155</td>
<td>97.888</td>
</tr>
<tr>
<td>$S_{g+m+c+sw+SW}$</td>
<td>5</td>
<td>110.737</td>
<td>3.734</td>
<td>0.021</td>
<td>0.155</td>
<td>100.143</td>
</tr>
<tr>
<td>$S_{g+m+ww}$</td>
<td>4</td>
<td>110.897</td>
<td>3.894</td>
<td>0.020</td>
<td>0.143</td>
<td>102.055</td>
</tr>
<tr>
<td>$S_{g+m+sw}$</td>
<td>6</td>
<td>111.151</td>
<td>4.148</td>
<td>0.017</td>
<td>0.126</td>
<td>98.311</td>
</tr>
<tr>
<td>$S_{g+m+sw+WW}$</td>
<td>5</td>
<td>111.302</td>
<td>4.298</td>
<td>0.016</td>
<td>0.117</td>
<td>100.708</td>
</tr>
<tr>
<td>$S_{g+m+WW}$</td>
<td>5</td>
<td>111.910</td>
<td>4.906</td>
<td>0.012</td>
<td>0.086</td>
<td>101.315</td>
</tr>
<tr>
<td>$S_{g+sw}$</td>
<td>4</td>
<td>111.921</td>
<td>4.917</td>
<td>0.012</td>
<td>0.086</td>
<td>103.528</td>
</tr>
<tr>
<td>$S_{g+WW}$</td>
<td>3</td>
<td>111.921</td>
<td>4.918</td>
<td>0.012</td>
<td>0.086</td>
<td>105.688</td>
</tr>
<tr>
<td>$S_{g+WW+WW}$</td>
<td>4</td>
<td>112.300</td>
<td>5.297</td>
<td>0.010</td>
<td>0.071</td>
<td>103.908</td>
</tr>
<tr>
<td>$S_{g+WW+SW}$</td>
<td>4</td>
<td>112.311</td>
<td>5.308</td>
<td>0.010</td>
<td>0.070</td>
<td>103.919</td>
</tr>
</tbody>
</table>

*Notes: Although we tested 37 models, we present results only for models with Akaike weights ≥ 0.01. Abbreviations are: g, gender; m, birthweight; c, coyote density; j, an irruption in the population of white-tailed jackrabbits; sw, summer wolf density; ww, winter wolf density; wf, wolf-free site; s, site; and y, year.

*† Number of estimable parameters, including the intercept.*
Table 2. Model-averaged estimates ($\hat{\delta}$, with SE and confidence limits) of pronghorn fawn survival during the first 60 days of life at three study sites in northwestern Wyoming, 2002–2004.

<table>
<thead>
<tr>
<th>Site</th>
<th>$\hat{\delta}$</th>
<th>SE</th>
<th>95% lower CL</th>
<th>95% upper CL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sites with coyotes and wolves</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gros Ventre 2003</td>
<td>0.255</td>
<td>0.071</td>
<td>0.141</td>
<td>0.417</td>
</tr>
<tr>
<td>Gros Ventre 2004</td>
<td>0.390</td>
<td>0.094</td>
<td>0.228</td>
<td>0.581</td>
</tr>
<tr>
<td>Elk Ranch 2003</td>
<td>0.259</td>
<td>0.085</td>
<td>0.127</td>
<td>0.454</td>
</tr>
<tr>
<td>Elk Ranch 2004</td>
<td>0.440</td>
<td>0.112</td>
<td>0.244</td>
<td>0.657</td>
</tr>
<tr>
<td>Site with coyotes and no wolves</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antelope Flats 2002</td>
<td>0.149</td>
<td>0.055</td>
<td>0.070</td>
<td>0.291</td>
</tr>
<tr>
<td>Antelope Flats 2003</td>
<td>0.049</td>
<td>0.037</td>
<td>0.011</td>
<td>0.193</td>
</tr>
<tr>
<td>Antelope Flats 2004</td>
<td>0.097</td>
<td>0.043</td>
<td>0.040</td>
<td>0.218</td>
</tr>
</tbody>
</table>

wolf density was also positively correlated with fawn survival ($r = 0.447, P = 0.314$), and negatively correlated with coyote density ($r = -0.521, P = 0.185$), but neither relationship was statistically significant.

**Discussion**

Did wolves precipitate a trophic-level interaction?

The traditional trophic cascades model is based on consumer-resource interactions at each link in a food chain (Paine 1980). Consequently, research on top-down effects resulting from reintroductions of large carnivores has focused on cascades precipitated by direct predator-prey interactions (Berger et al. 2001, Ripple et al. 2001, Terborgh et al. 2001, Fortin et al. 2005, Hebblewhite et al. 2005), to the extent that alternative top-down pathways through which large carnivores influence systems have largely been ignored. However, large carnivores such as wolves also exert top-down forcing on systems through interference competition and intraguild predation, and these interactions may also be important mediators of cascades.

That wolves precipitated a species-level trophic cascade (sensu Polis 1999) is evidenced by more than a four-fold difference in neonatal survival at sites used by wolves during either winter, or both winter and summer (Table 2). The corresponding negative correlation between coyote and wolf densities supports the hypothesis that interspecific interactions between these species facilitated the observed increase in pronghorn fawn survival. Whereas mean densities of resident coyotes were similar between wolf-free and wolf-abundant sites ($\bar{X} = 0.251 \pm 0.025$ coyotes/km$^2$ and $\bar{X} = 0.232 \pm 0.29$ coyotes/km$^2$, respectively; Student’s $t$ test, $P = 0.687$), the mean abundance of transient coyotes was significantly lower in areas used by wolves ($\bar{X} = 0.188 \pm 0.019$ coyotes/km$^2$ vs. $\bar{X} = 0.039 \pm 0.005$ coyotes/km$^2$; Student’s $t$ test, $P < 0.001$). Thus, differential effects of wolves on solitary coyotes may be an important mechanism by which wolves limit coyote populations (Berger and Gese 2007). This hypothesis is further supported by differences in mortality rates and cause-specific mortality of resident and transient coyotes in GTNP between 2001 and 2004. Annual mortality rates of resident coyotes were 26% at the wolf-free site, and 27% at the wolf-abundant site (Berger and Gese 2007). In contrast, those of transient coyotes averaged 46% and 66% in wolf-free and wolf-abundant areas, respectively (Berger and Gese 2007). And, whereas no resident coyote were killed by wolves, 67% of transient coyote deaths resulted from predation, with wolves accounting for 83% of predation-related mortality (Berger and Gese 2007).

Despite the strong correlations between coyote densities, winter wolf densities, and fawn survival, the variable for winter wolf density did not appear in any of the highest ranked models (i.e., models with AIC$_C < 2$; Table 1; Burnham and Anderson 2002). This supports the hypotheses that the effect of wolves on fawn survival is largely indirect and mediated by differences in coyote densities among the sites, as inclusion of the winter wolf density variable in the model explained no additional variation in fawn survival beyond that already captured by the coyote density variable.

Reductions in coyote densities in GTNP have not been as large as those documented elsewhere. For instance, coyote densities were reportedly reduced by 50% in YNP following wolf reintroduction, and coyotes were extirpated from Isle Royale within eight years of the arrival of wolves in the late 1940s (Krefting 1969, Smith et al. 2003). In contrast, coyote abundance in GTNP has declined by ~33% based on differential population densities at sites with and without wolves.

Several factors likely contributed to the lesser reduction in coyote densities we detected. For instance, the small size of the area (2314 km$^2$) and corresponding lack of refugia are thought to have contributed to the rapid extirpation of coyotes from Isle Royale (Peterson 1995b). In contrast, GTNP is not spatially closed and a single wolf pack occupied only a small portion of the Park during the course of this study. Thus, it is likely the coyote population in GTNP will experience additional reductions as the wolf population continues to increase and wolves expand into areas of the Park from which they are currently absent. Furthermore, competition between wolves and coyotes may have been mediated by a relative abundance of prey. Elk densities in GTNP are in the neighborhood of 6 elk/km$^2$, rising to ~76 elk/km$^2$ during winter when elk are concentrated on feed grounds (based on data from Smith et al. 2004). As elk are the primary prey of wolves (Smith et al. 2003), their relative abundance may increase wolf tolerance of coyotes at carcasses where agonistic encounters are most likely to occur (Switalski 2003).

**Effects of changes in neonatal survival and pronghorn population density**

Demographic modeling indicates that the observed differences in fawn survival between wolf-free and wolf-abundant areas were sufficient to alter the trajectory of
the pronghorn population in GTNP from a declining to an increasing trend (Berger 2007). Still, for increases in summer survival of pronghorn fawns to result in an actual increase in the pronghorn population in GTNP, several conditions must be met. First, mortality from coyote predation must be additive and not compensatory (Boyce et al. 1999). We found no evidence of any compensatory predation-related mortality in radio-collared fawns (Berger 2007), and prospects for compensatory density-dependent mortality appear unlikely given that the current pronghorn population in the Park is <10% of its historical size (Berger 2003). Second, fawns surviving the summer must also survive their first winter to be recruited into the population as yearlings. Whereas prospects for density-dependent population regulation appear unlikely on the summer range, conditions on the winter range, located on lands managed by the Bureau of Land Management some 190 km beyond Park borders, strongly differ. Habitat designated “crucial winter range” for pronghorn (Wyoming Game and Fish Department, Cheyenne, Wyoming, USA) is currently undergoing rapid conversion due to development of natural gas wells. As overwinter survival rates of juvenile ungulates are typically lower than those of adults (Gaillard et al. 1998), this age class is likely to be differentially susceptible to any reductions in carrying capacity stemming from habitat loss. Thus, increases in summer survival of fawns may be offset by increases in overwinter mortality, resulting in no net change, or even a decrease, in the pronghorn population. Third, fawns surviving their first winter must complete the return migration the following spring to be recruited into the Park population. Telemetry data indicate that approximately 80–85% of fawns return to the Park each year, with the remainder dispersing to other summer ranges (K. M. Berger, unpublished data). Although competition for forage could alter the proportion of fawns showing philopatry to their natal range, this possibility appears unlikely given the low population density.

**Contributing factors**

The detection of trophic cascades in terrestrial systems has often been elusive because interactions between species can be weak and diffuse (Polis et al. 2000). Although the food web in Greater Yellowstone is complex due to a large number of sympatric carnivores and herbivores (Berger and Smith 2005), the focal chain we studied was relatively simple in structure. Adult pronghorn are effectively predator-free owing to their speed (Byers 1997), and while bobcats (*Lynx rufus*) and golden eagles (*Aquila chrysaetos*) are important predators of fawns in some areas (Beale and Smith 1973, Byers 1997), both species occur at low densities at our field sites (K. M. Berger, personal observations). Wolves do kill pronghorn fawns opportunistically, but their large body mass (18–80 kg) relative to coyotes (11–18

**Fig. 6.** Correlations between (a) observed pronghorn fawn survival and coyote density, (b) observed pronghorn fawn survival and wolf density, and (c) coyote and wolf densities at three sites in northwestern Wyoming, 2002–2004. Note that the lines are fitted using correlation analysis (Gotelli and Ellison 2004), which uses a slightly different line-fitting algorithm than linear regression.
kg) makes it energetically inefficient for wolves to hunt systematically for pronghorn neonates (3–4 kg) with the same intensity as coyotes (Gittleman 1985, Byers 1997). Consequently, coyotes accounted for 71% of total mortality, and 97% of predation-related mortality, of pronghorn fawns in our system (Berger 2007). Thus, effects of changes in coyote predation on fawn survival may have been easier to discern due to a lack of compensatory predation.

Anthropogenic changes in pronghorn population densities may have contributed to the strength of the interaction between coyotes and pronghorn. Specifically, populations that have been reduced by severe winter weather or over-harvesting by humans may experience poor recruitment resulting from sustained levels of predation (Gasaway et al. 1983). Although a few thousand pronghorn have historically summered in the Park (Deloney 1948), the population was reduced in the late 1800s as a consequence of market hunting. Since the turn of the 20th century, the population has never numbered more than the low 400s, and is currently ~200 animals (Berger 2003). Thus, relatively high coyote densities coupled with relatively low densities of pronghorn may allow coyotes to consume nearly all of the estimated ~150 pronghorn fawns produced in the Park each summer (Berger 2007).

Populations of migratory ungulates may be regulated by bottom-up forces when carnivore densities are determined by the supply of resident herbivores (Sinclair 1995). However, alternative prey may maintain stable predator populations or enable high densities of predators (Polis 1999). Because pronghorn females rely on reproductive synchrony and predator swamping to maximize fitness (Gregg et al. 2001), low pronghorn densities relative to the number of coyotes sustained by resident herbivores such as elk may allow coyotes to effectively regulate the pronghorn population by consuming a large proportion of the fawns produced each year (i.e., a predator-pit; Holling 1965). The possibility of a predator-pit is suggested by a positive relationship between fawn survival and pronghorn population density ($r^2 = 0.257, P = 0.004$) in GTNP between 1981 and 2004 (Berger 2007).

The strength of the interaction between coyotes and pronghorn may also be enhanced by a lack of alternative prey. Notably, although jackrabbits are an important component of coyote diets in some areas (Clark 1972), black-tailed jackrabbits (Lepus californicus) do not occur in northwestern Wyoming (Best 1996), and white-tailed jackrabbits are functionally, if not actually, extinct in GTNP (Berger et al. 2006). Jackrabbits and pronghorn neonates are similarly sized (3–4 kg), and the absence of alternative prey may increase coyotes’ dependence on pronghorn fawns at a critical juncture when adult coyotes are experiencing energetic demands associated with provisioning pups.

An irruption in the jackrabbit population at the Gros Ventre site in 2004 provided an opportunity to explore this idea. Specifically, we included a dummy variable representing the jackrabbit irruption in the model of estimated fawn survival to test for evidence of additional variation in survival that was not adequately explained by the top-ranked model. The model that included the jackrabbit variable accounted for 5.6% of the Akaiake weights (Table 1), suggesting some support for our hypothesis (Burnham and Anderson 2002). However, this model had a similar deviance to the top-ranked model, and the $\Delta AIC_c = 2$ was a result of adding another parameter to the model that explained little additional variation (Burnham and Anderson 2002). Thus, we concluded there was weak evidence that an irruption in the jackrabbit population contributed to an increase in fawn survival at the GV site in 2004.

Finally, the strength of the interaction between coyotes and pronghorn may be enhanced by changes in coyote densities resulting from human alteration of resource availability. Specifically, whereas most elk migrated out of GTNP and the surrounding area prior to human settlement, currently an average of 7500 elk now winter just south of GTNP on the National Elk Refuge (Smith et al. 2004). Overwinter mortality of elk on the NER averages 2–3% (Smith 1991), resulting in an estimated 41,000 kg of gross carcass biomass during a typical winter (i.e., 7500 elk × 2% mortality × 273 kg/elk = 40950 kg). Coyotes are opportunistic, generalist predators and scavengers and their densities are limited by the availability of prey during winter (Gese 2004). Thus, the availability of abundant elk carcasses on the NER is likely to subsidize the winter diets of coyotes and maintain the population in GTNP at artificially elevated densities. Furthermore, because elk feeding suppresses temporal variation in elk mortality associated with mild and harsh winters, carcasses on the NER provide a stable food supply that may buffer the coyote population from weather-dependent fluctuations. That elk carrion is an important resource for coyotes is suggested by the coyote “aggregations” that form on the NER each winter (Camenzind 1978). Indeed, the availability of this seasonal food subsidy results in the seasonal migration of transient and resident coyotes from both the ER and AF sites (K. M. Berger, unpublished data).

**Conclusions**

In contrast with previous studies, the changes in herbivore populations that we observed resulted not from direct predation by a top carnivore, but rather as a result of indirect effects mediated by changes in mesocarnivore abundance. The strong, negative correlations between coyote and wolf densities, and coyote densities and fawn survival, support the hypothesis that mesopredator release of coyotes, resulting from the extirpation of wolves throughout much of North America, contributes to high rates of coyote predation on pronghorn fawns observed in some areas. Thus, from both management and conservation perspectives wolf restoration holds promise for reducing coyote predation.
rates on neonatal ungulates such as pronghorn, mule deer (Odocoileus hemionus), and white-tailed deer (Odocoileus virginianus). In particular, we expect that similar cascades should emerge in places such as Yellowstone National Park, where the pronghorn population has declined precipitously in recent years, coyote predation on pronghorn fawns is high, and wolves have reportedly reduced the coyote population by as much as 50% (Caslick 1998, Smith et al. 2003). Our results provide strong evidence of a species-level trophic cascade precipitated by wolf reclamation in the southern GYE, and support a growing body of research demonstrating the importance of top-down forces in structuring the dynamics of consumer–resource interactions in terrestrial systems (McLaren and Peterson 1994, Berger et al. 2001, Ripple et al. 2001, Terborgh et al. 2001, Fortin et al. 2005).

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LITERATURE CITED
Mountain lions prey selectively on prion-infected mule deer

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The possibility that predators choose prey selectively based on age or condition has been suggested but rarely tested. We examined whether mountain lions (Puma concolor) selectively prey upon mule deer (Odocoileus hemionus) infected with chronic wasting disease, a prion disease. We located kill sites of mountain lions in the northern Front Range of Colorado, USA, and compared disease prevalence among lion-killed adult (≥2 years old) deer with prevalence among sympatric deer taken by hunters in the vicinity of kill sites. Hunter-killed female deer were less likely to be infected than males (odds ratios (OR) = 0.2, 95% confidence intervals (CI) = 0.1–0.6; p = 0.015). However, both female (OR = 8.5, 95% CI = 2.3–30.9) and male deer (OR = 3.2, 95% CI = 1–10) killed by a mountain lion were more likely to be infected than same-sex deer killed in the vicinity by a hunter (p < 0.001), suggesting that mountain lions in this area actively selected prion-infected individuals when targeting adult mule deer as prey items.

Keywords: chronic wasting disease; predation; prion; Puma concolor; selection; vulnerability

1. INTRODUCTION

Theoretical models and some empirical evidence suggest that predators select prey based in part on their vulnerability (Emlen 1966; MacArthur & Pianka 1966; Curio 1976; Temple 1987). Selecting prey in poor condition may conserve energy or reduce the risk of injury (Mech 1970; Ackerman et al. 1984; Pierce et al. 2000). Thus, a prevailing idea in ecology is that predators capture young, old, sick, weak, injured or inexperienced individuals from prey populations in higher than expected proportions (Errington 1946; Slobodkin 1968; Curio 1976). Despite its wide acceptance, this idea rarely has been tested.

Mountain lions (Puma concolor) are ambush predators (Hornocker 1970; Logan & Swayne 2001). Young and/or solitary deer (Odocoileus spp.) are most vulnerable to mountain lion predation (Hornocker 1970; Logan & Swayne 2001). However, previous studies have not examined whether diseased deer are more vulnerable to or selected by mountain lions.

Chronic wasting disease (CWD) (Williams & Young 1980) is a naturally occurring prion disease of North American deer. Simulations suggest that selectively removing infected individuals via test-and-cull or predation could reduce prevalence (Gross & Miller 2001), and thus would be valuable in disease control. Clinical signs of CWD are progressive and include poor body condition, altered behaviour, incoordination and periods of somnolence (Williams & Young 1980). It follows that infected deer may be more susceptible to predation than uninfected individuals because they are less cautious and less able to recognize and respond to threats (Williams & Young 1980; Chase-Topping et al. 2005; Krumm et al. 2005; Miller et al. 2008). Here, we evaluated whether mountain lions are more likely to prey upon prion-infected mule deer (Odocoileus hemionus) than upon uninfected individuals.

2. MATERIAL AND METHODS

Nine captured mountain lions older than one year were fitted with GPS collars in the northern Front Range of Colorado, USA. GPS data were obtained through remote download. We used cluster analysis of greater than or equal to three location data points within 200 m over a 24 h period to determine the locations of possible kill sites (Anderson & Lindzey 2003). Once a cluster was identified, we used its centre in attempting to locate the kill site. If the prey item was a mule deer and appropriate tissues were available, samples were tested for prion infection. We also collected samples from other mountain-lion-killed mule deer carcasses found in the study area during the same time period. Prion diagnostic methods were as described in Miller & Conner (2005).

For comparison to lion-killed mule deer, we used data from mule deer sampled in the vicinity of identified lion-kill sites (hereafter referred to as ‘vicinity-sampled’). We defined vicinity as less than or equal to 3 km radius of a lion-kill site because from a previous study 86 percent of movements made by local mule deer were less than or equal to 3 km during non-migratory periods (Conner & Miller 2004). This approximately 28 km² area represented local prion infection risk. We only included vicinity samples from the same overall time period as the lion-killed samples. The source of vicinity samples was mule deer killed by hunters and tested using the same diagnostic methods as above.

To assess the differential probability of mountain lion predation, we compared the odds of infection (odds ratio (OR)) among lion-killed deer to that among vicinity-sampled deer. We used data from lion-killed deer that had greater than or equal to three vicinity samples in these analyses. Because prevalence in mule deer differs by age, sex and population (Miller & Conner 2005), we only used data for adult (≥2 years of age) deer and factored sex and population influences into our analyses. We estimated the prevalence among lion-killed deer and vicinity-sampled deer using least-squares means and their 95 per cent confidence intervals (CI) from a generalized linear mixed model approach (Proc GLIMMIX; SAS Institute 2008). We used a logistic model with the explanatory variables (fixed effects) sex, kill type (lion- or vicinity-), sex × kill type; we included source (the cluster of kills in the vicinity of a lion kill) as a random effect to account for spatial heterogeneity. Among the adult-lion-killed deer (10 infected and 31 uninfected) that had been assigned to age groups (2–4 years, 5–7 years or >8 years old) by examining dentition, we also compared the occurrence by infection status across three age classes post hoc using a Fisher exact 2 × 3 contingency table.

3. RESULTS

From January 2003 to July 2006, we found prey remains at 108 kill sites, including 62 mule deer carcasses. In all, there were 54 lion-killed deer carcasses that were greater than or equal to 2 years of age, had suitable tissue available and had greater than or equal to three associated vicinity kills.
gathered across several studies, we hypothesize that mountain lions were equally likely to be killed by either mountain lions or vehicles (relative risk ¼ 1.4–4.1) similar to those estimated from our data. However, a separate cohort study of mule deer survival at Table Mesa (also located within our study area) revealed that prion-infected deer had a much greater risk (3.7 ×, 95% CI ¼ 1.1–12.5) of being killed by mountain lions than by vehicles, even though uninfected deer in this area were equally likely to be killed by either mountain lions or vehicles (relative risk ¼ 0.6, 95% CI ¼ 0.2–2.4; Miller et al. 2008). From the observations gathered across several studies, we hypothesize that although much of the ‘selection’ we observed may be attributed to infected mule deer being less vigilant or fit and thus relatively vulnerable to ‘attack’ of one kind or another, mountain lions may also learn to recognize and more actively target diseased deer.

Other studies indicate that coursing predators like wolves (Canis lupus) and coyotes (C. latrans) select prey disproportionately if they appear impaired by malnutrition, age or disease (Crisler 1956; Mech 1970; Gese & Grothe 1995; Lingle & Wilson 2001). Although a stalking predator might not be expected to be as selective as a coursing predator, mountain lions apparently can be as selective—relative to the availability of different age and condition categories of prey—as coyotes (Pierce et al. 2000). The subtle behaviour changes in prion-infected deer may be better signals of vulnerability than body condition, and these cues may occur well before body condition noticeably declines (Williams & Young 1980; Chase-Topping et al. 2005; Krumm et al. 2005; Miller et al. 2008). The tendency for infected-lion-killed deer to be relatively young adults compared to uninfected-lion-killed deer (figure 1) suggests that such cues were sufficiently strong to draw attention to (or increase vulnerability of) individuals outside the age classes typically targeted by mountain lions hunting in this area.

### 4. DISCUSSION

Adult mule deer killed by mountain lions were more likely to be prion-infected than were deer killed more randomly in sympatric populations, suggesting that mountain lions were selecting for infected individuals when they targeted adult deer. In roughly the same geographical area where we sampled mountain-lion-kill sites, Krumm et al. (2005) found that deer killed in vehicle collisions had the odds of prion infection (OR ¼ 2.4, 95% CI ¼ 1.4–4.1) similar to those estimated from our data. However, a separate cohort study of mule deer survival at Table Mesa (also located within our study area) revealed that prion-infected deer had a much greater risk (3.7 ×, 95% CI ¼ 1.1–12.5) of being killed by mountain lions than by vehicles, even though uninfected deer in this area were equally likely to be killed by either mountain lions or vehicles (relative risk ¼ 0.6, 95% CI ¼ 0.2–2.4; Miller et al. 2008). From the observations gathered across several studies, we hypothesize that although much of the ‘selection’ we observed...
Intuitively, we expect predators to be more successful in capturing animals that are slow or less alert. The ‘sanitation effect’ of predators selecting weak individuals over prime, healthy specimens (Leopold 1933; Mech 1970) has been documented in several studies (Mech 1966; Kolenosky 1972; Schaller 1972). Although theory suggests that removing infected animals could ‘sanitize’ and slow the rate of prion transmission (Gross & Miller 2001), prevalence can be remarkably high in mule deer populations preyed upon by mountain lions (Miller et al. 2008). Prion transmission among deer can occur via several mechanisms, including indirect transmission from exposure to prions in the environment (Miller et al. 2004). We observed that mountain lions typically consumed greater than 85 percent of a deer carcass, often including brain tissue, and this may be beneficial in decreasing prion contamination at kill sites. However, the extent to which selective predation by mountain lions alters the dynamics of prion disease epidemics in natural mule deer populations remains unclear (Miller et al. 2008).

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Mexican wolves, elk, and aspen in Arizona: Is there a trophic cascade?

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**A B S T R A C T**

In 1998, Mexican gray wolves (*Canis lupus baileyi*) were introduced into the Blue Range Wolf Recovery Area (BRWRA) that spans adjacent portions of Arizona and New Mexico. In 2009 we selected three mixed-conifer sites on the Apache National Forest, within the BRWRA of east-central Arizona, to characterize long-term age structure of aspen (*Populus tremuloides*) and to check for the possible occurrence of a tri-trophic cascade involving Mexican wolves, Rocky Mountain elk (*Cervus elaphus nelsoni*), and aspen. These mixed-conifer sites included (a) a refugium site, (b) an old-growth site, and (c) a site thinned in 1991–1992. The refugium site was inaccessible to elk and cattle whereas the old-growth and thinned sites were accessible to elk but not cattle. Age structure results indicated that aspen recruitment (i.e., the growth of sprouts/seedlings into tall saplings, poles, and eventually trees) at the refugium site had been ongoing over a period of many decades. In contrast, aspen recruitment at the old-growth and thinned sites decreased significantly (*p* < 0.05) during the two most recent decades when elk populations, as indexed by annual harvest levels, were relatively “high”. From 2000 to 2008, only 2.9 Mexican wolves per 1000 elk were present on the Apache National Forest compared to 9.3 western gray wolves (*Canis lupus occidentalis*) per 1000 elk in Yellowstone National Park where tri-trophic cascades involving wolves, elk, and aspen have been reported. The low number of Mexican wolves relative to their primary prey (elk) suggests that an ecologically effective density of wolves has not become established in east-central Arizona. Furthermore, the lack of recent aspen recruitment in stands accessible to elk indicates an absence, to date, of a tri-trophic cascade.

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**1. Introduction**

Aspen (*Populus tremuloides*), also known as quaking aspen or trembling aspen, is the most widely distributed deciduous tree species in North America and unusual in reproducing primarily by sprouts (ramets) from a parent root system (Fowells, 1965; Perala, 1990). Areas that support aspen in the western United States (US) commonly contain a variety of woody and herbaceous plants that provide critical habitat and food-web support to many wildlife species (DeByle and Winokur, 1985). Historically, aspen forests occupied nearly 3.9 million hectares in eight western states (Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming) but had declined 60% by the end of the 20th century (Bartos, 2001). At the southern end of aspen’s range in the western US losses have been particularly severe with aspen declines of 96% and 88% in Arizona and New Mexico, respectively. Various factors can contribute to the loss of aspen including reduced fire frequency, conifer invasion, disease, a changing climate, intensive browsing by large herbivores, and others (DeByle and Winokur, 1985; Worrall et al., 2007).

The browsing of aspen stands by native large herbivores, such as elk (*Cervus elaphus*) and deer (*Odocoileus* spp.), has likely occurred over many thousands of years in the American West since the leaves and stems of young aspen plants are highly palatable to ungulates. Yet the capability of these stands to persist over long periods of time and to cover large areas indicates that ungulate herbivory may not have seriously limited aspen recruitment (growth of sprouts/seedlings into tall saplings, poles, and eventually trees). However, with the introduction of domestic livestock and reduced populations of large predators across large areas of the West during the late 1800s and early 1900s, followed by enlarged populations of wild ungulates during the latter half of the 20th century, browsing of aspen sprouts/seedlings had become an increasingly important factor affecting recruitment (Muegler and Bartos, 1977; DeByle and Winokur, 1985; Kay, 1997; Kay and Bartos, 2000).

Recent studies in Yellowstone National Park, an area where domestic livestock grazing has not occurred, point to an additional factor that may contribute to the long-term demise of aspen—the collapse of a tri-trophic cascade involving wolves, elk, and aspen. Following the extirpation of western gray wolves (*Canis lupus occidentalis*) from Yellowstone nearly a century ago, increased browsing by Rocky Mountain elk (*Cervus elaphus nelsoni*) not only suppressed the recruitment of aspen in the park’s northern winter ranges but also that of willows (*Salix* spp.), cottonwoods (*Popu-
and reduced elk densities following wolf reintroduction (White, 2001a; Kay, 2001a; Barmore, 2003; Ripple and Beschta, 2004a,b; Beschta, 2005). Increased elk herbivory and decreased aspen recruitment similarly occurred in the Canadian Rockies when wolf populations in Jasper, Yoho, and Kootenay National Parks of Alberta were suppressed during the mid-1900s (White et al., 1998; Beschta and Ripple, 2006). In Rocky Mountain National Park, where elk were reintroduced in the absence of wolves, intensive browsing by elk reduced aspen and willow recruitment (Hess, 1993; Zeigenfuss et al., 2002; Binkley, 2008). Unimpeded browsing by native large herbivores in the absence of apex predators is increasingly recognized as an important factor affecting the biodiversity and ecosystem services of native plant communities that comprise temperate and boreal ecosystems (Ripple et al., 2010).

During the winters of 1995–1996, gray wolves were reintroduced into Yellowstone National Park, thus completing the park’s historical predator guild. Soon thereafter studies began observing behavioral responses of elk (e.g., vigilance, use of habitat) due to the presence of wolves (Laundré et al., 2001; Mao et al., 2005; Halofsky and Ripple, 2008a). Altered patterns of browsing and reduced elk densities following wolf reintroduction (White and Garrott, 2005) also appeared to explain the spatially patchy release (increased heights of young woody plants in various locations) currently underway for willow, aspen, and cottonwood in Yellowstone’s northern winter ranges (Beyer et al., 2007; Ripple and Beschta, 2007; Halofsky and Ripple, 2008b; Beschta and Ripple, 2010). Similarly, aspen recruitment improved following recovery of wolf populations in Jasper National Park (Beschta and Ripple, 2006).

Like much of the American West, wolves in Arizona and New Mexico were heavily persecuted in the late 1800s and early 1900s. For example, in 1920 alone over 100 wolves were removed from these two states (Brown, 1983). Removals dropped to ~15 wolves/year in the 1930s and by the mid-1940s, or soon thereafter, wolves in Arizona and New Mexico had become functionally extirpated. However, in 1998 Mexican gray wolves (Canis lupus baileyi) from a captive breeding program were introduced into east-central Arizona and west-central New Mexico, an area designated as the Blue Range Wolf Recovery Area (BRWRA). While these introductions occurred approximately 200 km north of the historical range of Mexican wolves (see Brown, 1983), the BRWRA was thought to have suitable habitat and sufficient prey for maintaining a population of Mexican wolves (USFWS, 1996).

We undertook this study on the Apache National Forest (Fig. 1) where introduced Mexican wolves have been present for a decade. This national forest comprises the portion of the BRWRA that extends into east-central Arizona. It is also adjacent to the White Mountain Apache Reservation where wolves have become protected in recent years. Field reconnaissance of the Apache National Forest in the summer of 2008 indicated that aspen recruitment in recent decades has been generally absent across major portions of the Springerville and Alpine districts. Thus, our overall objective was to assess temporal patterns of aspen recruitment in mixed-conifer stands accessible to elk where we hypothesized that a tri-trophic cascade involving wolves–elk–aspen might again be occurring following the introduction of Mexican wolves, potentially contributing to improved aspen recruitment. The occurrence of such a trophic cascade would suggest recovery of an ecologically effective density of wolves (Soule et al., 2003).

2. Study area

Our study area was located along the southern portion of the Springerville District, Apache National Forest, approximately 20 km west of Alpine, Arizona. Here, mixed-conifer forests contained varying proportions of Douglas-fir (Pseudotsuga menziesii), Engelmann spruce (Picea englemannii), blue spruce (P. pungens), white fir (Abies concolor), subalpine fir (A. lasiocarpa), limber pine (Pinus flexilis), and ponderosa pine (P. ponderosa). Aspen, a desired browse species for elk and deer, commonly occurs within these mixed-conifer stands.

Grizzly bears (Ursus arctos), black bears (U. americanus), cougar (Puma concolor), gray wolves, Merriam elk (C. elaphus merriami), mule deer (O. hemionus), and Coues white-tailed deer (O. virginianus couesi) originally inhabited portions of the Mogollon Rim and White Mountains of east-central Arizona (Hoffmeister, 1986). However, the influx of Euro-Americans into this area eventually resulted in the regional extirpation of grizzly bears and wolves as well as extinction of Merriam elk. Rocky Mountain elk from Yellowstone were introduced into east-central Arizona in 1913 and, as previously indicated, Mexican wolves in 1998. The Mexican wolf is the southernmost and smallest subspecies of gray wolf in North America (Mech and Boitani, 2003).

Three aspen sites, at an elevation of ~2700 m, were chosen to represent different treatments to forest stands (Fig. 2). They included (a) a “refugium site” that was inaccessible to wild and domestic ungulates because of topographic barriers (i.e., broken rock, cliff faces), (b) an “old-growth site” that had not experienced logging, and (c) a “thinned site” at which a partial overstory removal of conifers, along with the piling and burning of slash, occurred in 1991–1992. While both the old-growth and thinned sites were easily accessible to wild ungulates, neither had been grazed by domestic livestock. The old-growth site had been fenced to exclude cattle and the thinned site was sufficiently far from the nearest meadow that cattle did not forage at this site.

3. Methods

To help assess potential environmental or land-use factors within the general vicinity of our study sites that might affect aspen recruitment, we assembled annual records of snowpack accumulation, grazing use, timber harvest, and big game harvest within the Apache National Forest for the period 1970–2008. To characterize annual snowpack amounts, we calculated the average January 15 through April 1 snowpack water equivalent for the Beaver Head, Coronado Trail, Hannagan Meadow, Maverick Fork, and Nutrioso snow courses. Domestic livestock grazing was summarized in animal unit months (AUMs, where one AUM represents the foraging
needs of a cow and calf over a period of one month) for the Udall and Big Lake Allotments; these allotments occur along the southern end of the Springerville District. Timber harvest volumes (board-feet/acre) were compiled for the adjacent Springerville and Alpine Districts; volumes were converted to m$^3$ using a conversion factor of 0.0024 bd-ft/m$^3$ (Manfredo and Sanders, 2008). Big game harvest records for Arizona game management unit 1 (which covers essentially all of the Springerville District and the northern portion of the Alpine District) were used to index the general abundance of elk, mule deer, and Coues white-tailed deer, as well as temporal trends in their populations (AGFD, 2009).

At each study site we measured diameter at breast height (DBH, cm) of aspen having a DBH ≥ 1 cm. Because the refugium site comprised an area of only 0.1 ha, we sampled aspen within the entire site. However, at the old-growth (>5.0 ha) and thinned (~2.5 ha) sites we utilized belt transects to delineate areas within which aspen ≥1 cm in DBH were sampled. At the old-growth site, two parallel belt transects (each 25 m × 200 m, with a random start and 30-m offset between transects) were used; at the thinned site, two parallel belt transects (one 25 m × 200 m and the second 25 m × 75 m, with a random start and 30-m offset) were used.

At each site we measured canopy cover (hemispherical densitometer), basal area (4.6 m$^2$/ha per stem basal area factor [BAF] wedge), and the height and density of aspen sprouts/seedlings within a circular 3-m radius plot (28.3 m$^2$). At the refugium site we undertook these measurements at two plot centers, 25 m apart, located near the center of the site. For the old-growth and thinned sites we undertook the same set of measurements at 25-m intervals along the centerline of each belt transect. We also measured the annual growth (CAG, cm) of young aspen, not visibly affected by shepherd’s crook (Venturia spp.), to illustrate the general productivity of each site. Shepherd’s crook, a disease that causes a characteristic blackening and bending of young aspen stems, was relatively common on sprouts/seedlings at all three sites. Because these diseased stems eventually die and break-off in a manner that is similar to that of the stem having been browsed, we were unable to utilize plant architecture measurements for assessing browsing patterns on young aspen (e.g., Ripple and Beschta, 2007). All plant measurements were conducted in late July of 2009.

We selected 33 trees at the old-growth site and 30 trees at the thinned site from which increment cores were obtained. The probability of selection was based on the frequency distribution of DBHs at each site. Cores were placed in plastic straws, sealed, and transported to Oregon State University where they were subsequently dried and sanded. Annual growth rings were counted with a 10× binocular microscope to establish the age (at breast height) represented by each core. From these ring counts, regression analysis was used to establish a relationship between tree age at breast height (yr) and DBH. We also obtained cross-sections (wafers) at ground level and at breast height (1.4 m) from three aspen saplings near the refugium site and determined the number of years required for them to attain breast height. The estimated age at breast height (from regression analysis) and the number of years to attain breast height were jointly utilized to estimate the establishment date of each measured aspen.

A histogram of stem frequency vs. establishment date was developed for each site to represent aspen age structure, by decade, over the period 1900–2008. Since annual estimates of elk populations were not available for this period we used annual elk harvest data to index general population trends (Toweill and Thomas, 2002). Based on harvest data we considered elk abundance to be “low” prior to 1990 and “high” after 1990. At each site we fitted an exponential regression through the age structure data from 1900 to 1989 (the period of “low” elk abundance) and used this relationship to assess if significant changes ($p < 0.05$) in aspen recruitment occurred after 1990 (“high” elk abundance).

In 2005, an elk exclosure (elevation 2500 m) was constructed approximately 1.2 km north of the Alpine, Arizona, on the city watershed. Along the southern edge of the exclosure, aspen sprouts were occurring both inside and outside of the fence. We undertook plant architecture measurements (Beschta and Ripple, 2007) of young aspen plants inside and outside of the fence to identify their relative patterns of height growth following construction of the exclosure.

Lastly, we utilized a ratio of predator/prey (wolves per 1000 elk) to index the potential ecological effectiveness of the Mexican wolf population in east-central Arizona. We calculated (a) the number of Mexican wolves per 1000 elk on the Apache National Forest (wolf and elk population estimates were obtained from the Mex-
ican Wolf Recovery Project, Alpine, Arizona) and (b) the number of gray wolves per 1000 elk in the northern range of Yellowstone National Park (Yellowstone National Park, Mammoth Hot Springs, Wyoming). These ratios were calculated annually from 1998 to 2008 for the Apache National Forest and from 1995 to 2008 for Yellowstone.

4. Results

Summaries of snowpack water equivalent, grazing use, timber harvest, and big game harvest on the Apache National Forest since 1970 indicated variability in temporal patterns of climate and land use (Fig. 3). Although snowpack conditions fluctuated considerably from year-to-year, since about 1995 snowpack water equivalents have been relatively low. For example, in 10 of the last 14 years water equivalents have been less than the long-term average of 11.0 cm (Fig. 3a) indicating that forest stands on the Apache National Forest have recently been experiencing relatively shallow winter snowpacks. Domestic grazing levels showed a slow increase in AUMs from 1970 to 1990 after which they decreased to less than half of their former levels (Fig. 3b). Timber harvests declined precipitously after the late 1980s and since 1995 have remained relatively low (Fig. 3c). Big game harvest data suggested that mule deer and Coues white-tailed deer on the forest have generally been less prevalent than elk, particularly in recent years (Fig. 3d). Furthermore, while mule deer harvests have been trending lower since the mid–1980s, elk harvests increased from the early 1980s until the mid-1990s, after which they remained relatively high.

The overstory canopy cover at our study sites ranged between 41 and 65% (Table 1). The old-growth site had the greatest basal area of conifer and aspen (10.5 and 19.6 m$^2$/ha, respectively) while the refugium site had the lowest basal area in these categories (5.7 and 4.6 m$^2$/ha, respectively). The thinned site had the highest densities of aspen sprouts/seedlings, perhaps reflecting the effects of overstory conifer removal in the early 1990s (Table 2). The CAG of sprouts/seedlings was greatest on the thinned site (49 cm) and least for the refugium site (35 cm).

Based on results from the 63 aspen increment cores, linear regression indicated the following relationship: tree age at breast height (yr) = 2.49 DBH ($r^2 = 0.85$, $p < 0.01$). Cross-sections obtained at the base and breast height of three aspen saplings indicated they had attained breast height within three years. Thus, the establishment date of each sampled aspen was calculated as: establishment date (yr) = 2009 − [(2.49 DBH) + 3].

At the refugium site, aspen age structure indicated recruitment had been ongoing since about 1940 and that a large number of stems were associated with younger age classes (Fig. 4a). In particular, recruitment had been relatively high during the last two decades. This age structure pattern is characteristic of an uneven-aged forest where recruitment is an ongoing process. The old-growth (Fig. 4b) and thinned (Fig. 4c) sites also showed a

![Figure 3](image)

**Fig. 3.** Annual (a) snowpack water equivalent (SWE, cm) averaged from January 15 to April 1 for the Beaver Head, Coronado Trail, Hannagan Meadow, Maverick Fork, and Nutrioso snow courses, (b) grazing use in animal unit months (AUMs) for the Udall and Big Lake grazing allotments, Springerville District, (c) timber harvest volume (m$^3$) on Alpine and Springerville Districts, and (d) harvest of elk, mule deer, and Coues white-tailed deer in game management unit 1, Apache National Forest. Solid lines are five-year moving averages.

Data sources: (a) Natural Resources Conservation Service; (b) and (c) US Forest Service, Apache National Forest; and (d) Arizona Game and Fish Department.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Density (#/ha)</th>
<th>Height (cm)</th>
<th>CAG (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Refugium</td>
<td>104</td>
<td>97 [27]</td>
<td>35 [15]</td>
</tr>
</tbody>
</table>

**Table 2**

Average density, height, and current annual growth (CAG) of aspen <1.5 m in height at each study site (standard deviation in brackets).

*Table 1* General terrain and forest conditions at each study site (standard deviation in brackets).

<table>
<thead>
<tr>
<th>Study site</th>
<th>Elevation (m)</th>
<th>Aspect and slope (%)</th>
<th>$n^a$</th>
<th>Canopy</th>
<th>Basal area$^a$</th>
<th>Conifer (m$^2$/ha)</th>
<th>Aspen (m$^2$/ha)</th>
<th>Total (m$^2$/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Refugium</td>
<td>2700</td>
<td>S, 0–20%</td>
<td>2</td>
<td>41 [20]</td>
<td>5.7 [1.6]</td>
<td>4.6 [0.8]</td>
<td>10.3 [1.6]</td>
<td></td>
</tr>
</tbody>
</table>

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$^a$ Number of plots for canopy cover and basal area measurements.

$^b$ Canopy cover measured with a hemispherical densitometer.

$^c$ Basal area measured with a 4.6 m$^2$/ha basal area factor (BAF) wedge.
pattern of nearly continuous recruitment from 1900 to 1989, during the period when annual elk harvests were relatively "low". However, a significant decrease in recruitment ($p < 0.05$) occurred during the two most recent decades when annual elk harvests were relatively “high” (Fig. 3d).

Outside of the elk exclosure near Alpine, aspen sprouts remained suppressed by intensive elk browsing and unable to grow above a height of 50 cm in recent years. In contrast, aspen sprouts inside the exclosure and which averaged only 34 cm in height in 2005 had attained an average height of 241 cm in 2009, an annual height increase of 52 cm/yr (Fig. 5).

Over the last eight years (2001–2008 inclusive), an average of 2.9 Mexican wolves per 1000 elk (standard deviation = 0.8) have been present on the Apache National Forest. This ratio is significantly less ($p < 0.05$, t-test, unequal variances) than the 9.3 gray wolves per 1,000 elk (standard deviation = 3.0) that occurred in northern Yellowstone over the last eight years (Fig. 6a). Furthermore, 2.9 Mexican wolves per 1000 elk is a much lower ratio than has been reported for gray wolves in other portions of North America (Fig. 6b).

5. Discussion

Temporal patterns of several environmental and land-use variables specific to the Apache National Forest, variables that might directly or indirectly affect patterns of aspen recruitment, are summarized in Fig. 3. Relatively shallow snowpacks occurred during the most recent one and one-half decades, thus indicating reduced springtime and early summer soil moisture for plant communities. However, mountainous areas of east-central Arizona, like much of Arizona and New Mexico, normally experience a period of summertime thunderstorm precipitation. From 1990 to 2008, total July and August precipitation averaged 21.6 cm annually at Alpine, Arizona, or approximately 9% higher than the long-term average for the period 1970–2008.

The declines in annual snowpack water equivalent for snow courses on the Apache National Forest over recent decades are symptomatic of reduced winter snowpacks observed in other mountainous areas of the western US during this same period (Mote, 2006). While declining snowpacks may have implications for plant communities and patterns of streamflow, they may also influence elk populations. For example, Creel and Creel (2009) found that the steady growth of Montana elk populations in recent decades was inversely correlated with declining snowpacks. When they coupled their analysis with regional predictions of global climate change over the next 20–50 years, results indicated increased elk population growth rates were likely if snowpack amounts continue to decline as predicted. However, it is not known whether such results can be applied to Arizona where contemporary mountain snowpacks are often relatively shallow and thus may not limit elk populations like the deeper snowpacks of Montana’s mountains.

Range managers have long known that intensive annual browsing by domestic livestock can effectively curtail the recruitment of aspen and other palatable woody species over extended periods (Sampson, 1919; Houston, 1954). Relatively recently Kay (2001b) assessed the long-term status and trends of aspen stands across
central Nevada and found a widespread absence of recruitment extending back many decades. This lack of recruitment was not associated with climatic variation, fire suppression, forest succession, or browsing by wild ungulates, but instead was attributed to annual browsing by domestic cattle and/or sheep. During our 2008 field reconnaissance of aspen stands, a paucity of aspen recruitment along the edges of meadows utilized by cattle was observed in the Udall and Big Lake allotments. These reductions in recruitment appeared to have begun more than half a century ago, long before elk numbers had begun to increase.

The harvesting of overstory trees can greatly increase the amount of light available to the forest floor, thus increasing the above-ground biomass of herbaceous and browse species. Increased productivity of understory plants can provide additional food-web support for wild ungulates (Patten, 1974), particularly in forest stands not utilized by livestock. Thus, the relatively high levels of forest harvesting in the 1970s and 1980s may have contributed to the increase in elk abundance (as indicated by increasing harvest levels of elk) that occurred from the early 1980s to the mid-1990s (Fig. 3d). However, Coues white-tailed deer and mule deer harvests did not similarly benefit. Coues white-tailed deer harvests have remained extremely low from 1970 to the present and mule deer harvests have generally been in decline since the 1970s. The extent to which inter-specific competition may be a factor in the opposing trends in elk and mule deer harvests over the last three decades is not known, but elk are generally able to out-compete mule deer for limited forage resources (Murie, 1951).

Increased availability of light at the forest floor following timber harvesting can also trigger an increase in the density and vigor of aspen sprouts (DeByle and Winokur, 1985). The thinned site had the greatest density of aspen reproduction (1905 stems/ha) and the largest CAG (49 cm) of the three sites, perhaps as a consequence of thinning that occurred at this site in the early 1990s. Thus, the significant downturn in aspen recruitment ($p < 0.05$) at the thinned site (Fig. 4c) since 1990 represented an unexpected outcome of thinning. The significant downturn in aspen recruitment ($p < 0.05$) for the old-growth site since 1990 was similarly unexpected since there were numerous canopy openings where mature conifers had died or blown down in recent decades. These results indicate that high levels of elk herbivory now appear to be preventing aspen recruitment in mixed conifer stands not utilized by livestock. They further suggest that silvicultural treatments which would normally result in increased aspen recruitment are unlikely to be effective in areas where elk herbivory is relatively high.

The number of aspen stems attaining breast height during the last two decades was relatively high at the refugium site where aspen recruitment has been ongoing over many decades. These high levels of aspen recruitment indicated that diminished snowpacks, year-to-year fluctuations in summertime precipitation, or other environmental factors were not preventing recruitment. Continued height growth in recent years of young aspen within the elk enclosure near Alpine, Arizona similarly indicated that climatic patterns have not limited their growth. In contrast, significantly decreased aspen recruitment ($p < 0.05$) occurred during the last two decades at the old-growth and the thinned sites, during a period of relatively high elk abundance.

The general pattern of elk harvests reported for the Apache National Forest reflects a similar trend in elk harvest that has occurred on a state-wide basis. Approximately 1,000 elk were harvested across Arizona in 1970 with harvest levels increasing to 10,600–13,700 elk in the 1990s (AGFD, 2009). As of 2005, there were an estimated 35,000 Rocky Mountain elk in Arizona. On the Coconino National Forest in north-central Arizona, Fairweather and Tkacz (1999) found that browsing impacts to aspen sprouts/seedlings from cattle, along with elk and deer, were a common occurrence in aspen stands. They further observed that young aspen stems were often “browsed all the way to the ground, year after year, until the resources [root reserves] are depleted and they stop sprouting altogether.” Browsing of aspen regeneration from large herbivores has been a major concern since the 1960s for the Coconino National Forest. Intensive ungulate herbivory was so prevalent that permanent exclusion fences were required to insure successful aspen recruitment following silvicultural treatments or fire (Bailey and Whitham, 2003; Stritar et al., 2010).

Although either elk or deer can damage aspen by persistently browsing new sprouts and by rubbing saplings or trees with antlers, DeByle and Winokur (1985) indicate that elk generally have a greater impact because: (1) elk are larger thus requiring more forage per animal, (2) elk are able to browse plants at higher levels, (3) elk chew the bark of aspen trees, and (4) elk may remain in aspen forests through most winters whereas snowpack depths usually force deer to lower elevations. Both barking and rubbing have been associated with increasing the susceptibility of aspen to the entry of pathogenic fungi which, in turn, can cause stem cankers and decay that contribute to the death of trees.

Browsing studies in the western US have often utilized aspen to assess temporal patterns of herbivory because it is a long-lived species and aspen sprouts/seedlings are highly palatable to ungulates. When combined with coring measurements that help establish the age structure of overstory aspen (or other tree species with palatable sprouts/seedlings), such approaches can provide important insights regarding historical browsing patterns associated with large herbivores (Beschta and Ripple, 2009). Although various studies have often confirmed that aspen in the western US is in serious decline (Bartos, 2001; Rehfeldt et al., 2009), little research has addressed the long-term impacts of increased herbivory on other woody browse or herbaceous species associated with aspen stands. Thus, there is a high need for public land managers to understand how historical and contemporary herbivory has not only affected the age structure of existing aspen stands, but also how it may have altered understory plant communities. While ungulate exclosures have various limitations (Sarr, 2002), they can quickly provide local information regarding the relative effects of large herbivores on plant communities and can be constructed (e.g., three-way exclosures) to help discern differences between the effects of wild vs. domestic ungulates.

Rocky Mountain elk, introduced following the extinction of Merriam elk, have been able to attain a relatively large population in Arizona in recent decades. The results of this study suggest that if contemporary elk population levels on the Apache National Forest are maintained into the future, a lack of aspen recruitment may continue even where aspen stands are inaccessible to livestock. In other areas of the western US where domestic livestock grazing has been absent, increased browsing by wild ungulates following the loss of large predators was similarly found to reduce/terminate the recruitment of palatable woody plants (Beschta and Ripple, 2009).

The introduction of Mexican wolves into the BMWRA was undertaken in an attempt to establish a sustainable population of this apex predator (USFWS, 1996). However, wolf numbers have no longer continued to increase in recent years and our results show that their presence has been ineffective at reversing declines in aspen recruitment within mixed-conifer stands, thus indicating this apex predator have not sufficiently affected elk behavior or populations to initiate a trophic cascade. This result contrasts with the Yellowstone experience where decreased browsing pressure and a spatially patchy increase in the heights of young aspen, cottonwood, and willow growth were measured within a few years following the reintroduction of gray wolves. We observed only a few locations on the Springerville and Alpine Districts in the general vicinity of our field sites were young aspen were beginning to increase in height in recent years, possibly indicating wolves were causing elk to avoid high-risk sites. However, the limited size of
these sites, the occurrence of recent fires and reduced grazing pressure in surrounding areas, both of which increase forage availability to wild ungulates, as well as the general occurrence of shepherd's crook (which precluded attempts to assess recent browsing history) prevented us from drawing any conclusions from these sites regarding a possible trophic cascade.  

Soulé et al. (2003) indicate an ecologically effective density of highly interactive species (such as wolves in terrestrial ecosystems) is one that would maintain critical ecological interactions and help ensure against ecosystem degradation. With regard to a tri-trophic cascade involving wolves, elk, and aspen, this would be a predator density sufficient to mediate the behavior and/or density of native herbivores thus regulating potential impacts to plant communities. The relatively low ratio of Mexican wolves per 1000 elk on the Apache National Forest, in comparison to gray wolves in northern Yellowstone (Fig. 6a) and other areas of north America (Fig. 6b), appears to indicate that Mexican wolves have not achieved an ecologically effective density in Arizona. Why Mexican wolf populations in Arizona, as well as the New Mexico portion of the BMWRA, have not increased in recent years is a perplexing issue for wolf recovery biologists and administrators since elk, the primary prey of Mexican wolves in the BMWRA, remain plentiful. Part of the problem may lie with the prey base for Mexican wolves. For example, Rocky Mountain elk, the principal prey of Mexican wolves in the BMWRA, are considerably larger than Couses white-tailed deer which historically represented the primary prey of Mexican wolves in their historical range (Leopold, 1959; Brown, 1983). Additional impediments to the growth of the Mexican wolf population likely include human-caused wolf mortality and other types of management disruptions (Povilaitis et al., 2006).

In the western US, the uncoupling of a tri-trophic cascades following the extirpation or displacement of large predators has been found across an array of biomes (Beschta and Ripple, 2009). For temperate and boreal forest ecosystems from around the world, there are additional examples of where tri-trophic cascades have become uncoupled with the loss of a large predator or, conversely, where tri-trophic cascades continue to exist or have become re-established with the reintroduction or recovery of a large predator (Jedrzejewska and Jedrzejewski, 1998; Ripple et al., 2010). Improving our understanding of the role of large predators within terrestrial ecosystems represents a major challenge to the scientific community. Allowing large predators to persist or reoccupy former habitats so that their ecological imprint can occur may be perhaps an even larger challenge to society.

6. Conclusions

Ongoing fluctuations and trends in climate do not appear to be the cause of reduced aspen recruitment in mixed-conifer forests in east-central Arizona. Where ungulate herbivory had been excluded (i.e., the refugium site and the ungulate exclosure near Alpine), young aspen sprouts/seedlings were able to grow taller regardless of climatic patterns. Instead, our results indicate that reduced aspen recruitment since the 1990s in mixed-conifer stands not accessible to livestock was likely due to increased elk herbivory. Thus, there is a need for additional assessments of the aspen age structure in stands across Arizona, as well as elsewhere in the western US, to determine the relative importance of wild vs. domestic ungulates in causing downturns in aspen recruitment. Such information would allow land managers to make more informed decisions regarding causes and potential solutions whenever a lack of aspen recruitment is encountered. Although Mexican wolves were introduced into the BMWRA in the late 1990s, they appear to not yet have attained an ecologically effective density as we were unable to document a trophic cascade (i.e., improved aspen recruitment). Unless wolf densities increase, it is possible that the potential ecologically beneficial effects of these apex predators in the mixed-conifer forests of east-central Arizona will not be achieved.

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Trophic Downgrading of Planet Earth


Until recently, large apex consumers were ubiquitous across the globe and had been for millions of years. The loss of these animals may be humankind’s most pervasive influence on nature. Although such losses are widely viewed as an ethical and aesthetic problem, recent research reveals extensive cascading effects of their disappearance in marine, terrestrial, and freshwater ecosystems worldwide. This empirical work supports long-standing theory about the role of top-down forcing in ecosystems but also highlights the unanticipated impacts of trophic cascades on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles. These findings emphasize the urgent need for interdisciplinary research to forecast the effects of trophic downgrading on process, function, and resilience in global ecosystems.

The history of life on Earth is punctuated by several mass extinction events (2), during which global biodiversity was sharply reduced. These events were followed by novel changes in the evolution of surviving species and the structure and function of their ecosystems. Our planet is presently in the early to middle stages of a sixth mass extinction (3), which, like those before it, will separate evolutionary winners from losers. However, this event differs from those that preceded it in two fundamental ways: (i) Modern extinctions are largely being caused by a single species, Homo sapiens, and (ii) from its onset in the late Pleistocene, the sixth mass extinction has been characterized by the loss of larger-bodied animals in general and of apex consumers in particular (4, 5).

The loss of apex consumers is arguably humankind’s most pervasive influence on the natural world. This is true in part because it has occurred globally and in part because extinctions are by their very nature perpetual, whereas most other environmental impacts are potentially reversible on decadal to millennial time scales. Recent research suggests that the disappearance of these animals reverberates further than previously anticipated (6–8), with far-reaching effects on processes as diverse as the dynamics of disease; fire; carbon sequestration; invasive species; and biogeochemical exchanges among Earth’s soil, water, and atmosphere.

Here, we review contemporary findings on the consequences of removing large apex consumers from nature—a process we refer to as trophic downgrading. Specifically, we highlight the ecological theory that predicts trophic downgrading, consider why these effects have been difficult to observe, and summarize the key empirical evidence for trophic downgrading, much of which has appeared in the literature since the beginning of the 21st century. In so doing, we demonstrate the influence of predation and herbivory across global ecosystems and bring to light the far-reaching impacts of trophic downgrading on the structure and dynamics of these systems. These findings suggest that trophic downgrading acts additively and synergistically with other anthropogenic impacts on nature, such as climate and land use change, habitat loss, and pollution.

Foundations in Theory

Ecological theory has long predicted that major shifts in ecosystems can follow changes in the abundance and distribution of apex consumers (9, 10). Three key elements of that theory provide the foundation for interpreting recurrent patterns suggestive of trophic downgrading in more recent empirical work across ecosystems. First is the idea that an ecosystem may be shaped by apex consumers, which dates back more than a century since the beginning of the 21st century. In

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Alternative stable states occur when perturbations of sufficient magnitude and direction push ecosystems from one basin of attraction to another (12). Tipping points (also known as thresholds or breakpoints) around which abrupt changes in ecosystem structure and function (a.k.a. phase shifts) occur, often characterize transitions between alternative stable states. Ecosystem phase shifts can also display hysteresis, a phenomenon in which the locations of tipping points between states differ with the directionality of change (13). A third key concept, connectivity, holds that ecosystems are built around interaction webs within which every species potentially can influence many other species. Such interactions, which include both biological processes (e.g., predation, competition, and mutualism) and physicochemical processes (e.g., the nourishing or limiting influences of water, temperature, and nutrients), link species together at an array of spatial scales (from millimeters to thousands of kilometers) in a highly complex network. Taken together, these relatively simple concepts set the stage for the idea of trophic downgrading.
The loss of apex consumers reduces food chain length, thus altering the intensity of herbivory and the abundance and composition of plants in largely predictable ways (10). The transitions in ecosystems that characterize such changes are often abrupt, are sometimes difficult to reverse, and commonly lead to radically different patterns and pathways of energy and material flux and sequestration.

The Cryptic Nature of Trophic Downgrading

The omnipresence of top-down control in ecosystems is not widely appreciated because several of its key components are difficult to observe. The main reason for this is that species interactions, which are invisible under static or equilibrial conditions, must be perturbed if one is to witness and describe them. Even with such perturbations, responses to the loss or addition of a species may require years or decades to become evident because of the long generation times of some species. Adding to these difficulties is the fact that populations of large apex consumers have long been reduced or extirpated from much of the world. The irony of this latter situation is that we often cannot unequivocally see the effects of large apex consumers until after they have been lost from an ecosystem, at which point the capacity to restore top-down control has also been lost. Another difficulty is that many of the processes associated with trophic downgrading occur on scales of tens to thousands of square kilometers, whereas most empirical studies of species interactions have been done on small or weakly motile species.

**Fig. 1.** Landscape-level effects of trophic cascades from five selected freshwater and marine ecosystems. (A) Shallow seafloor community at Amchitka Island (Aleutian archipelago) before (1971; photo credit: P.K. Dayton) and after (2009) the collapse of sea otter populations. Sea otters enhance kelp abundance (right) by limiting herbivorous sea urchins (left) (20). (B) A plot in the rocky intertidal zone of central California before (September 2001, right) and after (August 2003, left) seastar (*Pisaster ochraceus*) exclusion. *Pisaster* increases species diversity by preventing competitive dominance of mussels. [Photo credits: D. Hart] (C) Long Lake (Michigan) with largemouth bass present (right) and experimentally removed (left). Bass indirectly reduce phytoplankton (thereby increasing water clarity) by limiting smaller zooplanktivorous fishes, thus causing zooplankton to increase and phytoplankton to decline (26). (D) Coral reef ecosystems of uninhabited Jarvis Island (right, unfished) and neighboring Kiritimati Island (left, with an active reef fishery). Fishing alters the patterns of predation and herbivory, leading to shifted benthic dynamics, with the competitive advantage of reef-building corals and coralline algae diminished in concert with removal of large fish (66). (E) Pools in Brier Creek, a prairie margin stream in south-central Oklahoma with (right) and lacking (left) largemouth and spotted bass. The predatory bass extirpate herbivorous minnows, promoting the growth of benthic algae (67).
with short generation times that could be manipulated at small spatial scales. Although some influences of apex consumers (e.g., trophic cascades) seen in experiments scale up to systems with larger or more mobile species (14), others are harder to discern at small spatial and temporal scales (e.g., many of the indirect effects of trophic cascades on ecosystem processes described below). As a result, we have an incomplete and distorted picture of the influences of apex consumers across much of the natural world.

The Widespread Occurrence of Trophic Cascades

Despite these challenges, trophic cascades have now been documented in all of the world’s major biomes—from the poles to the tropics and in terrestrial, freshwater, and marine systems (table S1). Top-down forcing and trophic cascades often have striking effects on the abundance and species composition of autotrophs, leading to regime shifts and alternative states of ecosystems (15). When the impacts of apex consumers are reduced or removed or when systems are examined over sufficiently large scales of space and time, their influences are often obvious (Figs. 1 and 2). Although purposeful manipulations have produced the most statistically robust evidence, “natural experiments” (i.e., perturbations caused by population declines, extinctions, reintroductions, invasions, and various forms of natural resource management) corroborate the essential role of top-down interactions in structuring ecosystems involving species such as killer whales (Orcinus orca) (16), lions (Panthera leo) (17), wolves (Canis lupus) and cougars (Puma concolor) (18), the great sharks (19), sea otters (Enhydra lutris) (20), diverse mesopredators (21), and megaherbivores (22). Although the extent and quality of evidence differs among species and systems, top-down effects over spatial scales that are amenable to experimentation have proven robust to alternative explanations (23).

The impacts of trophic cascades on communities are far-reaching, yet the strength of these impacts will likely differ among species and ecosystems. For example, empirical research in Serengeti, Tanzania, showed that the presence or absence of apex predators had little short-term effect on resident megaherbivores [elephant (Loxodonta africana), hippopotamus (Hippopotamus amphibius), and rhinoceros (Diceros bicornis)] because these herbivores were virtually invulnerable to predation (24). Conversely, predation accounted for nearly all mortality in smaller herbivores [oribi (Ourebia ourebi), Thompson’s gazelle (Eudorcas thomsonii), and impala (Aepyceros melampus)], and these species showed dramatic increases in abundance and distribution after the local extinction of predators. Thus, top-down forcing in this system is more apparent in some species than others, at least when it is studied on relatively short time scales, although the aggregate ecological impact of apex consumers here, as elsewhere, remains great (24).

Other than the inclusion of top-down forcing, there is no rule of thumb on the interplay between apex consumers and autotrophs in intact ecosystems. This is largely a consequence of natural variation in food chain length (10). In some cases, the influence of apex consumers is to suppress herbivory and to increase the abundance and production of autotrophs. The sea otter/kelp forest system in the North Pacific Ocean (20) (Fig. 1A) and the wolf/ungulate/forest system in temperate and boreal North America (25) (Fig. 2C) function in this manner. Apex consumers in other systems reduce the abundance and production of autotrophs. The largemouth bass/planktivore/zooplankton/phytoplankton system in U.S. Midwestern lakes (26) (Fig. 1C) functions in such a manner.

Effects on Ecosystem Processes

Apart from small oceanic islands, all regions of our planet supported a megafauna before the
rise of Homo sapiens (4, 27). The apex consumers influence their associated ecosystems through top-down forcing and trophic cascades, which in turn often lead to myriad effects on other species and ecosystem processes (Figs. 3 and 4). Here, we describe some of the known or suspected indirect effects of losing these apex consumers.

**Herbivory and wildfire.** Wildfires burn up to 500 million ha of the global landscape annually, consuming an estimated 8700 Tg of dry plant biomass, releasing roughly 4000 Tg of carbon to the atmosphere, and costing billions of dollars in fire suppression and property loss (28). The frequency and extent of wildfire have been largely attributed to a warming and drying climate and fuel accumulation from protective wildland management practices. However, the global distribution and biomass of vegetation are poorly predicted by temperature and rainfall (29), and recent analyses suggest that interdependencies among predation (including disease), herbivory, plant communities, and fire may better explain the dynamics of vegetation. Such interdependencies are well illustrated in East Africa, where the introduction of rinderpest in the late 1800s decimated many native ungulate populations, including wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Reductions of these large herbivores caused an increase in plant biomass, which fueled wildfires during the dry season. Rinderpest was eliminated from East Africa in the 1960s through an extensive vaccination and control program. Because of this, wildebeest and buffalo populations had recovered to what was thought to be historically high levels by the early 1980s. The resulting increase in herbivory drove these systems from shrublands to grasslands, thus decreasing the fuel loads and reducing the frequency and intensity of wildfires (30) (Fig. 4). Other examples of the interplay between megafauna and wildfire are the increase in fire frequency after the late Pleistocene/early Holocene decline of megaherbivores in Australia (31) and the northeastern United States (32).

**Disease.** The apparent rise of infectious diseases across much of the globe is commonly attributed to climate change, eutrophication, and habitat deterioration. Although these factors are undoubtedly important, links also exist between disease and predation (33). For example, the reduction of lions and leopards from parts of sub-Saharan Africa has led to population outbreaks and changes in behavior of olive baboons (*Papio anubis*). The baboons, in turn, have been drawn into increasing contact with people because of their attraction to crops and other human food resources. The increased baboon densities and their expanded interface with human populations have led to higher rates of intestinal parasites in baboons and the humans who live in close proximity to them (17). A similar result, involving different species and processes, occurred in India, where the decline of vultures also led to increased health risks from rabies and anthrax (34). Further examples of the interplay between predation and disease exist for aquatic systems. The establishment of no-take marine reserves in the Channel Islands of southern California led to increases in the size and abundance of spiny lobsters (*Panulirus interruptus*) and declines in population densities of sea urchins, which are preyed on by the lobsters. The reduced urchin densities thwarted the spread of disease among individual sea urchins, which led to a lowered frequency of epidemics of sea urchin wasting disease within the reserves (35) (Fig. 4). In freshwater systems, the localized rise and fall of human malaria is associated with the impacts of predatory fishes on planktivores, which are in turn important consumers of mosquito larvae (36).

**Physical and chemical influences.** The influences of industrialization and agriculture on Earth’s physical environments and geochemical processes are widely known. However, the contributing effects of changes in the distribution and abundance of apex consumers to the physical and chemical nature of our biosphere—the atmosphere, soils, and water—are understudied and largely unappreciated. Even so, important connections between these entities have become apparent in the few instances where people have looked.

The atmosphere. Linkages between apex consumers and the atmosphere are known or suspected in freshwater, marine, and terrestrial ecosystems. Trophic cascades associated with the presence or absence of apex predatory fishes in lakes can affect phytoplankton density, in turn affecting the rate of primary production, the uptake rate of CO2, and the direction of carbon flux between lakes and the atmosphere. Where apex predatory fishes are present in sufficient numbers, they reduce the abundance of smaller planktivorous minnows, thus releasing zooplankton from limitation by planktivores and increasing consumption rates of phytoplankton by zooplankton (Fig. 1B). This trophic cascade causes lakes to switch from net sinks for atmospheric CO2 when predatory fishes are absent to net sources of atmospheric CO2 when
these fishes are present (37) (Fig. 4). Similar processes occur in the oceans and on land. Industrial whaling during the 20th century transferred some 105 million tons of carbon from great whales to the atmosphere (38), and even today whale feces return various limiting nutrients from the aphotic to photic zones, thereby directly enhancing primary productivity (39, 40) and its influence on carbon flux and sequestration. From land, the demise of Pleistocene megaherbivores may have contributed to or even largely accounted for the reduced atmospheric methane concentration and the resulting abrupt 9°C temperature decline that defines the Younger-Dryas period (41).

Soils. Leaf-eating herbivores profoundly influence soils and their associated biota through altered plant allocation patterns of carbon and nutrients to the roots and rhizosphere, changing the quantity and quality of litter that plants return to the soil. Ungulate herbivores further influence soils through trampling, compaction, and the return of dung and urine. The collective influence of these processes is often an effect on species composition of the vegetation and altered successional pathways (42, 43). Predators of these herbivores and the trophic cascades they set in motion reverse these belowground effects (44). For example, the reintroduction of wolves to Yellowstone National Park has reduced the positive indirect effects of ungulates on soil nitrogen mineralization and potentially the nitrogen supply for plant growth (45). In contrast, introduced rats (46) and arctic foxes (Fig. 4) (47) have reduced soil fertility and plant nutrition on high-latitude islands by disrupting seabirds and their sea-to-land nutrient subsidies, with striking effects on plant community composition.

Water. Large consumers influence the composition and quality of both fresh and salt water through a variety of mechanisms. For example, the collapse of large demersal fish led to a 20% reduction in silica supply to pelagic diatoms in the Baltic Sea (48). In rivers, mass spawning by salmon suspends sediments, thus increasing downstream sediment transport (49) (Fig. 4). This flushing of stream bed sediments by the spawning fish and the increased circulation of fresh water through the gravel interstices of the stream bed have positive feedbacks on salmon populations by increasing oxygen for incubating eggs and fry and decreasing the frequency with which bed-mobilizing floods kill salmon in these early life stages (50). Similarly, in terrestrial systems wolves protect riparian trees and shrubs from overbrowsing by large ungulates, in turn shading and cooling the adjacent streams, reducing stream bank erosion, and providing cover for fish and other aquatic life (51, 52).

Invasive species. A common feature of many successful invasive species is that they have left behind their natural predators and freed themselves from top-down control (53). Likewise, the loss of native predators leaves ecosystems more vulnerable to invasion by nonnative species (54). There are many examples of hypervulnerable invasions due to the absence or loss of top-down control in aquatic and terrestrial systems. The experimental exclusion of native birds from small areas in Hawaii resulted in an up to 80-fold increase in nonnative spider density (55) (Fig. 4). Other examples include the spread of the invasive brown tree snake (Boiga irregularis) on the otherwise vertebrate predator–free island of Guam (56), the facilitating influence of reduced fish predation on the invasion of zebra mussels (Dreissena polymorpha) in the Mississippi River (57), and reduced abundance and spread of the introduced European green crab (Carcinus maenas) by predation from native blue crabs (Callinectes sapidus) in eastern North America (58).

Biodiversity. Earth’s biodiversity (defined here as both species diversity and the associated functional diversity) is increasingly confined to formal protected areas. Although the establishment of protected areas mitigates certain threats to biodiversity—habitat loss and fragmentation, over-exploitation, and the spread of invasive species—when large apex consumers are missing, protected areas often fail to function as intended. The link between apex consumers and species diversity can occur via a number of interaction pathways, for example, by blocking competitive exclusion (predatory seastars in the rocky intertidal (59)), mesopredator release (coyotes (Canis latrans) maintaining small vertebrate species in chaparral habitats (Fig. 4) (60)), and indirect habitat effects [e.g., the loss of small vertebrates from overgrazed and degraded riparian habitats after the

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**Fig. 4.** Examples of the indirect effects of apex consumers and top-down forcing on diverse ecosystem processes, including wildfires (30); disease (35); composition of atmosphere (37), soil (47), and fresh water (49); invadability by exotic species (55); and species diversity (60). Interaction web linkages by which these processes are connected to apex consumers are shown in the center. Magnitude of effect is shown in graphs on right. Blue bars are data from systems containing the apex consumer; brown bars are data from systems lacking the apex consumer. Data replotted from original sources (cited above), except raw data on native bird diversity in chaparral habitats provided by K. Crooks.
loss of cougars (61) or wolves and grizzly bears (Ursus arctos) (62) from temperate and boreal forests of western North America.

Tree recruitment failure and the eventual transformation of forests to heaths and grasslands because of increased ungulate herbivory illustrates the influence of large apex consumers on functional diversity. This process is most clearly seen by contrasting areas where apex consumers have been absent for differing lengths of time. In North America, where wolves and other large carnivores were not extirpated until the early 20th century, the effects of their loss on plants is evident only as the recruitment failure of the younger trees. Because for controlling predators to enhance fish, wild game, and livestock, resource managers commonly base their actions on the assumption that physical processes are the ultimate driver of ecological change. Bottom-up forces are ubiquitous and fundamental, and they are necessary to account for the responses of ecosystems to perturbations, but they are not sufficient. Top-down forcing must be included in conceptual overviews if there is to be any real hope of understanding and managing the workings of nature.

References and Notes

A Paradigm Shift in Ecology

The accumulation of theoretical and empirical evidence calls for an altered perspective on top-down forcing in ecosystem dynamics. Many practicing ecologists still view large animals in genet, and apex consumers in particular, as ecological passengers riding atop the trophic pyramid but having little impact on the structure below. The influences of these animals, although acknowledged in particular cases, are generally regarded as anomalous, occurring in some systems but not in many others. This perception has generally led to the requirement of independent study and confirmation for each species and system before the null hypothesis that they serve no important ecological role can be rejected. We argue that the burden of proof be shifted to show, for any ecosystem, that consumers do (or did) not exert strong cascading effects.

Conclusions

Unanticipated changes in the distribution and abundance of key species have often been attributed to specified consequences in the “complexy of nature.” We propose that many of the ecological surprises that have confronted society over past centuries—pandemics, population collapses of species we value and eruptions of those we do not, major shifts in ecosystem states, and losses of diverse ecosystem services—were caused or facilitated by altered top-down forcing regimes associated with the loss of native apex consumers or the introduction of exotics. Our repeated failure to predict and moderate these events results not only from the complexity of nature but from fundamental misunderstandings of their root causes. Except for controlling predators to enhance fish, wild game, and livestock, resource managers commonly base their actions on the assumption that physical processes are the ultimate driver of ecological change. Bottom-up forces are ubiquitous and fundamental, and they are necessary to account for the responses of ecosystems to perturbations, but they are not sufficient. Top-down forcing must be included in conceptual overviews if there is to be any real hope of understanding and managing the workings of nature.

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ABSTRACT: Effective measures for controlling chronic wasting disease (CWD), a contagious prion disease of cervids, remain elusive. We review theoretic relationships between predation and host-parasite dynamics and describe a mathematical model to evaluate the potential influence of random removal through harvest or culling and selective predation by wolves (Canis lupus) upon CWD dynamics in deer (Odocoileus spp.) populations. Imposing nonselective mortality representing a 15% annual harvest or cull 51 yr after CWD introduction lowered both deer population size and steady state CWD. Selective (4×) mortality at the same 15% predation rate caused a more modest reduction in deer population size accompanied by a relatively rapid decline in CWD prevalence and elimination of the disease from a closed population. The impacts of selective predation on epidemic dynamics were sensitive to assumptions on parameter estimates; however, within expected ranges, the results of selective predation were consistent and robust. We suggest that as CWD distribution and wolf range overlap in the future, wolf predation may suppress disease emergence or limit prevalence.

Key words: Canis lupus, chronic wasting disease, deer, host-parasite, Odocoileus spp., predator-prey, selective predation, wolf.

INTRODUCTION

Disease emergence and reemergence threaten the abundance and viability of wildlife species worldwide (Daszak et al., 2000). Although a variety of factors appear to be contributing to the recent surges in diseases impacting natural populations, ecosystems altered by human activities seem particularly vulnerable to such effects (Harvell et al., 1999; Daszak et al., 2000, 2001; Kutz et al., 2005; Johnson et al., 2007; Pedersen et al., 2007). Ecologic imbalances can diminish the resilience of host species to natural fluctuations in pathogens and the host’s capacity to resist or recover from pathogen introductions. Such impacts on resiliency can be observed with alterations to host-parasite relationships resulting in changes in host survival and contact rates among susceptible and infected individuals (Harvell et al., 1999; Daszak et al., 2001; Kutz et al., 2005; Johnson et al., 2007; Pedersen et al., 2007).

Changes in predation rates or predator-prey dynamics are among the factors that may affect patterns of disease emergence, reemergence, and persistence (Choo et al., 2003; Packer et al., 2003; Holt and Roy, 2007). The potential effects of predation on epidemic dynamics vary depending on both the nature of predation occurring upon hosts and attributes of the host-parasite relationship. Nonselective predation could dampen epidemic dynamics by reducing host densities and contact rates or by lowering the total number of infected individuals in a host population (Heesterbeek and Roberts, 1995; Barlow, 1996; Packer et al., 2003). Similarly, selective predation on infected individuals could eliminate pathogens or prevent their establishment under some circumstances (Heesterbeek and Roberts, 1995; Gross and Miller, 2001; Packer et al., 2003).
Alternatively, both nonselective and selective predation might facilitate pathogen emergence and persistence in cases where resistant individuals become less abundant (Choisy and Rohani, 2006; Holt and Roy, 2007) and in cases where infected individuals are avoided by predators (Packer et al., 2003). It follows that ecosystems altered by removal of natural predators by humans may respond differently to endemic or novel pathogens than intact systems.

In light of the potential influence of predation on host-parasite dynamics, the role of predators should be considered in devising strategies for control of emerging or reemerging pathogens in natural populations. We review the theoretic relationships between predation and host-parasite dynamics, using the term parasite broadly to describe any infectious agent capable of infecting a host, utilizing host resources, and spreading to new hosts (Altizer et al., 2003). We then describe a simple mathematical model developed to evaluate how dynamics of prion disease in deer (Odocoileus spp.) populations may respond to nonrandom removal resulting from selective predation by wolves (Canis lupus) and compare this outcome with effects of random removal through harvest or culling.

**Predation and host-parasite dynamics**

*Nonselective predation:* The interplay among host regulation, immune response, and the pattern of predator selectivity determines whether predation reduces or increases the prevalence of disease in a population (Holt and Roy, 2007). Under many scenarios, increasing mortality rates in diseased populations can retard disease transmission and reduce disease prevalence (Barlow, 1996; Lafferty and Holt, 2003; Packer et al., 2003; Ostfeld and Holt, 2004). Increasing mortality slows transmission via two mechanisms. First, it reduces the average lifetime of infected individuals. Reduced lifespan, in turn, can truncate the time interval when animals are infectious, thereby reducing the number of infections produced per infected individual. Second, the effect of reduced intervals of infectivity is amplified by reductions in population density that occur as mortality increases; such reductions cause declines in the number of contacts between infected and susceptible individuals. Both of these mechanisms slow rates of transmission of disease. If these mechanisms cause the number of new infections produced per infected individual to fall below one, then the disease will be eliminated from the population.

*Selective predation:* Any elevation in mortality rate has the potential to cause the foregoing effects. Reductions in transmission rates and disease prevalence can be particularly large if mortality rates are disproportionately higher in the infected portion of the population than in the susceptible portion (Heesterbeek and Roberts, 1995). This explains why diseases that cause rapid death fail to persist. However, other, nondisease, agents of selective mortality can exert the same beneficial effect. For example, if predators prey selectively on diseased individuals, it is reasonable to expect that they might reduce disease prevalence much more rapidly than would occur if mortality were nonselective.

Evidence that predators have a greater selectivity for diseased prey has been widely observed. Voříšek et al. (1998) found parasitized voles in buzzards’ diets in a greater proportion than they occurred in the population. Birds with high blood parasite loads (Moller and Nielsen, 2007) and birds with weakened immune systems (Moller and Erritzoe, 2000) were preyed upon at higher rates than uncompromised birds. Murray et al. (1997) reported increased predation on snowshoe hares (Lepus americanus) with heavy burdens of the sublethal nematode *Obeliscoides cuniculi* during periods of limited food supplies.

It is logical to assume that predators’ high success with diseased prey may be due to poorer body condition of the prey and consequently prey’s slower avoidance behavior, decreased awareness, or re-
duced stamina. Studies have suggested that predators may also use visual pattern, scent, or behavioral cues to select compromised prey. Hudson et al. (1992) suggested that heavily parasitized female red grouse (Lagopus lagopus scoticus) emitted more scent, and were, as a result, more easily detected by mammalian predators. Larks (Calandrella rufescens) that were infected with poxvirus had shorter, lower-pitched distress calls than uninfected birds, indicating a behavioral change that could affect predation rates (Laiolo et al., 2007). Lafferty and Morris (1996) reported that parasitized killifish (Fundulus parvipinnis) exhibited more conspicuous behavior than uninfected killifish, and were also preyed upon more heavily by birds. Red-legged frog (Rana aurora) tadpoles also exhibited modified behavior when infected with yeast (Candida humicola), resulting in changes in thermoregulatory behavior, compromised predator avoidance behavior, and increases in being preyed upon (Lefcort and Blaustein, 1995). Examples of increased vulnerability to selective predation in large mammals are less numerous; however, diseased moose (Alces alces; Joly and Messier, 2004a) and bison (Bison bison; Joly and Messier, 2004b) appeared to be more susceptible to predation by wolves than apparently healthy animals. White-tailed deer (Odocoileus virginianus) killed by wolves may appear normal to human inspection, but subtle alterations may be present as demonstrated by the correlation of fawn and subadult survival to maternal and grand-maternal nutrition (Mech et al., 1991). Further, Krumm et al. (2009) recently reported that mountain lions (Puma concolor) prey selectively on prion-infected mule deer (Odocoileus hemionus) in Colorado, USA.

Wolves, selective predation, and prion disease dynamics

Chronic wasting disease (CWD; Williams and Young, 1980) is a contagious prion disease of at least four North American cervid species (Spraker et al., 1997; Baeten et al., 2007). The origins and evolutionary history of CWD are unclear, but uncontrolled epidemics have the potential to depress deer populations (Williams and Young, 1992; Miller et al., 2000, 2006; Gross and Miller, 2001; Williams et al., 2002) and to impact ecosystems dominated by these species (Hobbs, 1996). Epidemics of CWD are sustained naturally by horizontal transmission (Miller and Williams, 2003; Miller et al., 2006), with both infected animals and contaminated environments serving as sources of infection (Miller and Williams, 2003; Miller et al., 2004, 2006; Mathiason et al., 2006, 2009; Tamgüney et al., 2009). Under some conditions, the CWD agent persists in the environment for years in residues from excrement and infected carcasses (Miller et al., 2004). Mechanisms for both direct (animal-animal) and indirect (animal-environment-animal) prion transmission have been demonstrated empirically (Miller et al., 2004; Mathiason et al., 2006, 2009; Tamgüney et al., 2009), but models incorporating indirect transmission best represent epidemic dynamics in captive deer (Miller et al., 2006).

Effective measures for controlling CWD remain elusive. In the absence of vaccines or therapies, strategies undertaken to combat CWD have focused on depressing the abundance of host species either locally or regionally in an attempt to disrupt prion transmission (Williams et al., 2002; Grear et al., 2006; Conner et al., 2007). Thus far, control strategies relying on hunting or culling by humans to lower deer numbers and subsequently CWD prevalence have not yielded demonstrable effects (Conner et al., 2007). However, these results are not surprising given the limited duration of such management actions and because theory suggests that randomly removing individuals from an infected population should have less effect on epidemic dynamics than selectively removing infected individuals (Heesterbeek and Roberts, 1995; Gross and Miller,
2001). The protracted course of CWD in deer (Williams and Young, 1980, 1992; Fox et al., 2006) and occurrence of agent shedding well before the hallmark signs of emaciation and behavioral changes are discernable to human observers (Mathiason et al., 2009; Tamgïneý et al., 2009) suggest that selectively removing only obviously ill deer from a population would not be an effective control strategy (Gross and Miller, 2001). If infected deer were detectable earlier in the disease course, however, selective removal might be more effective than random removal in controlling epidemics (Gross and Miller, 2001; Wolfe et al., 2004).

Increased vulnerability of CWD-infected mule deer to vehicle collisions (Krumm et al., 2005) suggests that lowered vigilance also might make them more vulnerable to large predators. It follows that if natural predators were able to develop a search image for subtle behavioral changes of CWD infection in deer, then fostering predation upon CWD-infected deer populations might offer a viable adjunct or alternative to other control measures. Although mountain lions do appear to preferentially prey on mule deer infected with CWD (Krumm et al., 2009), epidemics persist in mule deer herds in the presence of mountain lion predation (Miller et al., 2008; Krumm et al., 2009). Based on the subtlety of the behavioral changes early in the course of CWD infection, we would expect coursing predators like wolves to show even greater potential selective capability than ambush predators like mountain lions; however, wolves were extirpated and packs are presently absent from the areas in North America where CWD is endemic in deer, so field data are not available for comparison. Consequently, to assess this possibility we developed and explored the behavior of models representing the effects of selective predation by wolves and compared these with nonselective predation, such as through harvest or culling, on CWD dynamics in deer.

MATERIALS AND METHODS

Model structure

We explored the potential impacts of predation on dynamics of deer populations using a simple model of interactions among infected animals, susceptible animals, and infectious residue in the environment in a closed population. We derived the model used here (Appendix A) from the indirect transmission model of Miller et al. (2006), which was the best approximating model of two CWD epidemics in a captive population of mule deer. Because of the similarities in CWD epidemiology between mule deer and whitetailed deer (Miller and Wild, 2004), here we generalize inferences to “deer.” We modified the best approximating model found by Miller et al. (2006) to portray disease dynamics in free-ranging populations as follows:

1) We assumed that transmission rates were approximately 25 times lower in natural populations than in captive ones. This assumption was based on the elevated densities of deer in captive populations (Miller et al., 2006). Adjusting transmission rates for differences in density was plausible; however, the magnitude of the adjustment for transmission was uncertain. Therefore we targeted this adjustment as one of the variables to be explored in simulation studies through the use of a scaling coefficient.

2) Per-capita birth rates were assumed to decline linearly with increasing population density.

3) We added a term representing predation. This term could be adjusted to reflect selective predation, where predators favored infected animals over susceptible ones, or nonselective predation, as would occur with hunting or culling, where removals were assumed to be random. In the case of selective predation on diseased animals, we also included a term to represent the extent to which predation mortality was compensatory with CWD mortality.

We sought to use the simplest model possible to achieve the greatest generality of results (Levins, 1966) and to reduce the number of parameters that had to be estimated. We avoided the use of an age-structured model, which would have required estimating unknown transmission rates for several age classes. Dynamics of the prey population was not coupled to the dynamics of predators and predation intensity did not change with prey abundance. In the interest of parsimony, we
used a constant relative rate for predation. Preliminary modeling included a type II functional response and did not yield results that were qualitatively different than those presented here. More importantly, by holding predation constant, we could be sure that observed dynamics resulted from the interplay between CWD and deer, rather than between deer and wolves (analogous to choosing to hold one factor constant in a designed experiment). Although our model is simple, we believe it represents the essential interactions in the deer-CWD system. As knowledge of parameters improves, more detailed models will be justified.

Model experiments

We exercised the model to examine how selective and nonselective predation may influence CWD prevalence. We made three model runs using our most plausible estimates of model parameters to examine differences among trajectories of diseased populations in the presence and absence of predation. We first conducted a reference simulation introducing a single infected animal into a population of 1,000 deer at time t=0 and allowed the model to equilibrate over 100 yr. In two experimental simulations, we introduced predation in year 51. In one of these simulations, predation was assumed to occur randomly; in the other, predators were assumed to favor infected individuals. In the case of selective predation, the modeled 15% predation rate was equivalent to about seven wolves removing 16 deer/wolf/yr (Mech and Peterson, 2003).

Although most parameters in the model were derived from Miller et al. (2006) or from reasonable assumptions on deer biology (See Table 1 in Appendix A for all parameter values), there was substantial uncertainty in our best guesses of the value of several parameters controlling the effects of the disease and of predation. Notable among these were the extent of predator selectivity for CWD-infected animals, the extent of compensation between CWD and predator mortality, and the adjustment for the rate of transmission in free-ranging populations. We explored consequences of these uncertainties by conducting model experiments varying these parameters singly and in pairs to examine the sensitivity of model predictions to uncertainty in their estimates.

RESULTS

In the absence of CWD and predation, the modeled deer population stabilized at an ecologic carrying capacity of about 1,000 animals. Adding a single infected deer in year 1 produced oscillatory dynamics typical of epidemics. With disease and no predation, the equilibrium density was 736 deer and disease prevalence was 29%. Thus, the disease reduced animal abundance in our model by almost a third (Fig. 1A, B). Our model resembles classic susceptible-infected (SI) models with an additional mortality source from predation and an environmental reservoir of infection. Models of this general type are known to have conditions that allow steady states (Miller et al., 2006), and the model used here shows that equilibrium.

Simulated selective and nonselective predation affected epidemic dynamics to different degrees. Imposing nonselective mortality representing a 15% annual harvest or cull in year 51 lowered both deer population size and steady state CWD prevalence; however, under the assumptions of this simulation, the disease was able to persist in the population (Fig. 1C, D). Selective (4X) mortality at the same 15% predation rate beginning in year 51 caused a more modest reduction in deer population size accompanied by a relatively rapid decline in CWD prevalence and elimination of the disease from this closed population (Fig. 1E, F). The impacts of selective predation on epidemic dynamics were sensitive to assumptions on vulnerability of infected animals and compensation between predation and mortality due to CWD, as well as overall predation and CWD transmission rates (Fig. 2). Doubling the vulnerability of infected animals to selective predation accelerated the rate of decline in prevalence (Fig. 2A). Increasing the proportion of compensatory deaths among infected deer dampened the predicted decline in prevalence (Fig. 2B); when compensation exceeded ca. 60%, selective predation had less of a predicted effect on epidemic dynamics than nonselective predation. The overall predation rate also affected the rate and magnitude of decline in steady state prevalence (Fig. 2C). Epidemic dynamics also were sensitive to assumptions on values for the scaling of transmission rate (Fig. 2D), with asymptotic prevalence varying by a
factor of more than 10 when changing the scaling coefficient from 20 to 40.

Our models predicted that interactions between the relative selectivity of predation and the degree to which mortality in infected deer is compensatory also will influence epidemic dynamics in emergent CWD foci (Fig. 3). Predicted CWD prevalence 20 yr after introducing a single infected deer into simulated populations subjected to 15% annual predation under different combinations of selectivity and compensation varied from \(~0\) to \(8\%\). In general, simulations suggested that even modest levels of selectivity might be expected to greatly diminish the persistence of CWD in a susceptible deer population provided that such pressure was largely additive; however, models predicted that sufficiently strong selection could still dampen the dynamics of emergent CWD epidemics even in cases where mortality among infected deer was largely compensatory.

**DISCUSSION**

Results from these simulations suggest that predation could markedly decrease prevalence of CWD under certain condi-
tions. Nonselective predation, as might occur with hunting or culling by humans, may decrease disease prevalence over time but the disease was not eliminated under modeled conditions (Fig. 1C, D). Alternatively, selective predation by wolves at the same rate would result in a more precipitous drop in CWD prevalence that would culminate in disease elimination in a closed system (Fig. 1E, F). Selective predation does not allow a larger population of susceptible animals to persist relative to the nonselective case because wolves are assumed to consume

**Figure 2.** Results of model experiments to examine sensitivity of variation in uncertain model parameters. Open circles show results from simulations with no predation, diamonds show nonselective predation at a rate of 0.15. A. Effect of variation in prey vulnerability to selective predation (v=2, solid line; 4, dashed line; 8, dotted line). Increasing values of v indicate greater selection for infected over susceptible animals. In all cases, compensation was held constant at 0.3 and predation rate at 0.15. B. Effect of variation in the level of compensation between predation and CWD mortality (c=0.1, solid line; 0.3, dashed line; 0.6, dotted line). Increasing values of c indicate greater compensation between predation and CWD. In all cases, selectivity was held constant at four and the predation rate at 0.15. C. Effect of variation in predation rate (δ; solid line, 0.10; dashed line, 0.30; dotted line, 0.50). In all cases, vulnerability to selective predation was held constant at 4 and compensation at 0.3. D. Effect of variation in the scaling coefficient for the transmission rate (solid line, 20; dashed line, 30; dotted line, 40). The scaling coefficient reduces the transmission rate to account for differences between captive and free-ranging deer. A scaling coefficient of 20 indicates that transmission is 20 time more rapid in captivity than in the wild. For other parameter values, see Table 1 in Appendix A.
more susceptible animals as infected ones become rare. Although the time required to achieve results depends in a fundamental way on assumptions about prey vulnerability to selective predation and the nature of compensation among different sources of mortality, as well as parameters regulating disease transmission, it appears that prevalence could be halved within a decade and eliminated within the century through sustained predation by a pack of wolves that removed 15% of deer per year in a closed population.

Although uncertainty in parameter estimates limits our confidence in predicting the precise timeframe required for control or elimination of disease, these time estimates provide a basis for comparison of approaches. What is most clear is a consistent and robust trend toward decreasing CWD prevalence in populations subject to predation, particularly selective predation, over a range of parameter estimates (Fig. 2). A similar decreasing trend would be predicted in a population subject to predation where CWD was repeatedly introduced at low levels (i.e., an open population); however, the slope of decline would be variable and elimination might never be achieved because high rates of disease reintroduction may offset selective predation of CWD-positive individuals. Although they are not the most likely scenarios, other combinations of parameters, in particular high excretion rates leading to increased levels of transmission, also may result in an inability to eliminate the disease within a reasonable period of time.

Simulation results suggested that selective predation could also dampen or eliminate the emergence of CWD in new locations (Fig. 3), adding support to speculation that the absence of large predators presents an amplification risk factor for establishment of CWD (Samuel et al., 2003). Our prediction may prove testable in the future as geographic distribution of CWD expands to areas such as the Greater Yellowstone Ecosystem and northern Wisconsin, USA, and Prince Albert National Park, Canada, where wolves are present but adjacent areas lack wolves. The simulated influences of large predators on the outcomes of CWD epizootics also may lend insight into circumstances surrounding the original emergence of CWD in Colorado, where wolves have been absent since 1943 and where mountain lion populations were suppressed by bounty hunting at the time of likely CWD emergence in the mid-1900s (Barrows and Holmes, 1990; Miller et al., 2000). The origins of CWD are unknown but may have been a result of spillover of scrapie from domestic sheep or may represent a spontaneous, naturally occurring spongiform encephalopathy of cervids (Williams and Young, 1992; Spraker et al., 1997). Regardless, our simulations suggest that had selective predation by wolves been present during that period, CWD may never have been established or detected. In combination with influences of human-assisted movement of infected cervids (Williams et al., 2002) and land use
alterations (Farnsworth et al., 2005), the absence of large predators, particularly wolves, over much of their native range in the United States (Laliberte and Ripple, 2004) has likely played a significant role in the current unnatural distribution and prevalence of this disease.

The decrease in CWD prevalence observed in simulations with selective predation is most likely a result of removing infectious individuals earlier in the disease course. Chronic wasting disease exhibits a prolonged disease course of about 18–36 mo (Williams and Miller, 2002). Transmission models (Miller et al., 2006) reveal little support for a disease latency period and instead support early onset of prion shedding, potentially from peripheral lymphoid tissue. Accumulation of abnormal prion protein (PrP<sup>cwd</sup>) in deer has been observed in alimentary tract–associated lymphoid tissues as early as 42 days following experimental oral inoculation (Sigurdson et al., 1999) and in tonsils as much as 20 mo prior to death from naturally occurring CWD (Wild et al., 2002). Moreover, orally inoculated deer shed infectious prions in saliva and feces 6–11 mo or more before the onset of clinical signs (Mathiason et al., 2009; Tamgüney et al., 2009). Therefore, early removal of infected individuals should markedly truncate CWD shedding and resultant opportunities for disease transmission.

The prolonged clinical course and type of clinical abnormalities associated with CWD make it the prototypic disease for selection by predators. Chronic wasting disease produces subtle changes in behavior and body condition that progress over weeks or months to overt signs of end-stage disease typified by loss of attentiveness or response to external stimuli, emaciation, and weakness (Williams and Young, 1980, 1992; Wild et al., 2002). Loss of attentiveness and cognitive function due to the neurodegenerative process likely account for the marked increase in risk for vehicle collision of CWD infected mule deer compared to hunter-harvested deer (Krumm et al., 2005). It follows that infected deer also would be less attentive to predators, and in later stages, that emaciation and weakness would decrease both their fight and flight response capabilities (Krumm et al., 2005, 2009; Miller et al., 2008); a nearly fourfold greater relative risk of infected mule deer succumbing to mountain lion predation (Miller et al., 2008) supports this notion. Furthermore, predators—particularly coursing predators such as wolves—focus on animals vulnerable due to odd behavior or compromised body condition (Temple, 1987; Mech et al., 1991). Field observations also suggest that predators can select CWD-infected deer: mule deer killed by mountain lions were much more likely (odds ratios ≥3.2) to be infected with CWD than same-sex deer killed in the vicinity by hunters (Krumm et al., 2009). Based on the prolonged course of CWD, the ability of wolves to detect vulnerable prey, and field observations of mountain lion predation patterns in a system where CWD occurs naturally, we believe that selective predation modeled at a rate four times higher than that of healthy deer is a reasonable, if not conservative, estimate.

Overall, our modeling results also are likely a conservative portrayal of the beneficial impacts that selective predation could have on damping prion epidemic dynamics in deer. The model we developed did not include carcasses of infected deer as a source of infectivity because necessary parameter estimates were not available (Miller et al., 2006). However, carcasses of CWD-infected deer would be an added source of environmental infectivity in natural systems (Miller et al., 2004), and thus their consumption by wolves or other carnivores either via selective predation or scavenging would be expected to reduce the contribution of carcass material to the overall pool of environmental infectivity through local dispersal and dilution (Krumm et al., 2009). Passage through the alimentary tract...
tract of wolves likely markedly degrades infectivity of tissues. In sheep, in vitro incubation of a dilute scrapie brain inoculum with alimentary tract fluids resulted in almost complete degradation of PrP (Jeffrey et al., 2006). Moreover, changes in deer behavior due to the presence of predators, i.e., predation risk effects or what has been termed the ecology of fear (Brown et al., 1999; Ripple and Beschta, 2004), include changes in use of space through habitat preferences or foraging patterns within a given habitat, or both (Lima and Dill, 1990). If deer move more within established home ranges due to fear of predation, then contact rates with environmental deposits of infectivity also might diminish. Given the sensitivity of epidemic dynamics to such contact rates, even relatively small reductions would further dampen epidemic dynamics beyond effects arising from selective predation on infected deer alone.

Although here we modeled wolf predation on deer, similar outcomes would be expected for wolf predation on other species susceptible to CWD. Hobbs (2006) used CWD and elk (Cervus elaphus nelsoni) population data from Rocky Mountain National Park (Colorado, USA) to model the impact on CWD that may be achieved through maintaining a pack of wolves in the park. Results from these simulations supported the idea that predation could drive decreases in CWD prevalence over a range of parameter estimates. Impacts by predators other than wolves may also reduce CWD prevalence to varying degrees, as seen in our results from nonselective removal by humans. We consider the wolf, a large coursing predator, to be most effective in selective removal of deer vulnerable from CWD infection; however, opportunistic mountain lions (Krumm et al., 2009), and potentially coyote (Canis latrans) packs, would likely benefit from lack of vigilance by CWD-affected deer as well.

The potential impact on wolves and other native North American predators from consumption of CWD-positive ruminants is unknown; however, no evidence of naturally occurring CWD has been reported outside four species in the family Cervidae. Limited surveillance of predators and scavengers in CWD-affected areas (Jennelle et al., 2009; Miller and Wild, unpubl. data) has not revealed evidence of abnormal prion accumulation. Naturally occurring transmissible spongiform encephalopathies (TSE) other than CWD have been documented in domestic mink (transmissible mink encephalopathy), domestic sheep and goats (scrapie), and domestic cattle (bovine spongiform encephalopathy [BSE]), as well as in humans (variant Creutzfeldt-Jacob disease) and domestic and captive wild felids (feline spongiform encephalopathy) that consumed BSE-contaminated feed (Hönnliman et al., 2007). Interestingly however, no TSE has been observed in a canid despite dietary challenge of BSE to dogs (Kirkwood and Cunningham, 1994). A species barrier is generally believed to be responsible for the specificity of prion diseases to their respective hosts, although some spillover, as with BSE, has been documented for at least one prion strain. Raymond et al. (2000) demonstrated a barrier at the molecular level that they suggest limits the susceptibility of non-cervid species to CWD. The dog and wolf are very similar in PrP sequence and quite different from cattle, domestic cats, and elk (Schätzl, 2007).

We suggest that predation, particularly wolf predation, may be a useful tool for management of CWD. Currently, the range of wolves (Boitani, 2003) does not overlap with the distribution of CWD (Chronic Wasting Disease Alliance, 2009) so our predictions on the effects of wolves on CWD prevalence remain untested. However, as wolf range expands through Wyoming and Wisconsin, USA, and Alberta and Saskatchewan, Canada, and into Colorado and Utah, USA, the possibility for such evaluation may occur. Alternatively, CWD may be detected in a new
geographic location where wolves are present. Based on our simulations, disease may be difficult to detect in these areas unless unique methods of surveillance, such as monitoring of wolf-killed cervids for presence of PrPres, are implemented. Beschta and Ripple (2009) suggest that restoration of large predators, such as wolves, provides a recovery strategy for native flora, functional predator-prey-scavenger food webs, and ecosystems degraded by overabundant wild ungulates. Wolf restoration also provides an opportunity to observe and evaluate the effects that selective predation may have on prevalence of an invariably fatal chronic disease in deer and elk. In areas where predator restoration is not possible, deployment of wolves as stewardship tools for the primary purpose of disease control could provide a novel approach to management.

Although somewhat novel, the concept of using wildlife species as stewardship tools to provide ecosystem services is not new. Restoration of bison to reestablish healthy landscapes of prairie vegetation in the United States (United States Department of the Interior, 2008) and large carnivore, (e.g., lion [Panthera leo]), translocations to restore ecologic integrity in fenced parks in Africa (Hayward et al., 2007) are occurring. Licht et al. (2010) propose use of small populations of wolves for ecosystem restoration in North America. Public tolerance of wildlife, particularly predators, may dictate intensive management in species used in such restoration efforts. Regardless of whether wolves are managed under natural regulation or primarily for fulfilling their ecologic role, they provide a promising approach for control of CWD that warrants further evaluation.

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LITERATURE CITED


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**APPENDIX A—MODEL STRUCTURE**

Using data from two epidemics of chronic wasting disease (CWD) in a captive population of mule deer (Odocoileus hemionus), Miller et al. (2006) found that models of indirect transmission of CWD from excreta had almost seven times more support in data than more traditional models of direct, animal-to-animal transmission. The best approximating model in their studies used three linked differential equations representing the number of infected and susceptible animals and the mass of infectious material in the environment:

\[
\frac{dS}{dt} = a(I+S) - S(\gamma E + m),
\]

\[
\frac{dI}{dt} = \gamma SE - I(m + \mu),
\]

\[
\frac{dE}{dt} = \epsilon I - \tau E,
\]

where

- $S =$ number of susceptible (uninfected) animals,
- $I =$ number of infected animals,
- $E =$ the mass of infectious material in the environment,
- $\epsilon =$ the per capita birth rate,
- $m =$ the per
capita death rate from causes other than CWD, \( \gamma \) = the indirect transmission coefficient, \( \mu \) = the additive, per capita death rate from CWD, \( \varepsilon \) = the per capita rate of excretion of infectious material by infected animals, and \( \tau \) = the mass specific rate of loss of infectious material from the environment.

This model is based on two assumptions, that the instantaneous per capita rate of infection was directly proportionate to the mass of infectious material in the environment (i.e., \( dI/dt = \gamma E I \)) and that the rate of uptake of infectious material by deer has negligible effects on the pool size.

We modified this model to include density-dependent effects on recruitment into the population and to include selective and nonselective predation:

\[
\frac{dS}{dt} = a(S+I) \left( 1 - \frac{S+I}{K_s} \right) - S(\gamma E + \mu) - (1 - p)\delta(S+I),
\]

\[
\frac{dI}{dt} = \gamma SE - I(m + \mu) - p(1 - c)\delta(S+I),
\]

\[
\frac{dE}{dt} = \varepsilon I - \tau E,
\]

where \( K_s \) is the population level where birth rate = 0 and \( \delta \) is the additive, instantaneous per capita rate of predation when predators select prey randomly. Predation rates were adjusted to account for selectivity by the term \( p \), which represents the proportion of the total kill that was infected. We calculated \( p \) as

\[
p = \frac{vI}{vI+S}
\]

where \( v \) is the vulnerability of infected animals relative to susceptible ones. Relative vulnerability is a multiplier giving the number of infected animals in the total kill per susceptible animal, assuming equal abundance of infected and susceptible. Thus, a value of \( v = 2 \) means that if susceptible and infected animals were equally abundant, wolves would selectively kill twice as many infected animals as susceptible ones. A value of \( v = 1 \) indicates no vulnerability of infected animals and increasing values of \( v \) above 1 indicate increasing vulnerability to selective predation.

If predators select prey totally at random, then the probability of dying from CWD is independent of the probability of dying from predation, as \( \delta \) is defined. In this case the probability that an infected animal will survive, \( \varphi \), over an interval of time = \( \Delta t \) is

\[
\varphi = e^{-(m+\mu+\delta)\Delta t}.
\]

However, when predators are selective, then it follows by definition that the probability of dying from predation is not independent of the probability of dying from the disease:

\[
\varphi = e^{-(m+\mu+\delta(1-c))\Delta t}.
\]

The term \( c \) allows us to represent the extent to which predation mortality compensates for CWD mortality. Because \( 1/(m+\mu+\delta) \) is the average lifetime of an infected animal assuming that disease mortality and predation mortality are completely additive, it follows that \( 1/(m+\mu+\delta(1-c)) - 1/(m+\mu+\delta) \) is the increase in the average lifetime of an infected animal that results because predation mortality may not fully add to disease mortality. The value of \( c \) ranges from 0 to 1. When \( c = 0 \), then predation mortality is completely additive with CWD mortality, as in equation (4). When \( c = 1 \), predation mortality is completely compensatory and does not add to deaths from disease (i.e., deer would have died from CWD within the year had they not been preyed upon).

To solve the system of equations in (2), we used numeric integration implemented in the lsoda package of the R computing environment (R Development Core Team, 2008). Values for parameters used in simulations are derived from Miller et al. (2006) and plausible assumptions about deer population dynamics in the absence of CWD (Table 1).
Table 1. Values for model parameters used in example simulations.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Value*</th>
<th>Reference or source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>Birth rate(^b) at population=0</td>
<td>0.6</td>
<td>Medin and Anderson, 1979</td>
</tr>
<tr>
<td>$m$</td>
<td>Non-CWD(^c) death rate(^d)</td>
<td>0.1</td>
<td>White and Bartmann, 1998</td>
</tr>
<tr>
<td>$K_a$</td>
<td>Population at which birth rate=0</td>
<td>1.230</td>
<td>Assigned</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Transmission rate(^e)</td>
<td>0.787</td>
<td>Miller et al., 2006</td>
</tr>
<tr>
<td>$\mu$</td>
<td>CWD death rate</td>
<td>0.567</td>
<td>Miller et al., 2006</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>Rate of excretion of infectious material</td>
<td>0.111</td>
<td>Miller et al., 2006</td>
</tr>
<tr>
<td>$\tau$</td>
<td>Rate of loss of infectious material from the environment</td>
<td>2.55</td>
<td>Miller et al., 2006</td>
</tr>
</tbody>
</table>

* Units for all rates are per year.

\(^b\) The birth rate in continuous time, which corresponds to a discrete time birth rate of 1.8 fawns per female.

\(^c\) CWD=chronic wasting disease.

\(^d\) The continuous-time death rate corresponds to an annual adult survival probability of 0.90.

\(^e\) The transmission rate was scaled to account for differences in density between the wild and the captive setting where it was measured by Miller et al. (2006). The default scaling factor was allowed for densities in paddocks that were 25 times higher than in the wild, thus $0.787/25$. 
Wolves–coyotes–foxes: a cascade among carnivores

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Abstract. Due to the widespread eradication of large canids and felids, top predators in many terrestrial ecosystems are now medium-sized carnivores such as coyotes. Coyotes have been shown to increase songbird and rodent abundance and diversity by suppressing populations of small carnivores such as domestic cats and foxes. The restoration of gray wolves to many parts of North America, however, could alter this interaction chain. Here we use a 30-year time series of wolf, coyote, and fox relative abundance from the state of Minnesota, USA, to show that wolves suppress coyote populations, which in turn releases foxes from top-down control by coyotes. In contrast to mesopredator release theory, which has often considered the consequence of top predator removal in a three-species interaction chain (e.g., coyote–fox–prey), the presence of the top predator releases the smaller predator in a four-species interaction chain. Thus, heavy predation by abundant small predators might be more similar to the historical ecosystem before top-predator extirpation. The restructuring of predator communities due to the loss or restoration of top predators is likely to alter the size spectrum of heavily consumed prey with important implications for biodiversity and human health.

Key words: coyote; fox; indirect effects; intraguild predation; mesopredator release; Minnesota, USA; predator interference; wolf.

INTRODUCTION

Cascading species interactions are critical to structuring ecological communities (Pace et al. 1999). Cascades are a type of indirect effect in which linear chains of direct effects propagate for three or more nodes (species or groups of species). Among trophic-level cascades are now well documented in both aquatic and terrestrial ecosystems (Terborgh and Estes 2010). Little attention, however, has been given to among-guild cascades. Such among-guild cascades whereby the largest or competitively dominant species directly suppresses a mid-sized guild member thus releasing the smallest guild member might important influence the composition of species guilds as well as the trophic levels above and below them.

As large predators are extirpated in certain parts of the world and recolonize in others, knowledge of such among-guild, or more specifically among-predator, cascades will be crucial to understanding and predicting changes in community composition. Among trophic-level cascades involving an apex predator that suppresses a smaller or mesopredator with consequent impacts on the mesopredator’s prey have been well studied in recent years. Mesopredator releases have been documented in over 60 systems worldwide (Ritchie and Johnson 2009) in species complexes as varied as African lions (Panthera leo) and wild dogs (Lycaon pictus) (Creel and Creel 1996, Creel 2001) to black-backed gulls (Larus marinus) and crabs (Ellis et al. 2007). In North America, coyotes (Canis latrans) have been shown to suppress numerous smaller predators ranging from domestic cats (Felis catus) to opossum (Didelphis virginiana) (Crooks and Soule 1999, Ritchie and Johnson 2009), though their impacts on suppressing fox populations (Vulpes vulpes, Urocyon cinereoargentus, and Vulpes velox) are the most well documented (Harrison et al. 1989, Ralls and White 1995, Henke and Bryant 1999, Fedriani et al. 2000, Kamler et al. 2003, Mezquida et al. 2006, Karki et al. 2007, Moehrensclager et al. 2007, Thompson and Gese 2007). The influence of coyotes in suppressing mesopredators has been shown to increase rodent and songbird diversity and boost duck nesting success (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999). Separately, wolves (Canis lupus) in Yellowstone have been shown to suppress coyote populations (Berger and Gese 2007) leading to higher pronghorn (Antilocapra americana) calf survival (Berger and Conner 2008, Berger et al. 2008). An among-predator cascade by which wolves suppress coyotes thus releasing foxes has not yet been demonstrated but is plausible because niche overlap between wolves and coyotes, and between coyotes and foxes, is high relative to niche overlap between wolves and foxes. A high degree of niche overlap is expected to lead to higher rates of interference competition, including spatiotemporal avoidance, kleptoparasitism, and direct killing. We hypothesize that this will cause wolves to suppress coyotes, and coyotes to suppress foxes, more than wolves suppress foxes.

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In Minnesota, gray wolves were extirpated from nearly all of the state by the early 1970s (Mech 1970). Since the passage of the endangered species act in 1973, wolves have recolonized much of the northern-forested part of the state, and are now present, but at low abundance in the center of the state, which is transitional between farmland and forest. In the southern part of the state, which is largely farmland, wolves are not present. Here we make use of an over 30-year time series of wolf, coyote, and fox relative abundance to test the hypothesis that wolves suppress coyote populations, resulting in a cascading release of fox populations.

**Methods**

The Minnesota Department of Natural Resources began monitoring terrestrial carnivore populations in 1975 using scent station surveys (Sargeant et al. 1998). The scent station survey technique has been used to monitor foxes, coyotes, wolves, bobcats, and bears (Conner et al. 1983), which are difficult to survey using traditional methods (e.g., distance sampling, mark–recapture). Each scent station uses a fatty-acid tab to attract carnivores and sifted soil to record their tracks the following morning. Ten stations are placed on each 4.3 km long survey route for one night between late August and mid-October, which avoids pseudoreplication due to temporal correlation in visitation. All routes are separated by at least 5 km to avoid recording animals on multiple routes. The survey routes cover three geographically and ecologically distinct habitat zones of Minnesota (southern farmland, middle transition, and northern forest; Fig. 1A). In each habitat zone, we use the percentage of scent stations visited by foxes, coyotes, and wolves as an index of abundance for each species.

There are both red and gray foxes in Minnesota, but red foxes are historically much more abundant. Red fox harvests were 20–40 times higher than gray fox harvests until red fox entered a protracted decline in the mid-1990s from which they have not recovered (Fig. 1). The fox indices that we report are intended to be for red fox alone, but gray fox may represent a relatively stable background rate unlikely to influence our results. Gray fox tracks are differentiated from red fox by size and the presence of prominent nail prints and ridge on the interdigital foot pad.

Tests of this survey technique against independent estimates of population abundance have verified its use as a proxy of both seasonal and annual relative abundance (Conner et al. 1983). While scent station surveys reflect real changes in populations over time, their statistical power to detect changes in abundance is positively related to visitation rate (Sargeant et al. 2003). In order to meet statistical power requirements, therefore, the Minnesota Department of Natural Resources operates between 2500 and 4000 scent stations, divided among the three habitat zones.

The three habitat zones have qualitatively distinct canid communities allowing us to test hypotheses about the interactions among wolves, coyotes, and foxes. Wolves are absent in farmland, scarce in the transition zone, and relatively abundant in the northern forests. Foxes and coyotes are present in all three zones. Each species is cosmopolitan in their habitat requirements, with high densities occurring in both open and forested habitats in certain areas throughout their North American range. We analyze the canid time series in these three zones to test the among-predator cascade hypothesis: wolves suppress coyotes, which releases the fox population.

**Statistical analysis**

To test the among-predator cascade hypothesis, we analyze the 30-year time series of fox, coyote, and wolf relative abundance using two complementary statistical approaches. First, we examine how the abundance of each species changes with the abundance of other species in each habitat zone over the 30-year time series. Second, we examine how the year-to-year changes in population growth rate of foxes and coyotes are influenced by density dependence and the presence of the other species.

In the first approach, we examine the long-term population trends of each species (Fig. 1B–D) with respect to one another in each habitat zone using linear and quadratic regression analysis. In particular, we test whether there has been a significantly greater decline of foxes where coyotes are more abundant, and a significantly smaller coyote population increase where wolves are more abundant. We also explore interspecific correlations between the three species by regressing the relative abundance of each species against each other in each zone. Note that temporal autocorrelation can increase Type I errors, so we include a separate $P$ value, $P_{ac}$, that accounts for temporal autocorrelation in the residuals by including a one-year lag term in the regression as indicated by the partial autocorrelation function.

In the second approach, we analyze fox, coyote, and wolf population time series with autoregressive linear models that test how the population growth rate of foxes and coyotes depends on intraspecific density dependence and interspecific competition. To demonstrate the biological relevance of our statistical models, we begin by modifying the discrete logistic growth equation for species $n$, where $n$ can equal $f$ or $c$ for foxes and coyotes, respectively. The model is then given by

$$n_{t+1} = n_t \exp \left[ a_n \left( 1 - \frac{n_t}{K_n} \right) \right] = n_t \exp [\beta_0 f + \beta_1 n_t]$$

(1)
where \( n_t \) is the population index of foxes or coyotes at time \( t \). The carrying capacity, \( K_n \), and the maximum intrinsic population growth rate, \( a_n \), are transformed into the regression coefficients \( b_{n0} \) and \( b_{n1} \). Rearranging terms and taking the natural logarithm yields the log-difference equation

\[
\ln \frac{n_{t+1}}{n_t} = \ln n_{t+1} - \ln n_t = b_{n0} + b_{n1} n_t.
\]

Replacing the log-difference with \( r_n(t) = \ln n_{t+1} - \ln n_t \) and using a Gaussian error structure, we derive the following regression model:

\[
r_n(t) = b_{n0} + b_{n1} n_t + e_{nt},
\]

\[ e_{nt} \sim \mathcal{N}(0, \sigma_n^2). \]

The parameter \( b_{n1} \) can now be interpreted as the strength of density dependence of species \( n \) on itself.

To provide a biologically meaningful method for including as covariates the time series of species other than focal species \( n \), we modify the discrete Lotka-Volterra competition equation for species \( n \), with two competing populations, \( p_1 \) and \( p_2 \). The model is given by

\[
n_{t+1} = n_t \exp \left[ \alpha_n \left( 1 - \frac{n_t + \alpha_{n1} p_{1t} + \alpha_{n2} p_{2t}}{K_n} \right) \right]
\]

where \( \alpha_{n1} \) and \( \alpha_{n2} \) are the competitive effects of species \( p_1 \) and \( p_2 \) on species \( n \), and \( \beta_{ni} (i = 0, \ldots, 3) \) are regression coefficients. This equation leads to the more complete statistical model that can explore the strength of competition between foxes, coyotes, and wolves given by

\[ n_{t+1} = n_t \exp \left[ b_{n0} + b_{n1} n_t + b_{n2} p_{1t} + b_{n3} p_{2t} \right] \]
where $\beta_{02}$ and $\beta_{33}$ can be interpreted as the strength of the negative or positive impact of species $p_1$ and $p_2$, respectively, on the population growth rate of species $n$. We additionally include interaction terms in our final statistical model because nonlinearities in the population dynamics and/or the time series may exist.

We make inferences using corrected Akaike Information Criterion (AICc; Hurvich and Tsai 1989, Burnham and Anderson 2002). Specifically, we calculate the AICc of models with all possible combinations of wolves, coyotes, foxes, and pairwise interaction terms in each zone. We use AIC weights to indicate our degree of confidence in each model relative to other potential models and we report the results for models with >15% AIC weight.

Using proportions as predictor variables can sometimes lead to violations of model assumptions such as normality of the residuals and constant variance. In these cases, proportions might need to be logit-transformed to map them to the whole real line. As such, we assessed residual and q-q plots using both proportions and logit-transformed proportions. Using proportions generally met model assumptions and using logit-transformed proportions did not change this. As such, we use raw visitation proportions as our index of population abundance throughout.

**Hypotheses**

Changes in the relative abundance of canids might be due to bottom-up changes in resources, interspecific interactions, or a combination of the two. Here, we consider three possible mechanisms: (1) a simple bottom-up model whereby populations of all three species in each zone increase when conditions are good and decrease when conditions are poor, (2) a habitat specific bottom-up model whereby bottom-up processes have primacy, but these vary according to habitat zone, and (3) an interactive model whereby changes in one or more canid populations directly or indirectly impact changes in another.

To provide support for the simple bottom-up model, we would expect populations of each species to be positively correlated throughout the state of Minnesota. To provide support for the habitat-specific model, we would expect populations of each species to be positively correlated within each habitat zone, but not necessarily across the entire state. To investigate whether certain species in one or more zones might be bottom-up regulated, we also used the winter North Atlantic Oscillation (NAO; Hurrell 1995) as a proxy for resource availability in our statistical analyses. While the NAO is not a direct measure of productivity, previous work has shown a strong correlation between the NAO and population dynamics of canid prey species in nearby areas such as snowshoe hare (Lepus americanus; Stenseth et al. 2004) and moose (Alces alces; Wilmers et al. 2006). As well, the NAO often predicts population dynamics data better than locally collected weather data (Stenseth et al. 2003). Finally, to provide support for the interactive model, we would expect some combination of negative and positive correlations among canid species. To support the among-predator cascade hypothesis in particular, we would expect wolves to have a negative and positive impact on coyote and fox populations, respectively, and for coyotes to have a negative impact on fox populations.

**RESULTS**

Changes in the relative abundance of wolves, coyotes, and foxes were best supported by the among-predator model over the bottom-up models. In the farmland zone, the fox population shows a strong decline as the coyote population grows (Fig. 2C). Conversely, in the forest zone where wolves are present, coyote and fox populations show no relationship (Fig. 2D), while wolves and foxes exhibit a strong positive relationship (Fig. 2E). The winter NAO was not a significant predictor in any of our regression models.

**Population trends**

The fox population trends in each zone were best explained by quadratic regression models with positive linear terms and negative quadratic terms (Fig. 1). The linear term in a quadratic model controls the slope of the initial population growth at population size zero. As the population size increases, the quadratic term begins to dominate the expression causing the population curve to bend over and decline. The more negative the coefficient on the quadratic term, the stronger the decline. Comparisons of the coefficients of the quadratic terms in the fox population trend in each zone indicate that the rate of decline is significantly higher in farmland over transition ($P < 0.01$), and in transition over forest ($P < 0.01$; Fig. 1). Corresponding to these fox trends, the coyote population increase was quadratic in the farm zone where wolves are absent ($P < 10^{-11}$, $r^2 = 0.86$), linear in the transition zone where wolves are slowly recovering ($P = 0.001$, $r^2 = 0.30$), and the coyote population decreased linearly in the forest zone where wolves have recovered strongly ($P = 0.02$, $r^2 = 0.17$), indicating top-down control of coyotes by wolves.

**Population fluctuations**

Examination of year-to-year changes in fox population growth rate revealed that the strength of fox density dependence in the single-species fox model (Eq. 1, $n = f$) was not significant and weakest in farmland, stronger in transition, and strongest in the forest, (Fig. 2A). The increase in the magnitude of the density-dependent coefficient, and variance of the model explained by density dependence ($r^2$) from farmland, where coyotes are abundant, to forest, where coyotes are relatively...
scarce, is suggestive of a release from interspecific competition with coyotes to self-regulation by foxes (Fig. 2A).

The strength of coyote density dependence in the single-species coyote model (Eq. 1, \( n = c \)) was weakest in forest, strongest in transition, and weak in farmland (Fig. 2B). This is generally consistent with the idea of bottom-up control in the farmland giving way to increasing among-predator control in the transition and the greatest among-predator control in the forest zone, with the exception that we would expect negative density dependence to be stronger in the farmland than in the transition. However, inspection of the coyote time series in the farmland reveals that the coyote population is still growing nearly exponentially so that this population has not yet experienced competition for food resources. Therefore it is not surprising that strong density dependence has not been achieved thus far in that zone.

The multispecies model predicting fox population growth rate (Eq. 2, \( n = f \)) revealed a strong negative effect of coyotes on fox population growth in the farmland zone, where wolves are absent (Table 1). This suggests that in the absence of wolves, coyotes strongly limit fox populations. In the forest zone with relatively abundant wolves, fox are released from top-down control by coyotes and show only a small positive correlation with coyotes (Table 1). This positive correlation is likely to come about when populations fluctuate in response to a shared food resource, a lower trophic level that we cannot explicitly account for in our model. In the transition zone, the best model explaining fox population growth rate included fox, coyote, and an interaction between the two (Table 1). This interaction reveals that when the coyote population is low, fox density-dependent effects dominate, but as the coyote population increases the fox population is regulated more by competition with coyotes than by density dependence.

Wolves did not have an important effect on fox population growth rate in the transition zone where they occur at low abundance. Wolves were not included in the best model (\( \Delta \text{AIC}_c = 0, \text{AIC weight} = 0.56 \)) and while they revealed a small negative effect on foxes in the
second best model ($\Delta$AIC$_c = 0.82$, AIC weight = 0.37), the effect was not significant ($P = 0.17$). Wolves, however, had a strong positive effect on fox population growth rate in the forest zone. In fact, the effect size is the strongest of any that we observe in any zone. The best model in the forest zone also includes a negative cross term for wolves and foxes, implying that as wolves increase, foxes are increasingly regulated by density dependence, which is evidence that wolves are allowing foxes to approach their carrying capacity. Direct inclusion of wolves into the multispecies coyote model (Eq. 2, $n = c$) did not reveal a significant negative effect of wolves on coyotes in either the transition or forest zones.

**DISCUSSION**

Taken as a whole, our analysis supports an among-predator cascade from wolves through coyotes to foxes. While the evidence we present is correlational, it is based on a plausible mechanism of increased interference competition between more closely sized canids. Wolves are more likely to kill coyotes than foxes because they might perceive coyotes as more direct competitors because of the coyote’s larger size and more similar diet preferences. This mechanism is supported by data demonstrating wolf suppression of coyotes (Berger and Conner 2008, Berger et al. 2008) and separately, coyote suppression of foxes (Harrison et al. 1989, Ralls and White 1995, Henke and Bryant 1999, Fedriani et al. 2000, Kamler et al. 2003, Mezquida et al. 2006, Karki et al. 2007, Moehrenschlager et al. 2007, Thompson and Gese 2007). While bottom-up forces surely play a role in this system, neither the simple nor habitat specific bottom-up models were sufficient to explain the pattern of alternating negative and positive effects among these three canid species. Other alternative hypotheses explaining these data might include land use change as a driver of change in canid populations over time, and underlying habitat differences among the three zones. Neither of these alternative hypotheses stands up when confronted with all the available data. Land use change occurs too slowly to account for interannual variations in population growth, while habitat differences are unlikely to explain the patterns we report here as both foxes and coyotes have achieved high densities in both forested and farm habitats here and elsewhere (Kays et al. 2008). Finally, disease, particularly mange, likely impacts populations of canids in Minnesota, but without data we could not include this in our analysis. Qualitatively, it does not appear that shared disease drives the among-predator interactions because the canid populations do not exhibit a temporally correlated decline. The uniformity of the coyote increase and fox decrease is more consistent with direct killing of foxes by coyotes rather than interspecies pathogen transmission.

Size asymmetric among-guild effects whereby larger competitors suppress smaller ones have been shown in various taxa including plants (Schwinning and Weiner 1998), insects (Rosenheim 1998), and fish (Muñoz and Ojeda 1998). Research in these systems has focused on pairwise interactions and their effects on lower trophic levels (e.g., Polis and Strong 1996, Sih et al. 1998). While the mechanisms driving among-guild interactions can vary from resource competition to interference competition or direct killing, our results indicate that indirect effects can cascade through a guild to impact the abundance of tertiary guild members. As a general rule, we would expect Fretwell’s (1977) idea that the parity of a food chain determines the alternate suppression and release of plant biomass to apply to chains of among-guild interactions as well. Namely that among-guild interaction chains with even numbers of species will result in the smallest competitor being suppressed while among-guild interaction chains with odd numbers of species will result in the smallest competitor being released.

Our results indicate that the restoration of wolves to areas across the northern hemisphere might lengthen species interaction chains. This is likely to result in an increase in smaller predators (or those that like foxes are suppressed by coyotes but not wolves) in wolf occupied habitat, and consequent changes in prey community composition. As coyotes have expanded their range in the absence of wolves, the resulting exclusion of foxes is expected to lead to much lower predation rates on small mammals because fox densities are on the order of 5–10 fox families (2 adults and 4–6 kits per family) per 10 km$^2$ (Trewella et al. 1988), but Eastern coyote densities are an order of magnitude lower at around 0.5 individuals per 10 km$^2$ in forested landscapes and around 1

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**TABLE 1.** The best model or group of models explaining fox population growth in the farmland, transition, and forest zones of Minnesota, USA, by Akaike weight ($w$).

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Farmland ($w = 0.73, R^2 = 0.43$)</th>
<th>Farmland ($w = 0.25, R^2 = 0.45$)</th>
<th>Transition ($w = 0.56, R^2 = 0.43$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h_0$</td>
<td>$0.613 (0.146)$</td>
<td>$0.683 (0.170)$</td>
<td>$1.27 (0.299)$</td>
</tr>
<tr>
<td>$f_t$</td>
<td>$-0.031 (± 0.009)$</td>
<td>$-0.040 (± 0.014)$</td>
<td>$-0.116 (± 0.028)$</td>
</tr>
<tr>
<td>$c_t$</td>
<td>$-0.114 (± 0.028)$</td>
<td>$-0.152 (± 0.054)$</td>
<td>$-0.429 (± 0.120)$</td>
</tr>
<tr>
<td>$w_t$</td>
<td>$0.006 (± 0.007)$</td>
<td>$0.42$</td>
<td>$0.039 (± 0.011)$</td>
</tr>
<tr>
<td>$f_t \times c_t$</td>
<td>$0.011 (± 0.42)$</td>
<td>$0.028$</td>
<td>$0.002$</td>
</tr>
</tbody>
</table>

*Note:* The covariate $h_0$ is the intercept parameter, $f_t$, $c_t$, and $w_t$, are the time-dependent fox, coyote, and wolf indices.
individual per 10 km² in rural landscapes (Tremblay et al. 1998, Patterson and Messier 2001, Way et al. 2002). Small mammals are present in only 2–13% of Eastern coyote scats, but in 11–50% of red fox scats (Major and Sherburne 1987). The numerical and dietary difference between foxes and coyotes can combine to result in a markedly lower predation rate on small mammals when coyotes exclude foxes.

While the three canid species have some dietary overlap, wolves are most efficient at killing large prey such as ungulates; coyotes are most efficient at killing intermediate-sized prey such as lagomorphs, squirrels, and ungulate neonates; and foxes are most efficient at killing small prey such as small rodents, invertebrates, and birds, but also lagomorphs (Major and Sherburne 1987, Gompper 2002). As such the size spectrum of canid prey communities are likely to vary depending on whether wolves are present or not. In ecosystems with wolves, large and small prey will experience higher rates of predation than intermediate-sized prey, whereas in ecosystems lacking wolves, intermediate-sized prey are likely to experience higher predation rates (Fig. 3).

Consistent with this idea, there is evidence that the increasing coyote population (in the absence of wolves) has caused the decline of white-tailed jackrabbits over the past 40 years in the farmland and transition zones of Minnesota (Haroldson 2008). This decline may reflect a loss of preferred habitat, but a resurgence in jackrabbit populations during the peak of pelt prices in the late 1970s and early 1980s (when furbearers were heavily trapped) is suggestive of a temporary release from predation.

### Table 1. Extended.

<table>
<thead>
<tr>
<th>Transition $(w = 0.37, R^2 = 0.47)$</th>
<th>Forest $(w = 0.51, R^2 = 0.52)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimate (SE)</td>
<td>$P$</td>
</tr>
<tr>
<td>1.27 (0.293)</td>
<td>0.0002</td>
</tr>
<tr>
<td>-0.115 (± 0.027)</td>
<td>0.0003</td>
</tr>
<tr>
<td>-0.398 (± 0.120)</td>
<td>0.003</td>
</tr>
<tr>
<td>-0.151 (± 0.106)</td>
<td>0.168</td>
</tr>
<tr>
<td>0.038 (± 0.011)</td>
<td>0.002</td>
</tr>
</tbody>
</table>

![Fig. 3. Hypothesized impact of the among-predator cascade on food-web dynamics (with interactions indicated by black arrows).](image)

(A) Without wolves, coyotes suppress fox populations such that preferred coyote prey items are preferentially consumed by the canid guild. (B) With wolves, the interaction web transitions from A to B (indicated by the curved gray arrows). Coyotes are suppressed, releasing foxes and leading to dominant fox and wolf prey items being preferentially consumed.
The discovery of this among-predator cascade opens the door to search for similar types of cascades and to explore their implications. For example, the change in the size spectrum of preferred prey might importantly impact human–ecosystem interactions. Common prey species are often responsible for the emergence of zoonotic infectious diseases, including hantavirus and Lyme disease (Ostfeld and Holt 2004). For instance, the dominant reservoir hosts for Lyme disease in North America are small mammals (LoGiudice et al. 2003, Brisson et al. 2007), and deer are an important reproductive host for adult ticks. A wolf and fox dominated predator community is expected to preferentially prey on these important hosts, and prey less on the medium-sized hosts that are incompetent Lyme disease reservoirs (LoGiudice et al. 2003).

This among-predator cascade also informs our understanding of mesopredator release in terrestrial systems. Mesopredator release theory has often considered the consequence of top predator removal in a three species interaction chain (i.e., coyote–fox–prey) where the coyote was considered the top predator (Ritchie and Johnson 2009). However, the historical interaction chain before the extirpation of wolves had four links. In a four-link system, the top predator releases the smaller predator. The implication is that a world where prey species are heavily preyed by abundant small predators (mesopredator release) may be similar to the historical ecosystem. As top predators recolonize their former ranges, ecological communities may be predictably restructured with consequences that are important to explore in future research.

Acknowledgments

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Madelia, Minnesota, USA.


In My Opinion

Can Restoring Wolves Aid in Lynx Recovery?

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ABSTRACT Herein, we examine the hypothesis that relatively low densities of snowshoe hares (Lepus americanus) and the imperiled status of lynx (Lynx canadensis) may be partially due to an ecological cascade caused by the extirpation of gray wolves (Canis lupus) in most of the conterminous United States decades ago. This hypothesis focuses on 2 plausible mechanisms, one involving “mesopredator release” of the coyote (C. latrans), which expanded its distribution and abundance continentally following the ecological extinction of wolves over the temperate portion of their geographic range. In the absence of wolves, coyotes may have affected lynx via increased predation on snowshoe hares, on which the lynx specializes, and/or by direct killing of lynx. The second mechanism involves increased browsing pressure by native and domestic ungulates following the declines in wolves. A recovery of long-absent wolf populations could potentially set off a chain of events triggering a long-term decrease in coyotes and ungulates, improved plant communities, and eventually an increase in hares and lynx. This prediction, and others that we make, are testable. Ecological implications for the lynx may be dependent upon whether wolves are allowed to achieve ecologically effective populations where they recolonize or are reintroduced in lynx habitat. We emphasize the importance of little-considered trophic and competitive interactions when attempting to recover an endangered carnivore such as the lynx. © 2011 The Wildlife Society.

KEY WORDS Canada lynx, Canis lupus, competition, coyote, endangered species, gray wolf, Lynx canadensis, mesopredator release, Lepus americanus, white-tailed jackrabbit.

Under the auspices of the Endangered Species Act of 1973, the Canada lynx (Lynx canadensis) was listed in 2000 as a threatened species across the conterminous United States (US; U.S. Fish and Wildlife Service 2000). This listing was in part a response to sharp declines in distribution and abundance of lynx in several states for which reliable historical trapping records were available during the latter stages of the 20th century (e.g., MN, MT, NH, and WA; Federal Register 2000). These “southern lynx” are poorly understood relative to conspecifics occupying the boreal forests of northern Canada and Alaska, USA; therefore, their conservation remains a subject of debate (Koehler et al. 2008, Murray et al. 2008). Lynx face numerous factors that could limit their distribution and abundance, including competition with other mid-sized carnivores and habitat alteration by stand-replacing fires, timber harvest, and insect outbreaks (Buskirk et al. 2000, Koehler et al. 2008, Murray et al. 2008). Even so, there is broad agreement that the fate of the lynx at lower latitudes is closely linked to the distribution and abundance of its obligate primary prey, the snowshoe hare (Lepus americanus; Kolbe et al. 2007, Murray et al. 2008). That is not to say that widespread abundance of snowshoe hares is the only condition for lynx recovery; however, it is a necessary one (Aubry et al. 2000, Murray et al. 2008).

Snowshoe hare populations occupying the forests of northern Canada and Alaska typically exhibit dramatic stable limit cycles with periods of 9–11 yr (Keith 1963, Krebs et al. 2001). The mechanism underlying the hare cycle across this region is debated vigorously, with 2 mechanistic pathways contending for priority. The first, a tri-trophic-level interaction among quantity of winter browse, hare population density, and densities of hare predators involves time-lagged density dependence. Under this mechanism, declining winter browse availability helps to slow the growth of hare populations during the increase phase of the cycle, but predation, especially by lynx, initiates the decline and represents the primary driver of changes in hare abundance (Wolff 1980, Hodges 2000a, Krebs et al. 2001). The second, a hare–winter–browse hypothesis, invokes plant secondary chemical responses to herbivory as the chief factor eliciting the hare cycle (Bryant et al. 2009). Decadal-scale climate fluctuation (Stenseth et al. 2002) is invoked with both mechanisms to account for broad geographic synchrony. Yet, neither primary mechanism is alleged to operate strongly in the temperate, or southern, portion of the distribution of the hare; rather, southern hare populations in the conterminous US appear to exhibit attenuated dynamics and exhibit only relatively low densities at population peaks (Murray 2000, Murray et al. 2008, but see Hodges 2000b).
Dampened dynamics in southern hare populations have been attributed to a combination of forest fragmentation and predation by prey-generalists (Wolff 1980, Wirsing et al. 2002, Griffin and Mills 2009). Specifically, both limited suitable habitat offering enough protective cover and persistent pressure from facultative predators (e.g., coyotes [Canis latrans]) appear to not only increase predation mortality to hares but also prevent the recruitment necessary to generate a cycle. By implication, forces that reduce forest fragmentation or suppress facultative hare predators could enhance the size of southern hare populations and perhaps promote cyclic dynamics. Increased hare abundance in this region can plausibly be expected to improve the viability of southern lynx populations.

The objective of this article is to briefly examine a hypothesis that chronically low densities of southern snowshoe hares and the imperiled status of lynx may be partially the result of an ecological cascade caused decades ago by the extirpation of the gray wolf (Canis lupus) over most of its conterminous US range. This hypothesis focuses on the subsequent ecological release of coyotes and of the ungulate prey of wolves and leads us to the prediction that wolf restoration could help facilitate lynx recovery in the conterminous US.

THE CONCEPTUAL MODEL

During the 1800s and early 1900s, gray wolves were extirpated throughout much of the conterminous US, and ungulate and coyote irruptions often followed the loss of wolves (Leopold et al. 1947, Presnall 1948, Prugh et al. 2009, Ripple et al. 2010). Herein, we describe a series of trophic and competitive interactions connecting wolves to lynx (Fig. 1). With wolves present, we hypothesize that coyotes would be maintained at low densities, resulting in little competition—either exploitative or interference—between coyotes and lynx. Interspecific interactions helped shape the evolution, structure, and function of carnivore communities, with exploitative competition occurring when one species limits populations of another by using a common resource. Interference competition involves harassment, kleptoparasitism, or outright killing of one species by another (Van Valkenburgh 1991, Merkle et al. 2009). In the absence of wolves, coyote densities and distributions generally expanded in the US—into the Midwest (Bekoff 1977), to the northeast as far as Newfoundland (Parker 1995), and as far northwest as Alaska (MacDonald and Cook 2009). And, because coyotes are known to be effective predators of hares (Wirsing et al. 2002), increased coyote populations can cause exploitative competition with lynx via higher predation pressure on hares (Buskirk et al. 2000, Bunnell et al. 2006). Further, interference competition between coyotes and lynx could limit densities of the latter, since examples of coyotes killing lynx have been reported (O’Donoghue et al. 1995). Interestingly, researchers have attributed declines in bobcat (Lynx rufus) populations to exploitation competition for prey caused by increasing coyote populations (Litvaitis and Harrison 1989), as well as increases in bobcats due to decreases in coyotes (Henke and Bryant 1999). Also, in the absence of wolves, population densities of wild cervids typically increase (Leopold et al. 1947), creating prey and winter-killed carrion subsidies to coyotes (Weaver 1979). These carrion subsidies have the potential to increase densities of facultative hare predators, and thereby predation on hares, during periods when lynx are ordinarily uncommon and predation on hares is low (Kolbe et al. 2007, Gompper and Vanak 2008). Note that coyotes may also benefit from the provision of wolf-killed carrion in wolf-dominated landscapes (Merkle et al. 2009), but we hold that interference competition with wolves would likely have a stronger negative effect on coyotes that any positive effects from this type of carrion subsidy. Additionally, we

Figure 1. Conceptual diagram showing how the (a) presence or (b) absence of wolves may affect lynx across multiple trophic levels. We hypothesize (a) that in the presence of wolves, this apex predator maintains coyote populations at low densities, thus minimizing the potential influence of coyotes on hares. However, (b) in the absence of wolves, coyote densities increase, causing exploitative competition with lynx through high predation pressure on hares. Furthermore, in the absence of wolves, wild ungulates may not only provide a prey and carrion subsidy to coyotes but can also increase herbivory levels upon forest understory plants that satisfy important habitat needs for hares. Changes in ungulate herbivory and interference competition are not shown on the above diagrams. Note: Wide arrows denote strong effects; thin arrows, weak effects; large ellipses denote high densities; small ellipses, low densities; concentric lines in ellipses, variable and/or cycling densities.
hypothesize that elevated coyote predation pressure can, in addition to that from other hare predators, contribute to trait-mediated effects on hare populations via behavioral and physiological pathways. For example, in the Yukon Territory of Canada, increased stress from high levels of predation risk has been documented to cause marked deterioration in hare reproductive rates (Boonstra et al. 1998) and quality of offspring (Sheriff et al. 2009). Such trait-mediated effects could result in sustained, rather than decadal periodic, reductions in hare reproduction.

In northern latitudes (e.g., Yukon) where wolves are present and where hares are the main prey for coyotes, populations of coyotes generally occur at relatively low densities, as well as cycle up and down in concert with hares and lynx (O’Donoghue et al. 1998, Sheriff et al. 2009). This is in contrast to wolf-free southern latitudes (e.g., the conterminous US) where coyote densities are commonly an order of magnitude higher than those in the north (O’Donoghue et al. 1998, Bekoff and Gese 2003). Coyote diets are also more varied in the south. For example, in Wisconsin, coyote numbers did not decrease with declining snowshoe hare densities, because of attendant buffering from alternative food sources (Niebauer and Rongstad 1977). Thus, coyotes in the south have the potential to suppress hares through both habitat switching and prey switching, while subsisting, as opportunists, on other food resources: ungal prey and carrion, fruits, smaller mammals, insects, birds, and human-generated garbage. Further, domestic cattle and sheep occur more broadly and at higher densities in the south than the north, which, for the southern portion of the range of the hare, could 1) increase the prey and carrion subsidy to coyotes, and 2) affect hare habitat through decreased forest understory vegetation due to herbivory. Most spatial overlap between lynx and livestock would occur at lower elevations of the lynx range because livestock are not generally distributed as high as lynx. Murie (1951) suggested that high densities of cattle in Arizona resulted in a lack of vegetative cover causing low densities of leporids.

To further explore hare dynamics in the south, we contrast hare populations in 2 unfragmented National Park settings: Isle Royale and Yellowstone. Neither park features livestock grazing. On Isle Royale, wolves colonized the park in 1949, and soon thereafter eliminated all coyotes from the island. With wolves and no coyotes, hares on Isle Royale cycled to high levels (Hodges 2000a). In Yellowstone National Park, Bailey (1930:125) described the distribution and abundance of snowshoe hares at around the time of the final eradication of wolves in this way: “Snowshoe rabbits are fairly abundant throughout the Canadian Zone timbered area.” Similarly, Murie (1940:124) reported snowshoe hares in Yellowstone to be abundant in the early 1900s, writing that, “… at Sylvan Pass in 1903, 15 or 20 hares were frequently reported seen in a day so that hares at that time must have been quite plentiful.” In contrast, a recent survey spanning the years 2002–2007 documented snowshoe hares as rare in Yellowstone (Hodges et al. 2009). This putative hare decline generally coincides with the absence of wolves and the consequent abundance of coyotes and high levels of herbivory from elk (cervus elaphus; Murie 1940, Berger and Gese 2007, Beschta and Ripple 2009). Ungulates can compete with small mammals for forage and reduced ungulate densities can cause increases in small mammals (Keesing 2000). Lynx were common in Yellowstone at the turn of the 20th century but, similar to hare trends, have since declined (Buskirk 1999). Thus, we hypothesize that even with a lack of human fragmentation of landscapes or livestock grazing—as observed in Yellowstone National Park—disrupted trophic and competitive interactions alone may have been enough to chronically depress hare and lynx populations. With wolves now reestablished in Yellowstone (as of 1995), a test of this hypothesis is possible because it appears that coyote densities significantly declined in parts of the Greater Yellowstone Area following wolf reintroduction (Berger and Gese 2007). Moreover, early evidence tentatively suggests that a hare recovery may be taking place; namely, the 6 hare sampling sites for which the aforementioned Yellowstone survey had the longest time series all showed an upward trend in hare abundance in the final year (2007; Hodges et al. 2009). More hare sampling in Yellowstone in the future will be required to determine whether this initial trend continues.

An alternative explanation for the low snowshoe hare densities observed in Yellowstone invokes human-caused fire suppression in altering the spatial patterning of various successional stages important to this species. Fortunately, this mechanism can be tested by examining patterns of hare abundance in relation to changes to lodgepole pine (Pinus contorta) communities brought about by the wildfires of 1988, and subsequent successional changes. Under the fire suppression hypothesis, for example, we would expect increases in hare abundance to coincide primarily with the regeneration of high sapling density in stands burned in 1988 (Bryant et al. 2009, Hodges et al. 2009) rather than depression of coyote numbers caused by the presence of wolves.

We considered whether other leporids might have been affected by the processes hypothesized above for snowshoe hares. Again, early on Bailey (1930:127) described white-tailed jackrabbits (Lepus townsendii) as common in northern Yellowstone National Park “... and along the open valley of the Lamar River.” However, white-tailed jackrabbits in the Yellowstone–Grand Teton region apparently declined over the course of the mid- to late 20th century in the absence of wolves, and were recently reported as rare (Gunter et al. 2009) or completely absent (Berger 2008a, b) from the shrub–steppe-dominated Lamar Valley. Could this decline of white-tailed jackrabbits have been caused by increased coyote populations and elk herbivory following wolf extirpation? We believe that this scenario is both plausible and consistent with our hypothesis. During the 7-decade wolf-free period in Yellowstone, the Lamar Valley had both high densities of coyotes (high predation pressure on leporids) and intensive herbivory (reduced shrub and understory cover) from elk (Murie 1940, Beschta and Ripple 2009). Also, during the wolf-free period and consistent with the food–subsidy portion of our hypothesis, Gese et al. (1996) found that coyote densities and litter sizes in the Lamar Valley were
directly correlated with the amount of elk carcass biomass (carrion).

The hypothesized negative effect of wolf removal on snowshoe hares and lynx that we describe here could be exacerbated by climate change. In the high-elevation regions of the conterminous US where lynx still occur, deep winter snow provides these boreal specialists with a competitive advantage over coyotes, which have a higher foot-load (Murray and Boutin 1991, Crête and Lariviere 2003). Accordingly, while both species can overlap where snow is deep (Kolbe et al. 2007), coyotes have been shown to be more abundant during winter than lynx at lower elevations where snow is shallow and the energetic cost of movement is affected by snow (Murray and Boutin 1991). Thus, if climate change results in warmer and less severe winters, declining snow pack could allow coyotes (released by the absence of wolves) to exploit hares at higher elevations. Accordingly, additional studies, with and without wolves, that elucidate the winter sympatry among southern coyotes, lynx, and hares at high elevations are required to test for this scenario. Results of this research could be important for lynx conservation efforts in the conterminous US (Kolbe et al. 2007).

CONCLUSIONS

If the removal of wolves initiated trophic and competitive adjustments resulting in the decline of hare and lynx populations in southern latitudes, would the restoration of this apex predator help their recovery? Based on the above considerations, we hypothesize that the answer is yes, but we are unsure as to what extent and how long it might take. A recovery of long-absent wolf populations could potentially set off a chain of events triggering a long-term decrease in coyotes and ungulates, recovery of previously degraded native plant communities, and eventually an increase in hares and possibly other leporids as well. Furthermore, we think the answer is at least partially dependent upon whether wolves are allowed to achieve ecologically effective populations (Soulé et al. 2003) where they recolonize or are reintroduced. For example, aggressive wolf harvesting may have important negative effects on hares and lynx as described above, as well as on other species of concern. We encourage managers and policy makers to consider the potential for the types of ecological cascades hypothesized herein when 1) significantly altering or fragmenting habitat via intensive herbivory from high numbers of livestock or wild ungulates, as well as from other management practices (e.g., logging), and 2) designing and implementing wolf and lynx management plans. Perhaps more importantly, we encourage ecologists to test—experimentally or with observational data—our hypotheses regarding community interactions originating with wolves, but manifested in the distribution and abundance of snowshoe hares and lynx. We have proposed mechanisms that involve food of hares (via ungulate densities), predation on hares (coyote populations released from top-down control by wolves and food subsidized by ungulates and humans), and behavioral–physiological effects on hares via temporally sustained predation and harassment by facultative hare predators. We propose exacerbation of these effects by an abiotic factor: altered patterns of snow depth and hardness in the face of climate change. All of these hypotheses are testable, at least indirectly.

Where wolf restoration is the objective, we believe that it is especially important to consider the ecological roles of these top predators in the ecosystem, rather than focusing solely on their demography (Estes et al. 2009). Accordingly, wolf recovery criteria in regions where hares and lynx occur and should include measures of coyote densities, to index predation on hares, and the recruitment of woody browse species, which provide food and cover for hares.

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LITERATURE CITED


Deer, predators, and the emergence of Lyme disease

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Lyme disease is the most prevalent vector-borne disease in North America, and both the annual incidence and geographic range are increasing. The emergence of Lyme disease has been attributed to a century-long recovery of deer, an important reproductive host for adult ticks. However, a growing body of evidence suggests that Lyme disease risk may now be more dynamically linked to fluctuations in the abundance of small-mammal hosts that are thought to infect the majority of ticks. The continuing and rapid increase in Lyme disease over the past two decades, long after the recolonization of deer, suggests that other factors, including changes in the ecology of small-mammal hosts may be responsible for the continuing emergence of Lyme disease. We present a theoretical model that illustrates how reductions in small-mammal predators can sharply increase Lyme disease risk. We then show that increases in Lyme disease in the northeastern and midwestern United States over the past three decades are frequently uncorrelated with deer abundance and instead coincide with a range-wide decline of a key small-mammal predator, the red fox, likely due to expansion of coyote populations. Further, across four states we find poor spatial correlation between deer abundance and Lyme disease incidence, but coyote abundance and fox rarity effectively predict the spatial distribution of Lyme disease in New York. These results suggest that changes in predator communities may have cascading impacts that facilitate the emergence of zoonotic diseases, the vast majority of which rely on hosts that occupy low trophic levels.

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There is growing recognition that changes in host community ecology and trophic interactions can contribute to the emergence of infectious diseases (1–3). In particular, the transmission of vector-borne zoonotic diseases to humans depends on multiple species interactions that influence host and vector abundance and infection prevalence. Most zoonotic pathogens are harbored by wildlife that occupy low trophic levels (1). The extirpation of top predators and the consequent restructuring of predator communities (4, 5) may thus increase the risk of zoonotic diseases if predation of reservoir hosts plays a key role in disease suppression. A paradigmatic case of disease emergence that is thought to be driven by changes in the host community is Lyme disease (Fig. 1).

Lyme disease is the most prevalent vector-borne disease in North America, and both the annual incidence and geographic range are still increasing (6). The disease is caused by the bacterium Borrelia burgdorferi, which is transmitted to humans in the eastern United States primarily by the nymphal stage of Ixodes scapularis ticks (7). The emergence of Lyme disease has been attributed to the century-long population recovery of deer, which are not competent hosts for transmitting B. burgdorferi to ticks but are nonetheless important reproductive hosts for adult ticks (7, 8). Support for this hypothesis comes partly from studies of experimental removal or exclusion of deer, which has often led to reduced tick densities (9). However, substantial research indicates that experimental or natural increases of deer density above a low threshold often have little effect on nymphal tick abundance (reviewed in ref. 10; see also refs. 11–13; Table S1). This research suggests that when deer are sufficiently abundant, other factors, such as hosts for immature ticks, may become limiting. Decades after the recolonization of deer, and despite a shift in management objectives from increasing deer populations to stabilizing or reducing them (14), Lyme disease cases have increased enormously (380% increase in Minnesota, 280% in Wisconsin, and 1,300% in Virginia from 1997 to 2007; Fig. S1), which suggests that other previously unidentified ecological changes may now be facilitating the emergence of Lyme disease. A growing body of evidence implicates small-mammal abundance as a key determinant of the density of infected nymphs, the primary measure of entomological risk for Lyme disease (12, 15, 16). Molecular evidence suggests that four species of small mammals (the white-footed mouse Peromyscus leucopus, Eastern chipmunk Tamias striatus, short-tailed shrew Sorex brevicauda, and masked shrew Sorex cinereus) are responsible for infecting 80–90% of ticks (17). Thus, it is possible that changes in the ecology of small mammals play a role in the continuing increase of Lyme disease. Small-mammal populations are influenced both by resource availability, which has been correlated with the subsequent density of infected nymphs (12, 15) and by predation (18). The latter finding has led to the suggestion that predation may play a key role in suppressing Lyme disease (1).

A major change in predator–prey interactions in North America over the last half-century has resulted from the range expansion and population growth of a new top predator—the coyote, Canis latrans, which has spread across the continent following the extirpation of gray wolves, Canis lupus (19). The expansion of coyotes likely suppressed the abundance of several small-mammal predators, with the reduction of foxes by interference competition with coyotes being the best documented (20–22). The replacement of foxes by coyotes would likely reduce predation rates on small-mammal prey (i.e., the reverse of mesopredator release) because red fox (Vulpes vulpes) densities are typically an order of magnitude higher than coyote densities (23–25), and small mammals make up a larger fraction of their diets, particularly in the eastern United States, where coyotes have hybridized with wolves (26) and rely far more on deer (27, 28). Further, red fox cache prey for later consumption and are therefore able to kill large quantities of prey when prey are abundant (e.g., after an acorn mast). The high abundance of foxes (29), their ability to kill large quantities of small mammals due to both dietary preference and prey-caching behavior, and their adaptability to human-dominated landscapes makes them potentially highly important to suppressing Lyme disease hosts in areas around human habitation. Thus, somewhat paradoxically, the expansion of coyotes likely decreased predation rates on small mammals by suppressing more-efficient predators (foxes).

Here we test the hypothesis that changes in predation have contributed to the continuing emergence of Lyme disease by analyzing disease models that explicitly incorporate predation intensity, and by examining spatial and temporal correlations at multiple scales between Lyme disease, coyote, fox, and deer abundance.

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We built a host density of infected nymphs if it increases the tick birth rate (Fig. 1). At intermediate predator densities, small changes in predation can cause large changes in Lyme disease risk. For example, a 20% reduction in predation near the inflection point in Fig. 1B more than doubles the density of infected nymphs. This nonlinearity is due to the interaction of predation with the quadratic shape of logistic population growth. Host densities near carrying capacity are by definition unproductive. Increasing the predation rate reduces host density, which increases population growth rates. When the host population is maximally productive near intermediate host densities, further increases in predation cannot be compensated for with more reproduction, which allows small increases in predation to cause greater reductions in host density (Fig. S3). Additionally, at these intermediate densities the host turnover rate is highest (maximal steady-state birth and death rates), which reduces host infection prevalence because hosts are born uninfected.

In this model, increasing deer abundance can also increase the density of infected nymphs if it increases the tick birth rate (Fig. 1B). However, the relationship between deer abundance and the tick birth rate is highly uncertain because adult ticks may be able to increasingly concentrate bloodmeals on fewer deer or alternate hosts as deer abundance declines. To explore the hypothesis that the relationship between deer and Lyme disease risk (density of infected nymphs) saturates (i.e., further increases in already abundant deer have little impact on nymph abundance), we reanalyzed data from deer removal studies that recorded deer abundance and the response of nymphs (30). Deer abundance was a poor predictor of tick abundance (measured as nymphs per mouse) 2 y later (Fig. 2A), which did not decline despite great reduction in deer abundance. Similarly, reducing deer density from >90 km⁻² to 10 km⁻² at Bluff Point coastal reserve in Groton, CT, only reduced tick density below 20 deer per km² (Fig. 2B) (31).

The model suggests that nymphal infection prevalence is only weakly influenced by the tick birth rate (Fig. 1C), because the fraction of ticks that are infected depends primarily on the composition of the host community and only weakly on the abundance of ticks. This finding is consistent with observations that nymphal infection prevalence does not decline inside deer exclosures (32), but does increase with small-mammal abundance (15, 16). The density of infected nymphs is a more direct Lyme disease risk factor than the infection prevalence of nymphs. If adult tick feeding rates saturate, then the key drivers of both the density and infection prevalence of nymphs would be hosts for immature ticks. Thus, the impact of predators would be greater than suggested here if reducing the density of hosts for immature ticks significantly reduces the tick birth rate (see additional model results in Figs. S4–S6).

**Results**

**Host–Vector Dynamical Model.** We built a host–vector model to determine how changes in predation might impact Lyme disease risk (Fig. 1, Methods, and Table S2), and found that predation can have a strong nonlinear influence on both the density and infection prevalence of nymphs (Fig. 1 and Fig. S2). At intermediate predator densities, small changes in predation can cause large changes in Lyme disease risk. For example, a 20% reduction in predation near the inflection point in Fig. 1B more than doubles the density of infected nymphs. This nonlinearity is due to the interaction of predation with the quadratic shape of logistic population growth. Host densities near carrying capacity are by definition unproductive. Increasing the predation rate reduces host density, which increases population growth rates. When the host population is maximally productive near intermediate host densities, further increases in predation cannot be compensated for with more reproduction, which allows small increases in predation to cause greater reductions in host density (Fig. S3). Additionally, at these intermediate densities the host turnover rate is highest (maximal steady-state birth and death rates), which reduces host infection prevalence because hosts are born uninfected.

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**Temporal Correlations.** Over the past 30 y, correlations between deer abundance and Lyme disease were not significant or mixed in direction (Fig. 3), regardless of whether we scaled antlered-deer harvest by hunting license sales or used raw antlered-deer harvest data (Tables S3 and S4). Thus, we examined the potential role of predators as drivers of Lyme incidence with data on proxies of coyote and fox abundance (i.e., harvest by hunters). Harvests varied up to 10-fold as coyotes increased and foxes declined during the emergence of Lyme disease (Fig. 3). In Minnesota, fox hunter harvest decreased 95% from a high of 78,000 in 1991 to a low of 4,000 in 2008, whereas coyote harvest increased 2,200% from a low of 2,000 in 1982 to 46,000 in recent years. In Wisconsin, coyote hunter harvests increased 660% from a low of 6,847 in 1984 to over 52,000 in 2009, whereas fox harvests decreased 80% from over 25,000 to under 5,000 over that time. In Pennsylvania, only 1,810 coyotes were harvested in 1990, but harvests increased nearly 1,600% to a high of over 30,000 in 2009. In Virginia, where Lyme disease cases have only recently increased (more than 300% increase from 2005 to 2007), coyotes have also increased only recently, averaging ~3,000 in the 1990s, reaching nearly 10,000 in 2004, and increasing to a recent high of nearly 25,000 (Fig. S1). Lyme disease cases were positively correlated with coyote abundance and negatively correlated with fox abundance in all four states (Fig. 3). The best models, using a model selection approach based on an information theoretic criterion (33), included measures of predator abundance for all four states. In contrast, deer abundance was present in the best fitting model only in Virginia (Fig. 3D).

**Spatial Correlations.** To test whether the spatial distribution of Lyme disease is correlated with the spatial distribution of deer or small-mammal predators, we examined Lyme disease incidence in Wisconsin, Pennsylvania, Virginia, and New York. Across space, Lyme disease incidence did not consistently increase with deer abundance. Deer and Lyme incidence were negatively correlated in Wisconsin and Pennsylvania, positively correlated in Virginia, and uncorrelated in New York (Fig. 4 C–F). In contrast, the spatial distribution of Lyme disease incidence in New York (the only state for which we had spatial data on predator abundance),...
is positively correlated with coyotes and negatively correlated with foxes (Fig. 4A and B), which suggests a more important role for variation in the abundance of predators than deer. Lyme disease is notably rare in western New York, where fox are abundant, despite having among the highest deer abundance in the state. It is worth noting that the nonlinear relationship between foxes and Lyme in Fig. 4B closely resembles model predictions (Fig. 1). Previously compiled data on catch-per-unit effort of red fox by trappers and buck harvest density match the spatial distribution of carnivores and deer derived from harvest-independent data (34).

**Temporal Correlations at Smaller Spatial Scales.** Harvest-independent data from multiple regions of Wisconsin also suggest that Lyme incidence is more tightly linked to changes in predator abundance (coyote increase and fox decrease leading to lower overall predation rates) than deer abundance. In Wisconsin, where Lyme disease incidence has increased greatly over the past decade, landowner wildlife surveys indicate that a fox decline and coyote increase occurred throughout the state (Fig. 5), which corroborates the statewide trends from hunter harvest data (Fig. 3). Deer observations have been stable or declining over this period (Fig. 5), although due to high deer abundance, these surveys may be a less-sensitive index for deer. However, on a fine spatial scale, deer density in management units with the highest Lyme incidence did not change over the last decade, whereas Lyme disease cases increased 300% (Fig. S7). Deer densities increased at most sites from the early 1980s until the mid 1990s, which may have caused the initial emergence of Lyme disease in Wisconsin. However, in the past 15 y, deer abundance has slowed markedly, with one-fourth of units showing no increase and several others increasing only a small percentage (Fig. S7).

**Discussion**

The increase in deer during the early 20th century is thought to have allowed tick populations to grow and spread from small remnant populations, and this likely contributed significantly to the initial rise in Lyme disease cases (7). However, in recent decades, Lyme disease has continued to increase substantially in many places where deer populations have stabilized (Figs. 2 and 4). Further, we detected no relationship between the spatial distribution of Lyme disease and deer abundance in four states (Fig. 4). The weak correlations between changes in deer and Lyme disease incidence is consistent with a saturation in the probability that an adult tick finds a host (e.g., deer) with deer density (Fig. 2). Additionally, recent work from New York found no relationship between threefold variation in deer abundance and the density of infected nymphs over 13 y (12), and there was no response in nymph abundance to a recent deer culling program in New Jersey (13). Thus, though there is convincing evidence linking deer to high nymph densities from deer exclosure...
studies, and from the complete or near-complete deer removal on islands, linking deer abundance to ticks when deer are abundant has been less successful, particularly at mainland sites where there are many other potential reproductive hosts for *Ixodes* ticks and where most Lyme disease cases are contracted (reviewed in Table S1).

At the same time, over the past three decades there has been a regional red fox decline coincident with an expanding coyote population. Both spatial and temporal evidence across multiple states suggest that these changes in predator abundance are more closely linked with increases in Lyme disease than are changes in deer abundance. Our theoretical model suggested that changes in predation can in fact lead to the observed increases in Lyme risk, in that both the density and infection prevalence of nymphal ticks are sensitive to reduced predation (Fig. 1). Taken together with the empirical data on spatial and temporal patterns of Lyme incidence, deer, and predator abundance, these results suggest that the red fox declines may have resulted in increased Lyme disease risk due to the loss of predation as an ecosystem service. Detailed studies and experimental manipulation of predators could help elucidate whether controlling Lyme disease might be best accomplished by

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**Fig. 4.** Spatial relationships among deer, predators, and Lyme disease. (A) In New York, observation rates from the bow-hunter wildlife survey indicate that Lyme disease incidence (cases per 100,000) is positively correlated with coyotes, (B) negatively correlated with foxes, and (C) unrelated to deer. Coyote observations are scaled by foxes to highlight the transition in the predator community and its impact on Lyme disease. (D) Deer as estimated by the buck harvest density are positively (but weakly) correlated with Lyme disease incidence in Virginia counties ($R^2 = 0.1, P = 0.001$). (E) In contrast, deer density estimates (from sex-age-kill models) are negatively correlated with Lyme incidence in Wisconsin counties ($R^2 = 0.06, P = 0.05$, but driven by few data points—not significant when removed) and (F) negatively correlated in Pennsylvania deer management units ($R^2 = 0.14, P = 0.09$, where the unit with the lowest deer density has the second-highest Lyme incidence. (Insets) Darker red indicates more-abundant wildlife populations and higher Lyme incidence (in four classes: 0–10, 10–50, 50–100, and >100 cases per 100,000).

**Fig. 5.** The percent of surveyed rural landowners who saw coyotes, foxes, and deer in five geographic regions of Wisconsin from 1999 to 2009 according to the annual Summer Wildlife Inquiry run by the Department of Natural Resources. Lyme incidence in each region is the weighted average (by area) of county-level incidence.
a combination of predator manipulation and severe reductions in deer densities necessary to reduce tick abundance.

More broadly, these results suggest a need to explore the role of predation in the community ecology of other emerging zoonotic diseases, which overwhelmingly rely on hosts that occupy low trophic levels (1). Due to the widespread eradication of large carnivores (4), top predators in many terrestrial ecosystems are now medium-sized carnivores such as coyotes (5). These medium-sized carnivores can indirectly increase the abundance and diversity of low trophic-level species, such as rodents and songbirds, by suppressing populations of smaller carnivores such as foxes (20). Strong interactions among predators (35) that lead to cascading effects on prey have been documented for over 60 systems worldwide (21). As top predators are extirpated in some parts of the world, and recolonize in others, it will be important to understand the consequences for community composition and for the abundance of low trophic-level species in particular. Such restructuring of predator communities may have unintended consequences for human disease.

Methods

Host-Vector Disease Model. We use a vector-borne, susceptible-infected (36) modeling framework that describes the dynamics of ticks and small-mammal hosts, and includes parameters to account for the density of alternate hosts and deer. We group multiple species into a functional group of small-mammal hosts with density, \( N_m \). The small-mammal host population growth rate, \( G(N_m) \), is logistic with maximum intrinsic growth rate, \( r \), and carrying capacity, \( K \). The mortality rate, \( M(N_m) \), follows a Holling type III functional response, which is characteristic of prey-switching generalist predator, with maximum predation rate, \( a \), half-saturation parameter, \( c \), and predator density, \( P \) (37–39). This functional response can exhibit alternative stable states in a small region of parameter space, but we stress that our results depend only on an S-shaped functional response, which is characteristic of switching or aggregating behavior in response to more-abundant prey (Fig. 53). An S-shaped functional response is also obtained with a type II functional response when predators respond numerically to increasing prey density (i.e., a combined numerical and functional response; SI Text, Parameters and Derivations).

The differential equation for the total host population is

\[
\frac{dN_m}{dt} = G(N_m) - M(N_m) - rN_m \left( 1 - \frac{N_m}{K} \right) - \frac{aP_mN_m^2}{c^2 + N_m^2} 
\]

The small-mammal host population consists of susceptible, \( S_m \), and infected, \( I_m \), classes. Susceptible hosts become infected with probability \( T_m \) when bitten by an infected nymph, \( J \). A fraction of tick bites occur on incompetent "dilution" hosts, \( F \), so that these hosts divert blood meals away from small mammals but also increase total host abundance. The tick bite rate, \( \beta(N_m + F) \), follows a type II functional response. Because each tick life stage requires a single blood meal, the functional response saturates at 1 as the abundance of hosts increases (i.e., all ticks can feed if there are infinite hosts). The half-saturation parameter, \( b_o \), represents the density of small mammals where half of ticks would be expected to feed. Thus, the tick bite rate can be interpreted as the fraction of ticks that successfully feed given the total population of hosts, \( N_m + F \).

The differential equations for susceptible and infected small-mammal hosts are

\[
\frac{dS_m}{dt} = G(N_m) - T_mPmS_m \frac{\beta(N_m + F)}{N_m + F} - rS_m - \frac{aP_mS_m^2}{c^2 + S_m^2}
\]

and

\[
\frac{dI_m}{dt} = T_mPmS_m \frac{\beta(N_m + F)}{N_m + F} - \frac{rI_m}{N_m} - \frac{aP_mI_m^2}{c^2 + I_m^2}
\]

where susceptible hosts are created by birth and lost by infection or predation, and infected hosts are created by infection and lost by predation.

We assume no increase in predation risk associated with being infected. Therefore, the relative abundance of the susceptible and infected classes determines the relative predation rate of each class.

Larval ticks, \( S_l \), which are all susceptible, have birth rate \( \nu \) and per-capita death rate \( \mu \). We use a constant birth rate that can be varied independently, because it is unknown how vertebrate biomass and community composition influence the tick birth rate. Any larval tick that successfully feeds on either a small-mammal host or dilution host leaves this class so that the differential equation for larva is

\[
\frac{dS_l}{dt} = \nu - \beta(N_m + F)S_l - \mu S_l
\]

Nymphs die at rate, \( \mu_n \), and also leave their class by successfully feeding. Nymphs become infected when larva successfully contract *Borrelia* from an infected host (i.e., this depends on the frequency of infected hosts) with probability \( T_m \). Thus, the differential equation for infected nymphs, \( I_n \), is

\[
\frac{dI_n}{dt} = \frac{\nu}{N_m} \left( \beta(N_m + F)S_l - \beta(N_m + F)I_n - \mu_n I_n \right)
\]

Uninfected nymphs, \( J_n \), can be uninfected because a susceptible or dilution host or because a larval tick fed on an infected host but did not contract *Borrelia*. The equation for uninfected nymphs thus has an additional term to account for the probability that feeding on an infected host did not cause infection, but can be simplified to

\[
\frac{dI_n}{dt} = \frac{\nu}{N_m} \beta(N_m + F)S_l + \frac{\nu}{N_m} (1 - T_m) - \frac{\nu}{N_m} \beta(N_m + F)I_n - \mu_n I_n
\]

We solved for the steady states as a function of the steady-state small-mammal density \( N_m \). The closed-form solutions, which are presented in SI Text, Steady-State Solutions, explicitly demonstrate the strength of the known multiple drivers of Lyme disease.

Data Analysis. Spatial Analysis. New York enlists bow hunters to survey wildlife from tree stands. We averaged the observation rates of each species from 2005 to 2007 in each management unit to compare with Lyme disease incidence from 2006 to 2008. Lyme disease incidence is recorded at a county scale, so we allocated incidence to management units as a weighted average based on the relative area of each county in each wildlife management unit groupings.

In Virginia we used buck harvest per square mile reported in the Virginia deer management plan (14) as a proxy for deer density. Both the harvest data and Lyme disease data are on the county spatial scale. Wisconsin and Pennsylvania produce deer density estimates using the sex-age-kill model (40), which estimates density in management units using data on harvest, age, and sex structure, and fawn-to-do ratios. Lyme disease incidence is recorded at a county scale. In Pennsylvania, wildlife management units are larger than counties, so we allocated Lyme incidence to management units as above. In Wisconsin, wildlife management units are smaller than counties, so we allocated deer density to counties based on the relative area of each wildlife management unit in each county. For Wisconsin, we additionally analyze changes in deer densities since 1981 in 25 randomly chosen management units intersecting counties with the highest incidence (Fig. 57).

Time-Series Methods. We use harvest-based proxies for white-tailed deer, coyote, and red fox abundance. To compare the populations of coyotes and foxes with annual Lyme disease cases, we use hunter harvest as a proxy for abundance. Any longitudinal changes in hunting effort are unlikely to be biased in favor of one of these species over another, suggesting that a decline in fox harvests and an increase in coyote harvests represent real population changes. Data on trapper harvest is more widely available but is not reliable because it is influenced by exogenous factors such as pelt prices and changes in trapping regulations designed to prevent incidental catch of high-value or endangered species. Many states, including the four we consider, have liberal...
As a proxy for deer abundance, we use antlered deer harvest, which is routinely used by wildlife management agencies to monitor trends in deer abundance. Antlered deer harvest is a robust estimate of the statewide deer population due to the large number of hunters that sample the deer population with success rates dependent on the abundance of deer. We scale antlered deer harvest by hunting license sales to capture changes in hunter participation (Fig. S8). Analysis of the hunter functional response from 10 datasets supports a type I functional response (41), which suggests that hunter success rates are expected to increase linearly, rather than simply monotonically, with deer density. Additionally, hunter success rates (Fig. S8; <25% in MN, PA, and WI, and <40% in VA) suggest increases in deer abundance would be represented by increased harvests, because hunters are not saturated with deer. Longitudinal hunter harvest data has been shown to correlate well with trends in deer density and has been used in the literature not only for crude population trends but also for more sophisticated time-series analysis (42–45).

Combining the available wildlife harvest time series, we evaluate the relative support of the predation and deer hypotheses. We additionally analyze antlered deer harvest data not corrected for license sales (Table S3) and harvests of deer, coyotes, and foxes all scaled by hunting license sales (Table S4) to ensure that our results are statistically robust to changes in hunter participation. We use deer (big game) license sales throughout because small-game hunters focus on a variety of species, and individuals may only report that they are coyote or fox hunters if they opportunistically kill one of these species incidental to other activities (46). The strength of each candidate model was evaluated using corrected Akaike Information Crite-

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The role of large predators in maintaining riparian plant communities and river morphology

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Abstract

Studies assessing the potential for large predators to affect, via trophic cascades, the dynamics of riparian plant communities and the morphology of river channels have been largely absent in the scientific literature. Herein, we examine the results of recent studies involving three national parks in the western United States: Yellowstone, Olympic, and Zion. Within each park, key large predators were extirpated or displaced in the early 1900s and subsequent browsing pressure by native ungulates initiated long-term declines in recruitment (i.e., growth of seedlings/shoots into small saplings and trees) of palatable woody species and
Research Article

Effects of Intraguild Predation: Evaluating Resource Competition between Two Canid Species with Apparent Niche Separation

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1. Introduction

Theorists of competition between animal species have long recognized the important role resources play in shaping the ecology of a species [1–3]. Today, with declines in animal populations being attributed to widespread loss of suitable habitat, many studies focus on determining the resources important to imperiled species and the extent resource use overlaps with competing species [4, 5]. Habitat degradation, resulting in the potential loss of distinct niche space, may increase the potential for competition between sympatric species [6, 7]. As resource overlap increases, species often rely on behavioral mechanisms to reduce competitive pressures [8–10]. Evidence of a species’ effort to isolate its niche frequently manifests itself as changes in the use of space, time, or food resources and is often accompanied by restricted distribution, decreased fitness, or a reduction in population size [11–13]. When studied for relatively short periods of time or without historical perspective, two species competing for the same resources are coexisting because of the employment of these isolation mechanisms.

Often, studies examining the effects of competition are initiated for populations which have already incorporated behavioral changes, or are even in decline, as a result of interspecific pressures (e.g., [12–14]). Since a species’ habitat selection is not independent of such pressures, quantifying resource use versus availability may give a false impression of optimal distribution and resource requirements [15, 16], although habitat selection may occur in response to other intrinsic and extrinsic factors (e.g., thermoregulation, energetics, prey choice). Management decisions based on apparent interspecific species compatibility, as indicated by nonoverlapping habitat use patterns, may be in error. To test whether declining species are distributed optimally with
2. Materials and Methods

2.1. Study Site. We conducted research on the Dugway Proving Ground (DPG), Utah, in the Great Basin ecosystem. Classified as a basin and range landscape, the area is dominated by relatively flat, low-elevation habitat interspersed with steep mountains. Elevations range from 1,288 to 2,154 m. Owing to its position in a double rain shadow, mean annual precipitation is 20.3 cm with evaporation exceeding 1,100 cm. The area is characterized by residential and industrial structures, open spaces, and urban. We reclassified a digital vegetation map with 10 m resolution to reflect these 7 categories. Species compositions of these 7 habitats are described in order of decreasing elevation, with the exception of the urban habitat. We used the minimum convex polygon of all canid telemetry locations to estimate the relative proportion of each habitat within the study area.

The plant composition of the shrub-steppe habitat (81 km², 13%) included juniper (Juniper osteosperma), big sagebrush (Artemisia tridentata), greasewood (Sarcobatus vermiculatus), horsebrush (Tetradymia glabrata), viscid rabbitbrush (Chrysothamnus viscidiflorus), forbs, and native bunch grasses. The grassland habitat (135 km², 21%), largely a product of increased fire frequency and disturbance, was dominated by cheatgrass (Bromus tectorum), tumbler mustard (Sisymbrium altissimum), and peppergrass (Lepidium perfoliatum). Stable dunes (120 km², 19%) were composed of four-wing saltbush (Atriplex canescens), greasewood, sage, horsebrush, viscid rabbitbrush, dune rabbitbrush (Chrysothamnus nauseosus var. turbinatus), and Indian rice grass (Stipa hymenoides). The greasewood habitat (65 km², 10%) was characterized by large, monospecific stands of greasewood. Chenopod habitat (107 km², 17%) was dominated by gray molly (Kochia americana) and shadscale (Atriplex confertifolia), with some greasewood. Indicator species of the pickeleweed habitat (124 km², 19%) were Gardner’s saltbush (Atriplex gardneri) and pickeleweed (Allenrolfea occidentalis); both specialized for wet, saline conditions. Urban habitat (5 km², 1%), being anthropomorphic in origin, was characterized by residential and industrial structures, office buildings, laboratories, debris, and paved surfaces, as well as non-native plants including Russian olive (Elaeagnus angustifolia), tamarisk (Tamarix ramosissima), and lawn.

2.2. Animal Capture. We used helicopter net gunning to capture coyotes [23, 24]. We used box and enclosure traps to capture kit foxes [25]. For both species, no chemical immobilization was used to process animals. Animals ≥1-yr-old were radio collared, ear tagged, and released at the site of capture.

2.3. Observed Canid Distributions. We plotted locations of each radioed animal on the digital vegetation map to determine the habitat use of kit foxes and coyotes. Locations were from homing in on the radioed animal or triangulation obtained from ground and aerial telemetry. Repeated blind trials with reference collars determined ground telemetry error to be <3° and aerial telemetry error to average <100 m; the error polygon for a location had to be <0.25 km² to be retained for analyses [17]. We used the computer program Locate II (Pacer, Truro, Nova Scotia, Canada) to determine the animal’s position from ≥3 compass bearings [26]. We located animals 4 times a week for the life of the animal, or to the end of the 30-month study. We minimized sampling bias by evenly distributing observations across 4 time periods (dawn, day, dusk, night) and 3 seasons (breeding, rearing, dispersal) corresponding to distinct behavioral phases [27–29]. We classed locations into day and night by monthly times for sunrise and sunset.
We analyzed animal locations using ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, Calif., USA) in combination with the digital vegetation map reclassified to represent the 7 habitat types. We buffered each location by 150 m in radius (larger than the size of the accepted error polygon of 0.25 km²) to define the area, not the point, the animal was using at the time of the location [17, 30, 31]. We employed the use of a buffer, whose length corresponded to the appropriate distance of awareness for the animals being studied, to more accurately represent space use [32, 33]. Standard analyses of telemetry data use computer algorithms (e.g., Locate II) to provide “best guess” coordinates and error polygons constructed from 3 bearings, or 2 bearings and a reference error. Researchers typically accept the “best guess” coordinates as the animal’s actual location to apply to a home range estimate or assess landscape use parameters (e.g., habitat type, slope, aspect). This practice fails to recognize the resolution of radio telemetry location accuracy and can lead to misrepresentation of an individual animal’s use patterns by incorporating arbitrary landscape. Individuals do not occupy space or make habitat use decisions based on a single dimension, as represented by a point location. More realistically, they exhibit some level of “awareness” for their surroundings through sight, smell, sound, and memory [34, 35]. Approaching the analysis of landscape use by incorporating an animal’s “awareness” shifts emphasis from use of a point location to an area of influence and preserves a more appropriate resolution of telemetry locations.

Animal awareness should be estimated separately for every species and should also account for site-specific landscape characteristics [36, 37]. Based on visual observations (n = 513) of coyotes and kit foxes on DPG’s open landscape, we estimated that 150 m was the average distance each species was immediately sensitive to its surroundings (i.e., became aware of an observers presence; [30, 31]. We defined this distance as the species “awareness” which was used to convert point locations to a circular area 150 m in radius. We then used ArcView’s Geoprocessing wizard extension to spatially join the buffered location to the habitat map. When summed over the course of the study, the corresponding polygons, infused with the proportions of habitats used, generated a 2-dimensional use profile for each canid [17]. Because kit foxes traveled and hunted alone, and coyotes also traveled alone as indicated by activity patterns and spatial proximity, we used the individual animal as the sample unit for all analyses.

Although previous analyses of canid distributions on DPG focused on examining interactions between individuals with spatially overlapping home ranges [17], occurrence of coyotes on DPG and, therefore their use of habitat, were ubiquitous across the study site. For comparison with predicted distributions, space use by coyotes was portrayed on the population level. However, space use by kit foxes, because of their discontinuous distribution, was reported in the context of mountain, grassland, city, and poverty (i.e., low-lying salt flats) landscape classes based upon topography and elevation [17]. Due to a heterogeneous landscape, and in order to insure the comparison of the most spatially related canids with the highest chance of interaction [26, 38], we grouped individuals of both species into either a “highland” or “lowland” landscape class. Shrub-steppe, grassland, and stable dune habitats defined the highland regions of the study area, while the lowlands were composed primarily of greasewood, chenopod, and pickleweed habitats. Space use patterns allowed for the further division of kit foxes into 4 landscape use subclasses [17]. We divided highland foxes into “mountain” and “grassland” sub-classes, while lowland foxes were separated into “city” and “poverty”. As well as focusing the analysis on the individuals with the highest potential for resource overlap, this strategy also examined habitat use at a finer scale than that of the study area, effectively reducing the confounding effects of habitat availability and its influence on the observed landscape use patterns of each species. As a result, differences in habitat use between study animals more closely reflected actual selection rather than differences in available habitat and prevented spurious comparisons of individual animals that did not overlap or occupy similar landscapes [17, 26, 38]. For both species, locations were pooled across years and seasons to provide an overall estimate of habitat use. However, the predicted distributions used the locations of individuals within each landscape class (see Section 2.6).

Comparisons between canid distributions were analyzed using a chi-square goodness-of-fit test [15]. For significant differences detected between distributions, we used Bailey simultaneous confidence intervals to determine if the observed use of habitat types was more or less frequent than the predicted use of each habitat type [39], as determined by prey distribution and abundance. We used Resource Selection for Windows (RSW) software to compute these comparative statistics [40].

2.4. Carnivore Diets. We collected and analyzed scats to determine both kit fox and coyote diets. Scats of these two sympatric canids were distinguished by size, shape, and odor [41, 42], as well as associated tracks and sign. We drove dirt road transects (114 km) monthly to collect scat for both species and clear the road for the next month’s survey. Transects were distributed throughout the study area and passed through all 7 habitats. A vehicle with a driver and 2 observers drove transects in both directions before considering them clear. A low amount of fox scats on transects necessitated similar clearing and collection of scats at den sites. We classified transects and den sites as either highland or lowland based upon topography and elevation [17]. Once collected, scats were placed in paper bags labeled with month, species, and elevation. After being air dried, scats were transferred to nylon stockings, washed in a washing machine, and air dried. We analyzed indigestible remains using a light microscope for hair identification, and a locally obtained specimen collection for the identification of teeth, bones, and exoskeletons. Presence of individual prey species in each scat was recorded and percent occurrence calculated (no. of occurrences of an item/total no. of occurrences of all food items). We used the number of individuals observed in each prey category comprising >10% of prey item occurrence to model canid distribution. While the size of each prey species varied, we used the occurrence of prey due to the lack of a biomass conversion for kit foxes and the major prey species in
their diet. Future studies incorporating a biomass conversion for each prey species could prove useful.

2.5. Prey Distribution and Abundance. We quantified the relative abundance of black-tailed jackrabbits (Lepus californicus) and kangaroo rats (Dipodomys ordi and Dipodomys microps) across the habitat types using spotlight surveys [43, 44]. Six road transects totaling 99 km were established in May 1999 and surveyed until August 2001. Spotlight transects overlapped but were not identical to scat transects. We conducted spotlight surveys in February, May, August, and November with each survey lasting 3 nights. All transects were driven each night, with at least 1 night between surveys to increase independence of locations. Surveys began 1 hour after sunset and consisted of 2 observers each using 1.5 million candle power spotlights to illuminate both sides of the road; vehicle speed was maintained at 16–24 kph. We recorded species, Universal Transverse Mercator (UTM) coordinates, and distance from the road for each individual observed; the distance for animals seen on the road was recorded as zero. Because of varying detection among habitats, we used strip transects with a maximum detection of 50 m for jackrabbits and 25 m for kangaroo rats to standardize the sampling area among all habitats (i.e., we used the lowest detection distance for all transects and habitats). We imported coordinates of observations into ArcView and overlaid them with the digital habitat map to determine the habitat class of each individual location. We calculated habitat availability by buffering each spotlight route by the detection distance (50 m for jackrabbits, 25 m for kangaroo rats) to produce a survey area. We used ArcView to determine the proportion of each habitat within each transects survey area.

We conducted small mammal trapping with Sherman live traps twice a year during prereproductive (June) and postreproductive (September) periods; 3 trapping grids were randomly placed in each habitat type. Each grid consisted of 64 traps placed 10 m apart in an 8 × 8 array. We baited each trap with peanut butter and oats, and each grid was active for a 4-night period. We baited and set traps just before dusk, then checked and closed them in the morning. Each animal captured was identified, weighed, sexed, and marked with black hair dye or a permanent marker before release.

We sampled nocturnal and diurnal insects using pitfall traps augmented with a drift fence [45]. Each pitfall array consisted of 3, 3 m arms arranged in a “Y”. At the ends of the arms and at the center of the array, we buried steel cans (15 × 17 cm) flush with the ground; 2 arrays were constructed in each of the habitats. We cleared the cans once in the morning and once at dusk for 3 days, allowing the identification of diurnal and nocturnal insect activity patterns. We operated the pitfall arrays at the end of the month, May–September, 1999 through 2001. Flush counts augmented invertebrate sampling by counting flying and hopping insects that were not susceptible to pitfall trapping [46]. One 50 m transect was measured off each corner of the 18 small mammal grids for a total of 4 transects per grid, 12 transects per habitat. We walked each transect once a month during the afternoon and recorded the number of lizards and insects flushing ≤2 m on either side of the observer, we walked transects during the same months the pitfall traps were operated.

2.6. Modeling the Predicted Canid Distributions. To determine if kit fox and coyote distribution patterns were being shaped by the heterogeneity of the underlying prey base (distribution by choice) or were instead being governed by interspecific carnivore interactions (distribution by force), we modeled “predicted” distributions for both canid species. Calculated from the distribution of prey populations and the diet of DPG’s canids, predicted distributions of canid foraging represent spatial strategy alternatives where, in the absence of competition, kit foxes and coyotes maximize their proximity to abundant prey resources [47]. In addition, we present an overall landscape use unrestricted from competition by combining all canids from all landscape classes to produce a simplified, population-wide spatial budget for each of the species. Differences between observed spatial strategies of canids and modeled predicted distributions were used to quantify competition’s role in shaping canid distribution on the landscape.

Proportions and rank of prey items in the diet of DPG’s canids were determined from percent occurrence data from the scat analysis. We included only prey types occurring in the diet ≥10% of the time in the predicted distribution model. For both kit foxes and coyotes, 4 prey classes met this criterion: insect, rodent, kangaroo rat, and rabbit. For each of the 4 dominant prey types, the number of individuals enumerated per vegetation community was converted to a proportion of each habitat class to create a resource matrix linking habitat to prey abundance. Future studies incorporating a conversion of the number of individuals of each species to prey biomass in each habitat type could increase the precision of the model, but would require density estimates of each prey species in each habitat type as well as knowledge of detection probabilities for each survey method.

To model the spatial response of kit foxes and coyotes to DPG’s prey matrix, we assumed that in the absence of competitive forces, canid populations would distribute themselves among vegetation types in proportion to the resources available to them [47–49]. Granted, other factors (e.g., prey vulnerability, temperature regimes, and soil types for dens) may have also influenced canid distribution, but we wanted to examine a relatively simple predictive model using prey distribution and abundance. The basic formula used to calculate the predicted distribution of canids was

\[
\text{Predicted distribution} = \sum_{j=1}^{p} \sum_{i=1}^{v} \left( A_{ij} D_i \right),
\]

Where \( A_{ij} \): Abundance of prey item \( i \) found in vegetation class \( j \), \( D_i \): Percent occurrence of prey item \( i \) in diet, \( p \): Number of prey classes, and \( v \): Number of vegetation classes.

Starting with the proportional distributions of the 4 dominant prey classes as their base, the predicted distribution models weighted the contribution of each prey species to the matrix by its percent occurrence in the diet. Summing the weighted proportions across the 4 prey classes produced a coarse spatial budget for kit fox and coyote populations.
based solely on the distribution of prey classes and their prominence in the diet.

3. Results

3.1. Observed Canid Distributions. We captured and monitored 26 coyotes (14 males, 12 females) and 28 kit foxes (17 males, 11 females) between December 1999 and August 2001. Sixteen coyotes (10 males, 6 females) and 17 kit foxes (9 males, 8 females) had sufficient locations for spatial analysis (i.e., area-observation curves reached an asymptote). During the study, we collected 1,781 and 1,559 locations on kit foxes and coyotes, respectively; >25% of these locations were visual observations during the set sampling time (i.e., mainly kit foxes lying on den mounds during the day). Continuous den monitoring and trapping efforts indicated that 90–95% of the kit foxes in the study area were captured and identified.

When averaged across the study area, coyotes (Figure 1(a)) showed preference for grassland (P < 0.0001), stable dune (P < 0.0001), and greasewood (P < 0.0001) habitats, with low but preferred use of urban areas (P < 0.001). Coyotes exhibited avoidance of chenopod (P < 0.0001), shrub-steppe (P < 0.0001), and pickleweed (P < 0.0001) habitats (Figure 1(a)). Habitat use by kit foxes varied dramatically (Figure 1(b)). Although “Mountain” foxes avoided greasewood (P < 0.0001), chenopod (P < 0.0001), and pickleweed (P < 0.0001), their use of shrub-steppe (P < 0.0001) was greater than predicted. “Mountain” foxes used grassland (P > 0.05) and stable dune (P > 0.05) habitats not different from their availability on the landscape. “Grassland” foxes showed overwhelming preference for the grasslands (P < 0.0001), while avoiding greasewood (P < 0.0001), chenopod (P < 0.0001), stable dune (P < 0.0001), pickleweed (P < 0.0001), and urban (P < 0.005) habitats; use of shrub-steppe (P > 0.05) habitat was not different than availability. “City” foxes showed preference for only the urban habitat (P < 0.0001), while using the greasewood (P < 0.001), grassland (P < 0.0001), stable dune (P < 0.0001), shrub-steppe (P < 0.0001), and pickleweed (P < 0.0001) habitats less than predicted; use of chenopod habitat was not different than availability (P > 0.05). “Poverty” foxes spent more time than predicted in pickleweed (P < 0.0001) and urban (P < 0.0001) habitats, while avoiding grasslands (P < 0.0001), shrub-steppe (P < 0.0001), and greasewood (P < 0.0001). “Poverty” foxes use of chenopod (P > 0.05) and stable dunes (P > 0.05) did not differ from their availability (Figure 1(b)).

3.2. Prey Distribution and Abundance. A total of 2,970 km were surveyed by spotlight counts with 1,708 jackrabbits and 1,028 kangaroo rats (mostly Dipodomys ordi) recorded. After standardizing for unequal transect lengths and proportion of each habitat type surveyed, the proportion of prey species recorded in each habitat were: shrub-steppe (black-tail jackrabbit [BTJ]: 26.3%, kangaroo rat [KR]: 34.9%), grassland (BTJ: 24.9%, KR: 36.3%), stable dunes (BTJ: 4.8%, KR: 13.8%), greasewood (BTJ: 23.5%, KR: 10.4%), chenopod (BTJ: 5.3%, KR: 0.4%), pickleweed (BTJ: 2.8%, KR: 0%), and urban (BTJ: 12.4%, KR: 4.2%).

Sherman live traps were operated for 18,432 trap nights between June 1999 and September 2000 for a total of 474 individual captures representing 9 small mammal species (Table 1). Community diversity as well as the abundance of small mammals, varied between habitats. Shrub steppe and stable dunes were the most diverse, while chenopod, pickleweed, and urban habitats were most limited in species composition (Table 1). Proportional abundance of all small mammals trapped by habitat type was: shrub steppe (25.6%), grassland (7.5%), stable dune (13.8%), greasewood (18.9%), chenopod (12.3%), pickleweed (9.9%), and urban (12.0%). Pitfall arrays were operated for 630 array nights and days. Although dozens of invertebrate species were trapped using this method, it proved most appropriate for assessing the relative abundance of Mormon crickets (Anabrus simplex), Jerusalem crickets (Stenopelmatus fuscus), and scorpions (Centruroides spp.). Although Mormon crickets were present in all habitats except pickleweed, they were overwhelmingly found in grassland (n = 1,466, 80%) and shrub steppe (n = 290, 16%) habitats (Table 2). Jerusalem cricket's had the highest abundance in stable dune (n = 17, 38%), grassland (n = 11, 24%), and shrub steppe (n = 11, 24%) habitats. The largest proportion of scorpions were in the stable dunes (n = 171, 49%), with a more even distribution across shrub-steppe (n = 56, 16%), chenopod (n = 45, 13%), and grasslands (n = 34, 10%).

A total of 54 km of flush counts were walked over the course of 15 summer months (Table 2). Grasshoppers (Orthoptera spp.) were found in grasslands (n = 1, 219, 72%), shrub steppe (n = 241, 14%), and greasewood (n = 100, 6%). Lizards (Sceloporus graciosus, Uta stansburiana, and Cnemidophorus tigris) were found primarily in stable dune (n = 32, 43%) and chenopod (n = 28, 37%) habitats.

3.3. Dietary Preferences. During the study, 1,131 coyote (691 lowland, 440 highland) and 294 kit fox (98 lowland, 196 highland) scats were collected. Thirty-eight different prey species were found in the 2 canids’ scat. Four (insect, rodent, kangaroo rat, rabbit) categories indicated significant importance in the diet (>10% occurrence) and were incorporated into the predicted distribution modeling (Figure 2). The percent occurrence of kangaroo rat remains of Dipodomys ordi and D. microps was 36.8% for kit foxes and 25.6% for coyotes. The rabbit species Sylvilagus nuttallii and Lepus californicus were represented in 11.1% of the prey occurrences of kit foxes and 31.9% of coyotes. The rodent category, including Reithrodonontomys megalotis, Peromyscus maniculatus, P. traei, Onychomys leucogaster, and Anomospermophilus leucurus represented 19.9% of the kit fox and 14.8% of the coyote prey occurrences identified. Insects, which include Mormon crickets (Anabrus simplex), Jerusalem crickets (Stenopelmatus fuscus), and grasshoppers (Orthoptera spp.), comprised 19.3% of kit fox and 13% of coyote scat occurrences. Scorpions (4.7% kit fox [KF], 1.1% coyote [Coy]), reptiles (1.1% KF, 2.1% Coy), birds (6.0% KF, 2.7% Coy), ungulates (0.2% KF, 5.8% Coy), native fruits and vegetation (0% KF, 2.2% Coy), miscellaneous mammals (0.2% KF, 0.6% Coy), and anthropomorphic foods (0.7% KF, 0.3% Coy) all were found in amounts deemed too small to give weight to the
Figure 1: Comparison of habitat type availability and use by (a) all coyotes, and (b) kit foxes in mountain, grassland, city, and poverty landscapes, Dugway Proving Ground, Utah, 1999–2001.


<table>
<thead>
<tr>
<th>Habitat</th>
<th>PEMA</th>
<th>REME</th>
<th>DIOR</th>
<th>ONLE</th>
<th>NELE</th>
<th>PETR</th>
<th>AMLE</th>
<th>DIMI</th>
<th>PEPA</th>
<th>No. of Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub-steppe</td>
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<td>14</td>
<td>30</td>
<td>1</td>
<td>15</td>
<td>9</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Grassland</td>
<td>23</td>
<td>10</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Stable dune</td>
<td>28</td>
<td>16</td>
<td>26</td>
<td>11</td>
<td>0</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Greasewood</td>
<td>63</td>
<td>24</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Chenopod</td>
<td>53</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Pickleweed</td>
<td>44</td>
<td>0</td>
<td>1</td>
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<td>0</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td></td>
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<tr>
<td>Urban</td>
<td>55</td>
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<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>342</td>
<td>66</td>
<td>58</td>
<td>17</td>
<td>15</td>
<td>14</td>
<td>8</td>
<td>7</td>
<td>3</td>
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</tbody>
</table>

Table 2: Abundance and distribution of prey species recorded during pitfall trapping and flush counts on Dugway Proving Ground, Utah, 1999–2001.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>No. of Jerusalem crickets</th>
<th>No. of Mormon crickets</th>
<th>No. of Scorpions</th>
<th>No. of grasshoppers</th>
<th>No. of lizards</th>
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</thead>
<tbody>
<tr>
<td>Shrub-steppe</td>
<td>11</td>
<td>290</td>
<td>56</td>
<td>241</td>
<td>3</td>
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<tr>
<td>Grassland</td>
<td>11</td>
<td>1466</td>
<td>34</td>
<td>1219</td>
<td>1</td>
</tr>
<tr>
<td>Stable dune</td>
<td>17</td>
<td>4</td>
<td>171</td>
<td>57</td>
<td>32</td>
</tr>
<tr>
<td>Greasewood</td>
<td>0</td>
<td>38</td>
<td>20</td>
<td>100</td>
<td>1</td>
</tr>
<tr>
<td>Chenopod</td>
<td>1</td>
<td>10</td>
<td>45</td>
<td>36</td>
<td>28</td>
</tr>
<tr>
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<td>3</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
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</tr>
<tr>
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<td>45</td>
<td>1818</td>
<td>349</td>
<td>1690</td>
<td>75</td>
</tr>
</tbody>
</table>

No scat of either species was found to contain kit fox remains. When combined for the calculation of predicted distribution models, the prey categories of insect, rodent, kangaroo rat, and rabbit, comprised 83.1 ± 3.5% of the prey occurrences in the year-round diet of both species.

3.4. Modeling the Predicted Canid Distributions. Modeled for the study area, the predicted use of habitat types by kit foxes was similar (Figure 3). Grassland (36.2% KF, 32.4% Coy), shrub-steppe (27.9% KF, 27.7% Coy), greasewood (12.5% KF, 15.6% Coy), and stable dune (11.1% KF,
9.7% Coy) habitats were predicted to obtain the most use. Less productive urban (5.3% KF, 7.3% Coy) and chenopod (4.0% KF, 4.4% Coy) habitats were predicted to receive low amounts of use, and pickleweed (2.9% KF, 2.9% Coy) habitat virtually no use.

Comparisons between predicted and observed distributions indicated a closer adherence to the predicted model by coyotes than kit foxes (Figure 4). Based upon prey availability (relative abundance) among the 7 habitat types, the predicted distribution showed that in certain habitats with high prey and high coyote use, kit foxes avoided these habitats. Conversely, in habitats with low prey and low coyote use, kit foxes demonstrated much higher use than expected on prey abundance alone. For example, the predicted distribution for urban habitat indicated that the canids should use it 3.3% of the time. Coyotes followed the prediction (3.1% of locations) while kit foxes showed a high preference exceeding that predicted by prey availability (16.0% of locations; $P < 0.001$). Similarly, the predicted model indicated that pickleweed should be used 1.6% of the time based on prey, with coyotes using pickleweed 1.0% of the time and kit foxes using it 14% of the locations ($P < 0.001$). In contrast, the predicted distribution for grassland habitat showed that the canids should spend 36.9% of their time based upon prey abundance. Coyotes were located in grasslands 39.2% of the time, while kit foxes avoided that habitat (19% of locations). Greasewood habitat was predicted to be used 16.4% of the time based on food availability, with coyotes preferring this habitat (22.6% of locations) more than predicted by food alone, while kit foxes avoided this habitat (8% of locations; $P < 0.001$). Overall, kit foxes showed strong avoidance of habitats utilized by coyotes, and their observed distribution was significantly different than the predicted distribution based upon food availability ($\chi^2 = 165.62, df = 6, P < 0.001$).

However, significant differences existed between most comparisons of observed versus predicted (modeled from prey distribution and abundance) distributions among both canids (Table 3). Relative to the predicted model, coyotes’ observed distribution demonstrated both strong avoidance of shrub-steppe and preference for stable dune habitats. Observed habitat use by “mountain” foxes, “grassland” foxes, “city” foxes, and “poverty” foxes showed their strongest divergence from predicted distributions to occur as a result of preferential use of the habitat types associated with their landscape class namesake. Foxes demonstrated avoidance of virtually all other habitat classes (Table 3).

4. Discussion

Initial studies examining canid distributions on DPG showed differential use of its habitats by coyotes and kit foxes [17]. Given evidence of such space use, the conclusion could be made that although the dietary overlap of these 2 species is high, the canids remain in a stable state of sympatry through the implementation of spatial isolation mechanisms, a strategy by which kit foxes are able to stave off competitive exclusion by partitioning their space use with coyotes. Although evidence of isolation mechanism use by kit foxes was apparent, determining the current canid interactions required examination of the underlying causes of their distribution.

The results of the quantitative assessments conducted in this study demonstrated that habitats varied significantly in their prey resources. Both prey species’ composition and abundance varied across the 7 habitat types examined, resulting in these habitats being differentially important to foraging canids. Pickleweed, chenopod, and urban habitats were characterized as being inhabited by the fewest number of individuals and species of small mammals, invertebrates, and lagomorphs. Although these habitats comprised a considerable proportion of the study area (37%), only kit foxes spent substantial amounts of their time in these resource-scarce habitats (Figure 1(b)). Coyotes generally demonstrated an aversion to these 3 resource-poor habitats (Table 3). Pickleweed and chenopod, in addition to poor prey abundance, were also characterized by an acute, seasonal lack of free water. Although free water is not considered a limiting factor for kit foxes, its absence likely resulted in the
further restriction of coyotes’ use of these landscapes thereby enhancing their refuge-like qualities for kit foxes [50].

Although shrub-steppe, stable dune, grassland, and greasewood habitats held the highest values for diversity and abundance of the prey items favored by canid species, their use by kit foxes was less than predicted (Figure 1(b)). Of the kit foxes 4 landscape classes, only the “mountain” foxes and the single pair of foxes using the grasslands showed a preference for these habitat types. In fact, greasewood, with the 2nd highest abundance of small mammals and 3rd highest abundance of lagomorphs, was universally avoided by kit foxes and never averaged more than 15% of any landscape class spatial budget (Table 3). In contrast, the spatial distribution of coyotes overlapped heavily with those habitats

Figure 4: Observed and predicted canid distributions for (a) coyotes, (b) mountain kit foxes, (c) grassland kit foxes, (d) city kit foxes, and (e) poverty kit foxes, Dugway Proving Ground, Utah, 1999–2001.
supporting abundant prey resources. Overall, the distribution of coyotes closely matched the heterogeneity of the landscape in a manner that maximized their access to prey resources.

The diet of kit foxes and coyotes, as determined from scat analysis, indicates a high level of overlap of both the species and proportions of prey consumed [17]. Of the prey categories analyzed, insects, rodents, kangaroo rats, and lagomorphs were the 4 most important components of both canids’ diets. This indicates that even when occupying relatively resource-poor habitats, kit foxes still managed to select prey items in proportions similar to those found in the diets.

Table 3: Comparisons between observed (lower and upper) and predicted canid distributions analyzed using the chi-square goodness-of-fit test [14]. Significant differences between distributions were detected using Bailey simultaneous confidence intervals. Habitats that were avoided were used less frequently than predicted; preferred habitats were used more than predicted.

<table>
<thead>
<tr>
<th>Habitat</th>
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<th>Predicted</th>
<th>Selection</th>
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<td>Upper</td>
<td></td>
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<td><strong>Coyotes: observed versus predicted</strong></td>
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of canids inhabiting higher quality habitats. This dietary resiliency likely requires more energy to maintain, either in the form of increased search time or larger territories, and thereby may have a negative effect on kit foxes’ fitness. In essence, by avoiding competition with coyotes through spatial isolation, kit foxes must forage in suboptimal habitats to meet their dietary requirements [51, 52].

While it has been demonstrated that asymmetrical spatial partitioning of coyotes and kit foxes was occurring in association with high levels of dietary overlap, the question of whether the spatial distributions of the 2 canids were based on resources (by choice) or competition (by force) still needs to be addressed. Classical niche apportioning theory supports that a species’ relative abundance is derived from the amount of limiting resources it controls [53–55]. It follows that in the absence of competitive forces, individuals should distribute themselves in patterns relative to the distribution of resources necessary for their survival and reproduction [56]. Although other researchers have successfully used removal of conspecifics to perturb faunal community conditions towards an ideal [57–59], such studies, when conducted on large, fecund, or protected species, may be too logistically difficult or politically unsavory to accomplish [60].

Given the extent of dietary overlap exhibited by the two canid species, it is not surprising that very similar predicted distributions were modeled for both coyotes and kit foxes (Figure 3). By demonstrating preferences for the same food resources in roughly the same proportions, it stood to reason that, in the absence of other selective forces, both canids should exhibit similar predicted distributions. However, while the observed distribution of coyotes paralleled the presence and absence of abundant prey, observed space use by kit foxes was clearly not in reaction to the distribution of food resources alone. Kit fox strategies, when examined from the context of space use, used geographic extremes (i.e., rugged terrain) not frequented by coyotes. The overall result was a reduction in fine-scale sympathy.

We made several assumptions when determining the predicted distribution of the two canids. Foremost was that prey abundance, in the absence of competition, was the only limiting resource governing the distribution canids on the study area. Denning sites, a factor which could possibly affect space use in canids, was assumed not to be limiting due to the flexibility in site selection observed during both historic and concurrent studies [17, 19]. Differences in the vulnerability of prey or the energy required to forage across the different habitats was not considered. Limitations arising from the simplified nature of the model were deemed acceptable within the context; the model was intended to provide a conceptual starting point for identifying the effects of competitive exclusion.

Of special interest was the use of the shrub-steppe habitat by both species. The only habitat with significant amounts of topography, the shrub-steppe, was characterized by steep, rugged terrain and abundant prey resources. Observed use of this habitat was in contrast with the predicted model for both canids. In particular, kit foxes using the mountain landscape occupied the shrub-steppe to a very high degree, while coyotes were observed to largely avoid this rugged landscape (Table 3). Landscape complexity and the energy required to forage in it likely decreased the use of shrub-steppe by coyotes, while simultaneously providing direct and indirect refuge for kit foxes in the form of improved cover and reduced competition. Similar benefits were provided by the structural complexity of the urban environments, allowing kit foxes to forage in nearby greasewood habitats normally dominated by coyotes. Foxes using the city landscape averaged 3 times the use of the greasewood habitat of the other 3 fox landscape classes combined. The unpredicted use of the shrub-steppe and urban habitats by kit foxes illustrates the complexity of habitat selection by a subordinate species in the presence of a very dominant species.

In conclusion, habitat selection by kit foxes appears to be a solution that reduces spatial overlap with coyotes while providing access to resources. Occupation of the spatial refuges provided by the rugged mountain ranges or the vacant alkali flats serve to both isolate and limit the number of kit fox territories possible on the landscape. Not unlike the characteristics exhibited by other remnant populations, DPG’s kit foxes have high dispersal mortality and limited mixing of subpopulations [17]. We believe that under current conditions, the long-term sustainability of DPG’s small kit fox population is questionable, and any conservation measures would need to address the effects of interspecific competition by coyotes.

Acknowledgments

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References


Minimum viable populations: is there a ‘magic number’ for conservation practitioners?

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Establishing species conservation priorities and recovery goals is often enhanced by extinction risk estimates. The need to set goals, even in data-deficient situations, has prompted researchers to ask whether general guidelines could replace individual estimates of extinction risk. To inform conservation policy, recent studies have revived the concept of the minimum viable population (MVP), the population size required to provide some specified probability of persistence for a given period of time. These studies conclude that long-term persistence requires ≥5000 adult individuals, an MVP threshold that is unaffected by taxonomy, life history or environmental conditions. Here, we re-evaluate this suggestion. We find that neither data nor theory supports its general applicability, raising questions about the utility of MVPs for conservation planning.

Conservation planning and the viability of populations
Establishing species conservation priorities and quantitative management objectives is enhanced by the ability to estimate the extinction risk faced by populations. In particular, two topical, linked concepts in conservation (triage and return on investment) often require an estimate of the risk faced by a population and the financial costs of strategies to mitigate that risk [1]. Early work on estimating extinction risk focused on population viability analysis (PVA) and related methods for estimating a threshold population size below which extinction risks were deemed unacceptably high (the so-called ‘minimum viable population’, MVP) [2–4] (Box 1). Formal application of these methods requires extensive, high-quality data, usually drawn from intensive, long-term studies [5–10]. Even with quality data, extinction probabilities will often be estimated with considerable uncertainty, unless populations are rapidly growing or declining [11], and forecasts of population fates should be restricted to short time horizons [10]. Unfortunately, for many species, especially those of conservation concern, quality long-term data on which to base estimates of persistence remain limited [12–14].

The need to make rapid decisions about conservation targets, often in the absence of necessary data, has prompted interest in identifying robust, general guidelines for MVPs [15,16]. Taking advantage of growing access to population and life-history data for large numbers of species, several recent papers [17–20] explore the credibility of a lower limit to robust MVPs. Despite apparent caution about overinterpreting the strength of evidence, the most recent review [20] asserts that ‘[t]he bottom line is that both the evolutionary and demographic constraints on populations require sizes to be at least 5000 adult individuals.’ A popular science summary of the article goes further, christening 5000 adults ‘a magic number’ that applies to ‘mammals, amphibians, insects, plants and the rest’ [21]. The conservation implications of this claim are profound, because it asserts that a population threshold of 5000 must be reached or exceeded, regardless of taxon (plant, invertebrate or vertebrate) or environmental context (either short-term stressors or more fundamental properties of the local environment).

Given the importance of managing for viable populations, it is essential that conservation biologists engage in robust debate regarding MVP. Our intention here is to focus on the analyses and conclusions from recent studies that advocate a universal threshold for MVP [17–20]. We begin by considering whether ecological principles support the notion of a universally applicable MVP threshold and by outlining crucial conservation policy outcomes of recent MVP papers [17–20]. Using data from three of the key papers [17–19], we identify aspects of analysis and interpretation that do not support the existence of a universally applicable estimate of MVP. Finally, we offer suggestions for how conservationists might proceed in the absence of such an estimate.

A universal threshold for MVP?
Traill et al. [20] argue that conservationists working in developing countries lack the resources to estimate MVPs accurately for conservation targets and, thus, that there is ‘a compelling argument to develop rules of thumb for population size extinction-risk thresholds.’ By contrast,
Box 1. History and estimation of a MVP

The MVP concept emerged in 1981 from Shaffer’s [2] pioneering paper that defined a minimum viable population as ‘the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.’ The criteria for evaluating viability (the time frame and associated extinction risk) were ‘tentatively and arbitrarily’ chosen by Shaffer, recognizing that risk criteria were within the purview of society as well as science. Operationally, time horizons of 50–100 years and extinction risk of 5% became the most frequently used criteria.

Shaffer [2] outlined five possible approaches for determining MVPs: experiments, biogeographic patterns, theoretical models, simulation models and genetic considerations. Experimentally manipulating the size of replicated populations and then following their trajectories is rarely possible in nature. Examining biogeographic patterns of distribution can lead to estimates of minimum area requirements, densities, or population sizes versus occupancy (i.e. incidence). However, because of the indirect tie to extinction, this approach is rarely used. Theoretical models can be used to predict the time required for a population of a given size to go extinct (see [26]), but the idiosyncratic or contextual situation that characterizes most wild populations precludes the application of such models to real-world conservation. Genetic considerations consisted of comparing an estimate of the effective size ($N_e$) of a population to the 50/500 ‘rule’ of conservation genetics (i.e. an $N_e$ exceeding 50 for short-term and 500 for long-term survivability). However, the 50/500 values of $N_e$ are simply viability goals for maintaining genetically diverse populations; they provide little direct connection with extinction risk.

The remaining method, simulation modelling (also known as PVA), is the most general and popular approach to estimating MVPs. A stochastic population projection model is constructed from estimates of the mean and variance of demographic rates (from studies of individuals) or from population growth rates (i.e. $r$ or $\lambda$, estimated from time series of counts or indices). Simulation models project populations into the future using Monte Carlo methods, incorporating chance events (e.g. demographic and environmental stochasticity, genetic effects of inbreeding and catastrophes) as well as other processes that affect the population, to produce extinction probabilities at specified time periods in the future. The minimum viable population size is found by iteratively changing the initial population size to find the smallest size that has a 95% chance of remaining extant at the end of the time period evaluated in the simulations.

The initial promise of MVP estimates as conservation yardsticks faded as conservation biologists realized that estimates of extinction risk from PVA models were often imprecise, inaccurate, contingent upon threats currently acting, and affected by model structure, study duration and other uncontrolled factors [5,71–73]. Many conservation biologists recognized that PVA models were best used for ranking relative extinction risk [5,50]. The focus on MVP was reversed to emphasize the importance of PVAs for understanding the relative probability of persistence for populations in a variety of scenarios. This approach, which focused on understanding population drivers and processes, was of broader utility to land managers and conservation practitioners. When used to evaluate multiple scenarios, PVA can bring together Caughley’s [25] small and declining population paradigms in a tool that helps practitioners search for solutions to conservation problems, rather than focusing only on a static, small population paradigm answer (MVP) [74].

we argue that there are compelling reasons to suspect that no single MVP is likely to apply adequately to all populations because extinction risks are often context dependent (Box 1), and manifest from a complex interaction between life history, environmental context and threat [22–24] that can be difficult to detect with noisy data [5,10]. Theory strongly suggests that the size of a population is only marginally relevant to the extinction risk when the rate of decline is rapid and continuous [25,26]. Characteristics of both a ‘fast life style’ associated with small body size and short generation times [27], and the ‘slow life style’ represented by large organisms with long generation times [24,28] can make some species and lineages more or less likely to go extinct, affecting any estimation of MVP. Moreover, extinction risks differ between lineages threatened by habitat loss, lineages threatened by human persecution and introduced novel predators [22,24] and lineages threatened by loss of food resources [29]. Thus, theory indicates that populations of equal size will vary greatly in their extinction risk depending on their life histories, long-term population growth rates, habitat quality and current threats.

The findings of recent MVP papers [17–19] are at odds with theoretical expectations. A brief overview of the approaches and findings used in these three recent papers is given in Table 1. These papers have been characterized by largely measured tones (see also [30]), with the authors using generally careful analyses to expose sources of uncertainty in estimates of MVP. Against that backdrop, the authors’ emergent conclusions [20] are surprising. In particular, the assertion that practitioners ‘must manage for biologically relevant MVPs [of] at least 5000 adult individuals’ [20] is made without reference to the specifics of the situation of any population. The suggestion that funding could be allocated on the basis of the numerical distance of a population from 5000 adults [20], if strictly implemented, does not adequately acknowledge that some populations might persist safely at lower population sizes, whereas others might need to be considerably larger to ensure persistence. The concern that ‘while scientists debate MVP variance, the extinction crisis deepens’ [20], discourages further discussion of the issue. However, if a generally applicable MVP is to guide policy and funding allocation, then a robust debate culminating in a workable consensus is essential. Such a debate has yet to occur, but will need to focus on the value judgements inherent in estimating MVPs, as well as on the methods underlying MVP estimates. In the next section, we direct our attention to the latter.

What do data on MVP tell us?

Using 5000 individuals as a rule-of-thumb for the MVP of a population (the robust conservation threshold advocated by Traill et al. [20,21]) would disregard substantial uncertainty in existing estimates of MVPs that suggests that 5000 is likely to be a very poor estimate for any specific population. Analyses underlying the derivation of the 5000 benchmark are complex and, inevitably, analytical decisions were required to make disparate data comparable for a wide range of species and from a large number of sources. Here, we focus on three important issues. Technical details are provided to support our arguments. We demonstrate that uncertainty and contingency in the data have not been accounted for adequately, and that a failure to find taxonomic or ecological differences in measures of central tendency among highly variable data does not, in and of
### Table 1. Data sets and analyses used to estimate MVPs, and results and conclusions from papers advocating the use of generally applicable MVP thresholds

<table>
<thead>
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<th>Data analysed</th>
<th>MVP analyses</th>
<th>Results and conclusions</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Demographic data on 102 vertebrate species; estimates of the frequency and magnitude of catastrophes, and default assumptions about the consequences of inbreeding depression</td>
<td>Standard PVA software package (VORTEX [81]) used to estimate MVPs conferring a 99% probability of persistence for 40 generations; estimates standardized to their expected values if 40 generations of demographic data were available (see Box 2)</td>
<td>No statistically significant difference detected among MVPs across taxa; overall mean standardized MVP = 7316. '[C]onservation programs, for wild populations, need to be designed to conserve habitat capable of supporting approximately 7000 adult vertebrates to ensure long-term persistence’</td>
<td>[17]</td>
</tr>
<tr>
<td>Time series data (acquired from the Global Population Dynamics Database [82]) on 1198 populations of plants, vertebrates and invertebrates</td>
<td>Information theoretic approaches used to assess support among five population growth models ranging in complexity from a random walk to a δ-logistic [80,83]. Numerical simulations based on each model determined initial population size (i.e. the MVP) conferring 99% probability of persistence for 40 generations or 90% probability of persistence for 100 years. Average MVP determined for each criterion by model averaging [84]</td>
<td>Median MVP = 1181 and 1377 for 40-generation and 100-year criteria, respectively; ’a striking lack of predictability in MVP’; ‘although MVPs provide a useful rule of thumb for species conservation, they should not be used as precise conservation targets’</td>
<td>[18]</td>
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<tr>
<td>287 published MVP estimates, covering 212 species</td>
<td>Meta-analysis; all published estimates of MVP standardized to those expected if the generating model had sought a 99% probability of persistence for 40 generations, and had included both inbreeding depression and the potential for catastrophes</td>
<td>Model including desired probability and time-frame for persistence, the inclusion of inbreeding effects, and the inclusion of catastrophes explained 6.3% of the deviance among published MVP estimates. Median standardized MVP = 4169; ‘a species’ or population’s MVP is context-specific, and there are no simple short-cuts to its derivation’</td>
<td>[19]</td>
</tr>
</tbody>
</table>

Box 2. Data standardization and uncertainty

Environmental stochasticity is a major driver of the dynamics of many populations. To model the effects of environmental stochasticity, it is necessary to have good estimates of variance in vital rates, which, in turn, require data collected over many years to sample the extent of environmental variation [5,75]. Short studies will often underestimate the range of vital rate variation, providing optimistic estimates of population stability and viability [78]. As a result, Reed and colleagues found that raw estimates of MVP (termed MVPA) produced by VORTEX were strongly affected by the study length (in generations; SLG) from which data were drawn [17]; they ‘corrected’ MVP estimates to the value expected from 40 generations of population data (MVPC) using the process depicted in Figure I. Essentially, the correction amounts to extrapolating an estimated MVP at point a along a line parallel to the regression (Equation (1)):

\[
\ln(MVP_{a}) = \beta_{0} + \beta_{1}(\ln(SLG)) + \epsilon
\]

until it intersects a study length of 40 generations at point c.

Two aspects of this process are problematic. First, the correction approach assumes that a regression of estimated \(\ln(MVP)\) against \(\ln(SLG)\) for any individual population would have an independent intercept, but a common slope defined by the overall regression of 102 different populations. Thus, the correction method is predicated on the belief that collecting an equal amount of additional data on individual populations (i.e. increasing the study lengths by a given number of generations) would increase each estimated MVP by the same absolute amount. No theory exists to support this assumption.

The second concern is that the regression equation used to standardize MVPs to a span of 40 generations included only two investigations with \(>15\) generations of data. Assessing the consequences of this is problematic. Although theory exists to guide the assessment of prediction intervals around a standard regression (Figure I), such theory cannot be applied in a straightforward manner to data points assumed to lie on independent regression lines, with a shared slope but independent intercepts. Owing to this complexity, we consider only that component of uncertainty in MVPC estimates [17] that is associated with error in the estimated regression slope.

We examined the uncertainty in MVPC based on the statistics associated with re-fitting Reed et al.’s regression model to the data presented in their appendix [17]. If we assume that MVPA and SLG are known, such that the variance associated with these quantities is zero, then the variance associated with each corrected estimate \(i\) of MVP (MVPC) is given by Equation (2):

\[
\text{Var}(\ln(MVPC_{i})) = \text{Var}(\hat{\beta}_{1})(\ln(40/SLG_{i}))^{2}
\]

The 95% confidence interval for each corrected value, which we call an extrapolation interval, can then be estimated using Equation (3):

\[
\ln(MVPC_{i}) \pm 1.96\sqrt{\text{Var}(\ln(MVPC_{i}))}
\]

We observed that the extrapolation intervals for the 102 species analysed by Reed et al. [17] failed to include the universal MVP of 5000 adult individuals in 60% of the cases (Figure II).

Although this analysis illustrates the high degree of uncertainty surrounding efforts to estimate persistence over the long term with limited empirical data, uncertainty is still greatly underestimated here. For example, assigning an SLG to each study in [17] assumes that generation length is a fixed life-history property within species. However, it is well known that estimating mean generation time is a challenge among species with overlapping generations [77,78], and examples illustrate that intraspecific generation length estimates can vary substantially (e.g. Ethiopian wolf generation time estimates range from 3 to 8 years [79]). Thus, the uncertainty bounds associated with the extrapolation process reported here are, at best, minimum estimates.
itself, provide evidence for a generally applicable MVP threshold.

**Standardization and extrapolation**

Reed *et al.* observed a strong effect of study duration on MVP estimates [17]. Furthermore, variation in vital rates among species with different life histories (e.g. large- versus small-bodied animals) was reduced when scaled to a common generation length [31]. To account for these observations, MVP estimates were ‘corrected’ to MVPC, the value expected if 40 generations of population data had been available [17–19]. The standardization process by which this was achieved, together with the statistical shortcomings of that approach, are summarized in Box 2. Reconsidering uncertainty in the data, we estimated that the lower and upper bound of the corrected (standardized) MVP for each individual population studied ranged from a minimum of 425 individuals to a maximum of 54,712 individuals (Box 2,
Figure II). This outcome suggests to us, as it has to others, that the size of populations required for long-term persistence ‘...are generally believed to be highly circumstance and species specific, depending on the environment and life history characteristics of the species’ [31].

A similar process was used by Traill et al. to standardize the MVPs estimated through many disparate modelling exercises [19]. A statistical model was used to standardize MVP estimates to control for varying methodology in the literature (Table 1). As with the standardization process applied by Reed et al. (Box 2), this amounts to assuming that the effect of a given factor (e.g. the inclusion of inbreeding effects) across populations would apply with the same absolute magnitude within each population. Although it would be testable, no theory exists to support this notion. Even accepting the standardization process, it is telling that the fitted model explained only 6.3% of the deviance among MVP estimates; remaining variability is presumably attributable to inherent differences among the focal populations and their environmental context (see following section). The explanatory power of the fitted model does little to justify the claim [20] that, ‘[d]ifferences between published MVP estimates, even for the same species, can also be explained by the different survival probabilities and timescales used.’

Density dependence and stability

Density dependence is profoundly important to the regulation of many natural populations, and fundamental to the recovery of populations from perturbation. The form of density dependence can exert a strong influence on extinction probabilities associated with different population sizes [32,33]. Papers analysing MVPs [17–19] have differed in their treatment of density dependence, leading to some contradictory interpretations of the importance of the phenomenon (Box 4). Clearly, a failure to include density dependence appropriately is likely to inflate estimates of MVP substantially. The difficulty of inferring the form of density dependence, even from relatively long population time series, highlights that meaningful estimates of MVP are likely to be derived only from very long, and therefore rare, data sets [8].

Re-evaluating support for a generally applicable MVP threshold

Reconsideration of the underlying data indicates that uncertainty in MVP estimates is substantial, regardless of the analytical approach used in recent treatments [17–19]. The vast uncertainty associated with MVP estimates for single populations or groups of populations probably underlies the tendency to find no evidence for statistical differences of MVPs among taxa [17] or strong life-history predictors of MVP size [18,19]. An alternative, more robust interpretation of that finding is that there is no significant difference in MVPs between taxa simply because there is such enormous variation in MVPs within taxa. Indeed, variation among populations is perhaps the most striking finding of recent analyses; for example, within-species estimates of standardized MVP varied more than 100-fold for the whooping crane (Grus americana), Eurasian beaver (Castor fiber), muskox (Ovibos moschatus), and others ([19] see Table S1 in supplementary material online). Thus, regardless of the taxon to which a population belongs, any ‘rule of thumb’ MVP is likely to be a poor estimate of
Box 3. Outlier MVPs

In our re-examination of the Brook et al. supplemental data [18], it was apparent that their original Figure 1 truncated observations at ln(MVP) = 20 (≈0.5 billion individuals). A replotting of their figure based on all observations in their supplemental data (n = 1198) revealed that the number of species with MVPs that exceeded 0.5 billion individuals varied by the population growth model fitted to the time-series data (Figure I), with higher frequencies of exceptionally large MVPs associated with models lacking density dependence (Figure la,b). These large MVP estimates could be an artefact of the method used to estimate MVP, for it seems difficult to argue that species such as the rough-legged hawk (Buteo lagopus), northern harrier (Circus cyaneus), or rook (Corvus frugilegus) require >1 billion individuals (model-averaged estimate) to remain viable, unless the studies supplying the empirical data were on populations subject to strong deterministic threats or severe catastrophic events. To remove the potential bias caused by what could be termed ‘methodological outliers’, we deleted any observations with an estimated ln(MVP) >20. This filtering shifted the median MVP estimate from 1181 (n = 1198) to 462 (n = 756) using the 40-generation criterion. If we further restricted our consideration to those species with relatively stable populations (−0.02 ≤ r < 0.02), then the median MVP was further reduced to 280 individuals (n = 339).

Our point here is not to argue that MVP targets should be lower than those advocated by others [17–20], but to highlight two observations: (i) median MVP estimates are sensitive to the set of species used in their estimation; and (ii) there appear to be legitimate circumstances where reported MVPs can be overly pessimistic. Both of these observations indicate that summary statistics applied to empirically derived estimates of MVP are characterized by a degree of sensitivity that is inconsistent with the notion of a robust universal MVP.

Figure I. Full frequency distributions of ln[MVP] from Brook et al. supplemental data [18] among five population growth models (a–e) and model-averaged (f) estimates using Brook et al.’s 40-generation (dashed line) and 100-year (solid line) viability criteria. Potential methodological outliers are associated with a frequency spike at ln(MVP) > 20.
Alternatives to a ‘magic number’ for viability

Our reconsideration of recent MVP papers suggests that there are good reasons for managers and conservation practitioners to regard advocacy of a universal MVP threshold with considerable scepticism. That, in turn, prompts two questions. First, if published estimates of MVP are insufficient to identify the characteristics of a population or organism that will determine its approximate MVP, can one identify those attributes? Second, if one is unable to identify (and, therefore, plan for) a generally applicable minimum number of individuals to conserve, what are the consequences for conservation?

The concept of viable minima is of interest not only to conservation biologists. Minimum population densities are closely tied to several aspects of ecology, such as understanding consumer–resource relationships, the use of energy within ecosystems and the relative roles of factors that limit population persistence, whether genetic, behavioural or energetic. Although relationships between population density and body size have long been a focus of macroecology [34], theory has not yet been used to predict the lower limits to this relationship [35]. Viable minima are also closely tied to Allee effects [36] and, in particular, to the concept of ‘Allee thresholds’ (the point at which mean per-capita population growth rates become negative) [37]. This suggests that alternative, active fields of ecology could yield insights into the factors that predispose a population to be tolerant of low densities and (given an understanding of space use) small population sizes. It would be useful for researchers in those areas to consider how their work might relate to traits affecting MVP.

**Box 4. MVPs and density dependence**

Reed et al. recognized the importance of density dependence and included it where its impact on vital rates had been measured, or where there were strong indications of its operation [17]. Although they gave no details of the number of their studied populations for which adequate data on density dependence were available, we can gain a sense of their empirical challenge by examining the frequency distribution of study lengths for the populations considered. Study duration estimates for each population that we derived from Reed et al.’s appendix [17] show that over a quarter of the 102 populations used had been studied for one generation or less, half had been studied for less than two generations, and only one population had a study length that exceeded 25 generations (Box 2, Figure I). With these limitations on the temporal extent of available data, establishing plausible patterns of density dependence would be difficult for most, if not all, of the populations for which MVP was estimated.

A more rigorous approach was taken by Brook et al., who analysed evidence for different forms of density dependence in population time series [18]. They found strong evidence that the inclusion of negative density dependence had an important bearing on MVP estimates. MVPs determined from shorter time series (which lacked strong evidence of density dependence) were more pessimistic (i.e. larger) than those based on longer time series (from which, evidence of density dependence was typically strong); overall, the estimated MVP was approximately an order of magnitude larger for short than for long time series [18].

Brook et al.’s [18] findings suggest an intriguing contrast with the earlier findings of Reed et al. [17]. Specifically, although Reed et al. found that longer studies led to more pessimistic MVP estimates, it appears that when density dependence is incorporated, the insights gained from longer studies provide reasons for greater optimism (smaller MVP estimates). Although some authors have subsequently expressed doubts about the model used to determine the form of density dependence [80], the emergent message remains that a failure to include density dependence is likely to inflate estimates of MVP substantially.

Given the clear importance of density dependence, it is perhaps surprising that Traill et al. found no evidence that the way in which density dependence was incorporated into models had a bearing on the estimated MVP [19]. Nevertheless, it is likely that the role of density dependence is more complex than could be detected by Traill et al.’s statistical approach. In particular, there are good reasons to expect that the form of density dependence would interact with other aspects of modelling and environmental context to influence MVP estimates.
If, at present, it is not possible to identify a universally applicable MVP, what might be the consequences for conservation? Traill et al. have linked uncertainty over MVPs to the current extinction crisis [20]. Thus, it is reasonable to ask to what extent the failure to agree on a universally applicable MVP contributes to the current extinction crisis? It seems more probable that: (i) extinctions occur because of a failure to identify and treat the causes of population declines [25,38], not because populations are assumed to be safe when, in fact, they are not; and (ii) failures to treat the major causes of decline are often related to political or economic issues [39–42], rather than to a lack of adequate scientific information on population viability.

What, then, is the utility of estimates for MVPs? In spite of the enthusiasm with which the MVP concept was initially embraced by conservation biologists, we can distil from literature only two advantages of having an estimate of MVP. First, an MVP can serve as a useful tool to persuade policy-makers that extinction is a possibility and action is required [43,44]. In this way, PVA and other quantitative criteria are used to classify taxonomically diverse species into threat categories under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species [45], identifying populations that merit further scrutiny. In these cases, policy-makers should interpret estimates of extinction risk and its accompanied uncertainty for various scenarios, rather than comparing recent estimates of population size to an estimate of a ‘secure’ MVP population size. Second, MVPs can be used to determine conservation targets, either proactively or reactively (sensu [46]). Proactive targets set minimum size thresholds that, if reached, would place populations in unacceptable danger. Reactive targets suggest objectives for population recovery programs (e.g. delisting decisions). Value judgements are likely to differ in the two cases. Reactive MVPs could be used in prioritization, for example, as a tool for determining probable return on investment and, thus, as an aid to ecological triage [20]. Specifically, Traill et al. suggest prioritizing spending based on the distance a population is below a generalized target size of 5000 adults, in conjunction with the cost and likelihood of elevating the population to that target [20], ‘...to abandon hopelessly-case species in favour of greater returns elsewhere’ [21]. Given the poor support for a universal MVP, this approach lacks credibility.

In keeping with numerous other authors (e.g. [9,45,47–54]), we recognize the value of PVA in bringing together relevant information on a population, formalizing understanding of the important processes, exposing gaps in knowledge, and serving as a focus for both scientists and policy-makers. However, in agreement with those same authors, we recommend against using the outcomes of such modelling exercises to set conservation targets unless there are strong reasons to believe that modelling outcomes are robust and defensible for the focal population. Embracing a single, estimated MVP threshold would release biologists from the obligation to assess the situation of the focal population, thereby forfeiting the diagnostic benefits that emerge from doing so [25]. Much of modern conservation is directed towards landscape- or ecosystem-level processes [55–57]. However, in situations in which populations remain the focus of conservation action, particularly when trying to salvage populations that are already in trouble, we suggest that there is no substitute for diagnosing and treating the mechanisms behind the decline of a population [25,38], actions that are unlikely to be informed by using a ‘magic number’ to set a target for conservation.

Conclusions

We applaud recent efforts [17–20] to encourage more quantitative approaches to evaluating population viability than a reliance on the oft-cited 50/500 MVP rule of conservation genetics [58,59]. The findings that MVP estimates are sensitive to the duration over which data were gathered and that meta-analytic comparisons among MVP estimates require rigorous standardization emphasize the need to obtain good estimates of demographic variability. We also suspect (as have others long before [60]) that multiple populations totalling thousands (not hundreds) of individuals will be needed to ensure long-term persistence. Nevertheless, MVP estimates both among and within species show striking variation for many reasons. The fundamentally contingent nature of MVPs means that we cannot support a universally applicable MVP threshold.

Ecology has been characterized as a science built on ‘contingent generalizations’ [61,62]. Such contingency has long been acknowledged in the PVA literature [2] and continues to fool attempts to generalize about crucial levels of habitat or abundance [16,63], even among populations of a single species [64]. Uncertainty, even when dealing with populations of the same species, suggests that generalizing among species is a dangerous undertaking. Failing to account for uncertainty is a common problem in conservation [65], and can lead to biased expectations and to the misdirection of scarce conservation resources [66].

The MVP concept is a key example of one of the hardest questions faced in conservation biology: how much is enough? Key national legislations governing endangered species decisions (e.g. the US Endangered Species Act, Canada’s Species at Risk Act, and Australia’s Environmental Protection and Biodiversity Act), as well as efforts by national and international organizations committed to species conservation [67], use MVP concepts that can revolve around listing decisions (has the species declined to a number that is threatened with extinction?), delisting decisions (has it recovered enough that it is no longer so threatened?), extinction risk categorizations, and determining the number and size of protected areas that a threatened species needs. MVP analyses and PVA modelling can be used to assist in these decisions, but their value is constrained by large uncertainty in model outcomes [68]. Realistic MVPs might well be in the thousands for many life histories, but uncertainty around any guideline figure would be of a similar order of magnitude. The extinction of the passenger pigeon (Ectopistes migratorius), perhaps the most abundant land bird in North America during the 1800 s (numbering 3–5 billion individuals [69]), stands as a sobering reminder that population size alone is no guarantee against extinction. As others have remarked, ‘population viability analysis is an inexact science,’ [17] and there is ‘no single ‘magic’ population size that guarantees’ population persistence [70].
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Appendix A. Supplementary data
Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2011.03.001.

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From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape

Andrea T Morehouse and Mark S Boyce

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Large carnivores have important influences on ecosystem structure and function (Ripple and Beschta 2004), but conflicts with agriculture often limit management options. Predation on livestock is a concern wherever wolves (Canis lupus) and livestock overlap, yet research across North America indicates that wild ungulates, not livestock, are the main prey in wolf diets (Bjorge and Gunson 1983; Fritts et al. 1992; Peterson and Ciucci 2003). Understanding wolf diets is particularly important in agricultural landscapes, where the response to livestock predation may be to remove entire wolf packs.

The primary period of concern regarding livestock loss is summer and early fall, when cattle (Bos taurus) graze freely on public land, often in high densities, with little to no monitoring (Bjorge and Gunson 1983; Gunson 1983; Fritts et al. 1992). Grazing season timing coincides with the wolf pup-rearing season (Figure 1); the nutritional demands of wolves are considerable during this period, due to the need to satisfy growing pups. This potentially heightens the risk of predation on cattle throughout the grazing season (Fritts et al. 2003). The change in the abundance of cattle within the wolf-pack territories – from absent during the non-grazing season to high densities during the grazing season – may result in prey switching (Murdoch 1969) and an increased amount of cattle in the diet of wolves.

Wolf diets are typically assessed using scat analysis or, more recently, field searches of clusters of global positioning system telemetry relocations (Sand et al. 2005; Webb et al. 2008). The majority of studies on wolf kill sites have been undertaken in winter, when prey remains are easier to find, but such diet analyses do not account for seasonal variation in diet (Sand et al. 2008). Assessing wolf diets during the summer is more challenging, because small prey, such as deer (Odocoileus spp) fawns and elk (Cervus elaphus) calves, are rapidly consumed (Peterson and Ciucci 2003), and the lack of snow makes tracking wolves more difficult. Consequently, summer diets have been studied using scat analysis, although this only reveals what the wolves ate and not necessarily what they killed. In North America, most predator-compensation programs require physical evidence to indicate that the animal was killed by wolves before a livestock producer can receive compensation (Bergman and Mack 2007). The GPS cluster method can identify prey remains for evidence of predation on cattle (Figure 2), but this method can be biased toward large-bodied prey and might not accurately reflect total wolf diet composition (Sand et al. 2005).

In Alberta, Canada, the highest levels of predation on cattle occurred in the southwestern corner of the province, an area which represents only 3% of Alberta’s land area, but accounts for 37% of all paid claims (Alberta Conservation Association unpublished data). Southwestern Alberta is a heavily ranched landscape, characterized by an abrupt change in topography, where the Rocky Mountains meet the prairies; here, predation is a year-round problem for cattle producers, as wildlife habitats overlap grazing lands, so that the potential for conflict between predators and cattle is higher than elsewhere in the province.

Predation on cattle in Alberta is largely attributable to wolves, accounting for 74% of all monies paid through
the provincial predator-compensation program between 2000 and 2010 (Table 1). Moreover, the number of claims and the amount of money paid through such claims has risen over the past decade (Table 1). Despite increasing conflicts between wolves and cattle in southwestern Alberta, no study has assessed year-round wolf diets in this region. We used GPS cluster visits and scat analysis to test the hypothesis that an increase in cattle abundance in the grazing season results in a seasonal increase in the amount of cattle in wolf diets.

**Methods**

We captured four wolves from three packs using padded-jaw leg-hold traps or helicopter netgunning (University of Alberta Animal Care Protocol #565712). We collared the captured wolves with upload-capable Lotek 7000SU GPS radiocollars set to a one-hour duty cycle (Lotek Engineering, Newmarket, Canada). We monitored these individuals from 20 June 2008 through 14 October 2009. Individual wolves wore GPS radiocollars for 118–351 consecutive days (x = 215, SE = 51.86).

**GPS clusters**

We downloaded GPS telemetry data from the ground every 7–10 days during the grazing season and every 2–3 weeks during the non-grazing season. Location data were plotted in ArcMap 9.2 (ESRI, Redlands, CA), and clusters were identified as any location where the wolf spent ≥3 hours and GPS locations were within 100 m of each other. We visited GPS-cluster sites 1–47 days (x = 12.76, SE = 0.27) after the wolves were first detected there; however, den sites were visited several weeks later.

**Table 1. Compensation payments (in Canadian dollars) paid to livestock producers through Alberta’s predator compensation program, 2000–2010**

<table>
<thead>
<tr>
<th>Year</th>
<th>Total compensation paid (CANS)</th>
<th>Compensation paid due to wolf predation on, or injury to, cattle (CANS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000–2001</td>
<td>68 128</td>
<td>45 321</td>
</tr>
<tr>
<td>2001–2002</td>
<td>78 031</td>
<td>48 376</td>
</tr>
<tr>
<td>2002–2003</td>
<td>60 561</td>
<td>40 274</td>
</tr>
<tr>
<td>2003–2004</td>
<td>91 784</td>
<td>66 814</td>
</tr>
<tr>
<td>2004–2005</td>
<td>49 179</td>
<td>35 555</td>
</tr>
<tr>
<td>2005–2006</td>
<td>95 588</td>
<td>78 491</td>
</tr>
<tr>
<td>2006–2007</td>
<td>91 577</td>
<td>68 281</td>
</tr>
<tr>
<td>2007–2008</td>
<td>118 858</td>
<td>86 814</td>
</tr>
<tr>
<td>2008–2009</td>
<td>145 925</td>
<td>123 857</td>
</tr>
<tr>
<td>2009–2010</td>
<td>144 374</td>
<td>110 046</td>
</tr>
<tr>
<td>Total</td>
<td>944 006</td>
<td>703 829</td>
</tr>
</tbody>
</table>

Notes: 1 Includes payments for death or injury to all domestic livestock (cattle, bison, sheep, swine, and goats) due to black bears, grizzly bears, wolves, cougars, and eagles. 2 Includes only payments for death and injury to cattle due to wolves.
We searched clusters in cardinal directions, following methods detailed by Knopff et al. (2009). We assigned a “kill” status to the site if we found prey remains that closely matched the time period during which wolves were present, and there was evidence that the animal had been killed by wolves (Peterson and Ciucci 2003; Webb et al. 2008). We examined prey remains to identify species, sex, age, and any abnormalities. Wild ungulates were aged in the field as young-of-the-year (<1 year), yearling (<1 year but <2 years), or adult (>2 years) based on tooth-eruption patterns. Cattle ages were confirmed by the producer. Sites were classified as scavenge events if there was clear evidence the animal had not been killed by wolves (ie other predator kills, boneyards [where carcasses are dumped], hunter kills, and road kills).

We compared prey composition from GPS clusters between seasons using a chi-square test. We used frequency of prey detections, body mass of prey, and expected prey consumption to estimate relative biomass of each prey species in wolf diets. Using estimates of consumable biomass available in the literature (Głowaciński and Profus 1997; Hayes et al. 2000; Jedrzejewski et al. 2002; Sand et al. 2008), we assumed wolves consumed 65% of the live mass of large-bodied prey (>100 kg), 75% of medium-bodied prey (20–100 kg), and 90% of small-bodied prey (<20 kg). We calculated average live weights of Alberta ungulates adjusted for age and season. If the age of found prey was unknown, we used an average of all three age classes for the given season. Livestock weights were estimated by a local grazing co-op (M Roberts pers comm). Biomass of each species is expressed as a percentage of total estimated biomass consumed. Scavenging events were excluded from prey biomass calculations.

Scat

We collected scat samples opportunistically along roads, trails, at GPS-cluster sites, and at den and resting sites known as rendezvous areas. Scats were collected, stored, and analyzed using established methods (see WebPanel 1 for details). We calculated the frequency of prey items occurring in scats and expressed these data as a percentage that represents the occurrence of each prey item relative to the total number of prey items. An “item” is defined as the occurrence of a particular prey species in the scat sample; if, for example, both deer and ground squirrel were detected in a scat sample, that sample would be said to have two prey items. We also estimated relative biomass consumed by wolves using Weaver’s (1993) regression equation \( \hat{y} = 0.439 + 0.008x \), which describes the mass of prey (kg) \( \hat{y} \) consumed per collectable scat as a function of body mass of prey (kg) \( x \). We derived percent biomass by expressing the estimated consumed biomass of each species relative to the total biomass consumed. We adjusted prey weights to reflect the distribution of age classes found at kill sites in each season. When possible, scats were grouped by season. If it was not possible to know which season the scat was from (eg scats collected at dens and rendezvous sites visited after wolves had departed), no seasonal status was assigned and samples were used only for total diet assessment. We compared frequency of prey items in wolf scats across seasons using a chi-square test. For analysis, prey items < 10 kg were pooled due to small sample sizes. We also compared frequency of prey items across methods (GPS clusters vs scat samples) using a chi-square test.

Results

We visited 698 GPS cluster sites (mean number of clusters/wolf = 174.5, SE = 39.94). We found 181 kill sites and 32 scavenge sites. With one exception, we found only a single prey item per kill site. Wild ungulates and cattle made up 100% of prey items found by the GPS cluster technique, and composition of these sites varied seasonally (Figures 4a and b). We examined 319 scats and identified 675 prey items (mean prey items/scat = 2.12, SE = 0.05). Wild ungulates and cattle accounted for 72.3% of all prey occurrences in scat, but 91.4% of the estimated relative biomass consumed (WebFigure 1).

Both methods indicated a seasonal prey shift, from wild ungulates during the non-grazing season to cattle in the grazing season (kill sites: \( \chi^2 = 34.05, P < 0.001 \); scats: \( \chi^2 = 47.76, P < 0.001 \)). Cattle comprised 73.9% of the estimated biomass consumed during the grazing season (Figure 4d). GPS cluster visits indicate scavenging was more prevalent during the non-grazing season, with 85% of these scavenging events consisting of wolf visits to ranch-
Changes in wolf diet composition

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ers’ boneyards. Patterns were consistent across wolf packs.
Frequency ranking of large-bodied prey (e.g., cattle, deer, elk, and moose) was the same across methods in the grazing season ($\chi^2 = 3.57$, $0.5 > P > 0.25$), but differed across methods in the non-grazing season ($\chi^2 = 9.49$, $P < 0.05$). In the non-grazing season, deer were found most frequently at kill sites, and evidence of elk consumption was found most frequently in scat.

Discussion

Most studies of wolf diets in North America indicate that wolves primarily prey on wild ungulates (Peterson and Ciucci 2003). In our study area, however, cattle made up a larger component of wolf diet than has been reported in previous studies, especially during the livestock-grazing season; this supports our hypothesis that an increase in cattle abundance would lead to an increase in predation on cattle by wolves. During the course of our study, we identified the remains of 50 cattle at wolf kill sites from three packs, or roughly 17 cattle killed per pack per year. In contrast, the Northern Rocky Mountain Distinct Population Segment (Idaho, Montana, Wyoming, eastern one-third of Washington and Oregon, and a small part of north-central Utah) reported 192 confirmed cattle losses to 242 wolf packs in 2009 – down from 214 confirmed cattle losses to 217 wolf packs in 2008 (Sime and Bangs 2010) – or < 1 head of cattle per pack.

To our knowledge, our study is the first to use the GPS-cluster method to assess wolf diets in a ranching landscape. This method allowed us to locate cattle that would otherwise be classified as “missing” when livestock producers removed cattle from grazing allotments at the end of the grazing season. Local producers have long suspected that missing livestock could be attributed to wolf predation, but lacked evidence to support this claim. In Alberta, the predator-compensation program pays 100% of the market value for confirmed predator kills of livestock, and 50% of the market value for “probable” kills (Bergman and Mack 2007). The program, however, no longer pays for missing animals (Gunson 1992). Missing animals are therefore a primary concern of livestock producers, since they receive no compensation payments for them (Bergman and Mack 2007). Producers occasionally received compensation for animals found by our GPS cluster method, compensation they otherwise would not have received. Missing livestock are recognized as a problem elsewhere as well (Bangs et al. 1998). Nyhus et al. (2005) estimated that, in Wyoming, for every confirmed livestock loss due to grizzly bears (*Ursus arctos horribilis*), there was the equivalent of another two-thirds of an animal that was never located. Because wolves tend to scatter bones and other remains at some distance from a kill site (Sand et al. 2008), the numbers of missing cattle may be even higher, especially in areas where locating remains is difficult (e.g., in thick vegetation).

As expected, GPS clusters reflected a bias towards large-bodied prey, whereas scat analysis detected smaller prey items. Evidence of small prey ($\leq 10$ kg) occurred in wolf scat frequently but accounted for < 8% of the total estimated biomass consumed. A key worry with the GPS-cluster method is its inability to detect small prey, such as neonate ungulates (Sand et al. 2008; Webb et al. 2008). Our results, however, suggest we did not miss many young-of-the-year ungulates because there was no significant dif-
ference in prey occurrence between kill sites and scat analysis during the grazing season. Had we missed ungulate neonates in our GPS-cluster searches, we would have expected to see a higher proportion of deer and elk remains in scat when compared to the GPS-cluster kill sites.

Scat analysis does not provide details about wolf predation. We observed several instances of scavenging during the non-grazing season; scavenging sites made up 19% of GPS-cluster sites at which prey were found. Almost all scavenging events were on dead cattle, which increased the percent occurrence and estimated percent biomass of cattle remains in scat during the non-grazing season. The number of scavenging incidents in the grazing season was low and spread across prey species; there is therefore no reason to believe that cattle were over-represented in the scat analysis for this period.

While both GPS cluster data and scat analysis indicated a strong seasonal shift in wolf diets, the mechanism driving wolf prey selection remains unclear. It may be that prey selection remains constant, and the increased amount of cattle in the wolves’ diet is attributable to the increased numbers of cattle arriving in the area during the grazing season. Alternatively, the evidence of increased amounts of cattle in wolf diets could be explained by prey switching, whereby the wolves’ selection of cattle as prey increases as the relative abundance of cattle increases (Murdoch 1969). Seasonal differences in prey vulnerability may also influence wolf prey selection (Lingle et al. 2008). We recommend further use of the GPS-cluster method because it provides information on what the wolves killed, not just what they consumed.

Wolf visits to ranchers’ boneyards accounted for 85% of non-grazing-season scavenging events. These piles of dead livestock are a growing problem in southwestern Alberta, and have become even more prevalent since the detection of bovine spongiform encephalopathy (BSE, or “mad cow disease”) in Canadian cattle in 2003. Prior to BSE, rendering trucks removed dead stock free of charge and used the carcasses in dog-food and cattle feed supplements. However, changes in regulations by the Canadian Food Inspection Agency (CFIA) now prohibit the inclusion of specific risk material (SRM, ie tissues capable of transmitting BSE) in livestock feed, pet food, and fertilizer (CFIA 2007). SRM must now be disposed of separately, either through burial or incineration. Rendering companies pass on the costs of dealing with these new regulations to producers; these costs are prohibitively expensive for local producers, causing many to pile up carcasses in boneyards instead. Natural disposal, in the form of wildlife scavenging from boneyards, is currently legal in Alberta and is one of five government-approved livestock-carcass disposal options (Province of Alberta 2009). All large carnivores in southwestern Alberta have been reported to scavenge from these boneyards. Ironically, the CFIA regulations designed to prevent the spread of the BSE-causing prions might actually be promoting further contamination; if the cattle carcasses in boneyards are contaminated with BSE, there is a risk that it may spread to the carnivores feeding on them (Williams and Miller 2003).

Boneyards represented an important food source for wolves during winter, and they often made repeated visits to these locations. This is especially problematic because boneyards are required to be a minimum of only 400 m from livestock facilities and residences (Province of Alberta 2009). This brings carnivores into close contact with other stock-growing activities (eg calving), which could result in further conflict between wildlife and ranchers. Bear-proof metal storage bins have been suggested as an alternative to boneyards, to reduce scavenging and prevent carnivores from becoming accustomed to feeding on livestock (Northrup 2010). Restricting access to attractants (eg carcasses, grain bins, garbage dumps, etc) is a powerful tool for both conservation and management of carnivores (eg Bino et al. 2010). Partnerships are being developed in Canada and the US, to assist producers in securing funding for metal storage bins (eg Blackfoot Challenge and Drywood Yarrow Conservation Partnership). These programs offer a sensible solution for preventing BSE spread (Northrup 2010).

We caution that our results are from an area of intense overlap between wolves and cattle grazing; predation on cattle is less prevalent in many other areas of western Alberta.
North America (eg Webb et al. 2008). We recommend further use of the GPS-cluster method to help identify wolf diets in ranching landscapes, particularly in areas where missing animals are a concern among cattle producers. Wolves and other carnivores are important components of healthy ecosystems, but maintaining wolves on the landscape is largely dependent on societal values. Tolerance of carnivores diminishes as conflicts with livestock, pets, and people increase. Finding ways to reduce wolf–livestock conflicts is therefore fundamental to ensuring future coexistence between humans and wolves.

Acknowledgements

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References

WebPanel 1. Wolf scat analysis methods

To avoid accidental collection of non-wolf scats, we collected only scats that were ≥ 30 mm in diameter (Weaver and Fritts 1979). Scats ≤ 30 mm were collected only if they were in the vicinity of a known den or rendezvous area, or if they were accompanied by fresh wolf tracks and there was no evidence that coyotes were present at the site (Arjo et al. 2002). Scats were collected in plastic ziplock bags, which were labeled with the date of collection, GPS location, and suspected pack. Samples were then frozen for later analysis. Prior to analysis, scat samples were autoclaved, washed in a sieve, and dried (Reynolds and Aebischer 1991). We identified mammal hairs in the scat to species by microscopic examination of the medulla and cuticular scale patterns (Moore et al. 1974; Kennedy and Carbyn 1981). White-tailed deer (Odocoileus virginianus) and mule deer (O hemionus) were pooled due to the difficulty in distinguishing between these species (Moore et al. 1974). Similarly, marten (Martes americana), fisher (Martes pennanti), and ermine (Mustela erminea) were pooled as “mustelids”; Richardson’s ground squirrels (Urocitellus richardsonii) and Columbian ground squirrels (Urocitellus columbianus) were pooled as “squirrels”; and mice, voles, and shrews were pooled as “small rodents”. We used Alberta-specific live weights for our biomass calculations for both scat- and kill-site analysis (Schladweiler and Stevens 1973; Renecker and Samuel 1991; Stelfox 1993; Cook 2002; Hudson and Haigh 2002; Schwartz 2007).

## References


Developing Metapopulation Connectivity Criteria from Genetic and Habitat Data to Recover the Endangered Mexican Wolf

CARLOS CARROLL, RICHARD J. FREDRICKSON, AND ROBERT C. LACY

Abstract: Restoring connectivity between fragmented populations is an important tool for alleviating genetic threats to endangered species. Yet recovery plans typically lack quantitative criteria for ensuring such population connectivity. We demonstrate how models that integrate habitat, genetic, and demographic data can be used to develop connectivity criteria for the endangered Mexican wolf (Canis lupus baileyi), which is currently being restored to the wild from a captive population descended from 7 founders. We used population viability analysis that incorporated pedigree data to evaluate the relation between connectivity and persistence for a restored Mexican wolf metapopulation of 3 populations of equal size. Decreasing dispersal rates greatly increased extinction risk for small populations (<150–200), especially as dispersal rates dropped below 0.5 genetically effective migrants per generation. We compared observed migration rates in the Northern Rocky Mountains (NRM) wolf metapopulation to 2 habitat-based effective distance metrics, least-cost and resistance distance. We then used effective distance between potential primary core populations in a restored Mexican wolf metapopulation to evaluate potential dispersal rates. Although potential connectivity was lower in the Mexican wolf versus the NRM wolf metapopulation, a connectivity rate of >0.5 genetically effective migrants per generation may be achievable via natural dispersal under current landscape conditions. When sufficient data are available, these methods allow planners to move beyond general aspirational connectivity goals or rules of thumb to develop objective and measurable connectivity criteria that more effectively support species recovery. The shift from simple connectivity rules of thumb to species-specific analyses parallels the previous shift from general minimum-viable-population thresholds to detailed viability modeling in endangered species recovery planning.

Keywords: Canis lupus baileyi, circuit theory, conservation planning, Endangered Species Act, least-cost distance, metapopulations, population viability

Desarrollo de Criterios de Conectividad Metapoblacional a Partir de Datos Genéticos y de Hábitat para Recuperar al Lobo Mexicano en Peligro de Extinción

Resumen: Restaurar la conectividad entre poblaciones fragmentadas es una herramienta importante para aliviar las amenazas genéticas para las especies en peligro. A pesar de esto, los planes de recuperación tipicamente carecen de criterios cuantitativos para asegurar la conectividad de dicha población. Demostramos cómo los modelos que integran los datos de hábitat, genéticos y demográficos pueden ser utilizados para desarrollar criterios de conectividad para el lobo mexicano (Canis lupus baileyi) que se encuentra en peligro y actualmente está siendo reintroducido a la vida silvestre a partir de poblaciones cautivas que descienden de 7 fundadores. Usamos el análisis de viabilidad poblacional, que incorporó datos del árbol genealógico, para evaluar la relación entre la conectividad y la persistencia para una metapoblación restaurada de lobo mexicano con 3 poblaciones de igual tamaño. La disminución de las tasas de dispersión aumentó el riesgo de extinción de poblaciones pequeñas (<150-200), especialmente cuando las tasas de dispersión bajaban más allá de 0.5 migrantes genéticamente efectivos por generación. Comparamos tasas de migración observadas en la metapoblación de lobos de las Montañas Rocallosas del Norte con 2 medidas efectivas de distancia
Introduction

Efforts to recover endangered species increasingly involve measures to ensure population connectivity between core habitat areas to enhance population persistence and maintain evolutionary potential (Lowe & Allendorf 2010). The U.S. Endangered Species Act (ESA) requires that recovery plans define “objective and measurable” recovery criteria that comprehensively address the threats that led to listing of the taxa as threatened or endangered (16 U.S.C. §1533 [f][1][B][iii]). However, recovery plans that mention connectivity typically include only aspirational objectives or general rules of thumb (USFWS 1987). Here, we used a case study of recovery planning for the endangered Mexican wolf (Canis lupus baileyi) to demonstrate why quantitative connectivity criteria can form an important element of recovery plans and how such criteria can be developed and implemented.

As descendants of the first wave of colonization of North America by the gray wolf (Canis lupus), Mexican wolves represent the most genetically unique New World wolf lineage and one of the most endangered mammals in North America (Vonholdt et al. 2011; Wayne & Hedrick 2011). One population of approximately 75 individuals currently exists in the wild, with approximately 300 additional individuals maintained in captivity (Siminski 2012). Genetic threats are greater for the Mexican wolf than for other wolf subspecies because 7 wild founder individuals were the source of all wolves in both the captive and reintroduced populations (Hedrick & Fredrickson 2008). Negative effects of inbreeding on litter size are evident in captive and wild populations of Mexican wolves (Fredrickson et al. 2007). In other small and isolated wolf populations in Europe and North America, inbreeding accumulation has reduced litter size and increased incidence of skeletal defects (Liberg et al. 2005; Räikkonen et al. 2009). Dispersal of even a single migrant into such inbred populations can dramatically affect genetic structure and population performance (Vilà et al. 2003).

Wolves are among the most vagile of all terrestrial mammals and can disperse over 800 km (Forbes & Boyd 1997). Wolves were historically present throughout their range in the contiguous 48 states as a largely continuous population with some degree of genetic isolation by distance and additional heterogeneity reflecting ecological factors (Vonholdt et al. 2011). Due to habitat loss, over-exploitation, and other factors, future wolf distribution in the United States outside of Alaska is likely to consist of many relatively disjunct subpopulations, and these subpopulations will be small relative to historic population sizes (> 300,000; Leonard et al. 2005). However, given the species’ vagility, achieving connectivity via natural dispersal may be feasible within such a metapopulation. Rigorous assessment of the influence of connectivity as well as population size on viability is thus a necessary component in wolf recovery planning (Wayne & Hedrick 2011).

We demonstrate how results from population viability analyses can be combined with habitat data to develop quantitative recovery criteria for population connectivity. We used population viability analysis (PVA) that incorporated pedigree data to address the relation between connectivity and persistence for the species. Pedigree data for the existing wild population and for new populations founded by hypothetical captive pairings designed to minimize relatedness allowed us to realistically assess the effects of genetic management on restoration success. We then used habitat-based effective-distance metrics to determine the level of natural dispersal feasible given expected management and landscape characteristics. These models also allow identification of specific linkage areas in which connectivity conservation efforts can be focused. When sufficient data are available, these methods allow planners to move beyond general aspirational connectivity goals or rules of thumb to develop objective and measurable connectivity criteria that more effectively support species recovery.

Methods

Context of Case Study

We used information from previously published studies to determine what areas within the southwestern United States and northern Mexico contained sufficient habitat
Connectivity as a Recovery Criterion

We parameterized Vortex with available information from the wild Mexican wolf population (Fredrickson et al. 2007), the Northern Rocky Mountains (NRM) metapopulation (Smith et al. 2010), and other wolf populations (Supporting Information). We did not base model parameterization solely on data from the existing wild Mexican wolf population for 2 reasons. First, we analyzed potential persistence of populations reintroduced to new areas whose demographic rates may not match those of any extant population. Second, the existing wild population remains heavily manipulated via management removals and re-releases. Human-caused wolf mortalities in the existing wild population constituted 81% of the

Vortex Simulations of Population Viability

The Vortex model simulates the effects of both deterministic forces and demographic, environmental, and genetic stochastic events on wildlife populations (Lacy 2000; Lacy & Pollak 2012). Vortex simulates a population by stepping through a series of events that describe an annual cycle of a sexually reproducing, diploid organism. Vortex tracks the sex, age, and parentage of each individual in the population as demographic events are simulated. Vortex allows the user to specify the pedigree of the starting population and uses the genetic relationships among founders to derive inbreeding coefficients and other genetic metrics in subsequent simulated generations. Vortex allows tracking of both demographic metrics (population size, time to extinction) and genetic metrics (heterozygosity, allelic diversity, and inbreeding coefficient).

We adapted the Vortex model structure to make it appropriate for analysis of connectivity effects for a species with a complex social breeding system. We incorporated into the model the persistent monopolization of breeding opportunities by male and female alpha individuals. Once an individual achieves alpha status it will generally retain that status until death. This aspect of the wolf social system reduces genetic effective population size (Ne) and thus may enhance inbreeding effects. We also modified Vortex to track the observed number of genetically effective migrants per generation (here termed migrant and defined as the total number of individuals from all other populations that produces at least one offspring in the recipient population). These results were used to assess the effects of dispersal on population persistence and inform development of a recovery criterion for population connectivity. Alternative recovery criteria for population size were evaluated by creating a numeric threshold above which a percentage (10-16%) (Table 1) of any surplus individuals were removed annually. Further details, metadata, and sample input files documenting model structure are provided in Supporting Information.

We used a 2-stage process to evaluate potential recovery criteria for the Mexican wolf. Stage 1 consisted of a PVA in which population performance across a range of scenarios was compared with alternative population size and connectivity criteria. In stage 2, we used effective-distance metrics derived from habitat data to evaluate what rates of dispersal could be expected between the reintroduced populations. By combining information from these 2 stages, we were able to evaluate what combination of population size and connectivity criteria allowed recovery of a metapopulation of Mexican wolves given current habitat conditions.

PVA is a structured method of integrating information on diverse threats to a population’s persistence. Due to the magnitude of genetic threats to the Mexican wolf, we used an individual-based population simulation model (Vortex) (Lacy 2000; Lacy & Pollak 2012) that allows exploration of how genetic threat factors vary with population size and metapopulation structure. We combined the Vortex results with data from a previously published model (Carroll et al. 2006) that evaluated the distribution of potential wolf habitat in the southwestern United States.

Carroll et al. (2006) used a spatially explicit population model that allowed detailed treatment of spatial population dynamics and habitat configuration but lacked consideration of genetic issues. Their results suggest that the southwestern United States has 3 core areas with long-term capacity to support populations of several hundred wolves each. These 3 areas, each of which contains a core area of public lands subject to conservation mandates, are in eastern Arizona and western New Mexico (i.e., Blue Range, the location of the current wild population), northern Arizona and southern Utah (Grand Canyon), and northern New Mexico and southern Colorado (Southern Rockies) (Carroll et al. 2006). Based on the number and location of potential core areas, we structured our analysis to evaluate performance of a metapopulation of 3 populations and varied population size and connectivity across a range of plausible recovery criteria.

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Table 1. Results of sensitivity analysis of Vortex population model assessed using standardized coefficients from logistic regression of parameter sets against probability of extinction and quasi extinction.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Maximum</th>
<th>z value for probability of extinction</th>
<th>z value for probability of quasi-ex-150</th>
<th>z value for probability of quasi-ex-250</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult mortality(^b)</td>
<td>18.32</td>
<td>27.48</td>
<td>167.46</td>
<td>162.48</td>
<td>111.15</td>
</tr>
<tr>
<td>Percentage of females in breeding pool</td>
<td>40</td>
<td>60</td>
<td>-160.67</td>
<td>-156.80</td>
<td>-104.49</td>
</tr>
<tr>
<td>Population size threshold</td>
<td>50</td>
<td>350</td>
<td>-158.63</td>
<td>-136.53</td>
<td>-72.03</td>
</tr>
<tr>
<td>Strength of inbreeding depression(^c)</td>
<td>6.586</td>
<td>9.789</td>
<td>152.81</td>
<td>141.54</td>
<td>92.90</td>
</tr>
<tr>
<td>Density dependent reproduction(^d)</td>
<td>categorical</td>
<td></td>
<td>-92.42</td>
<td>-54.95</td>
<td>-8.35</td>
</tr>
<tr>
<td>Effective migrants per generation</td>
<td>0.0</td>
<td>2.4</td>
<td>-88.13</td>
<td>-56.17</td>
<td>-35.49</td>
</tr>
<tr>
<td>Average number of years between disease events</td>
<td>4</td>
<td>6</td>
<td>76.54</td>
<td>81.23</td>
<td>41.31</td>
</tr>
<tr>
<td>Pup mortality(^e)</td>
<td>19.52</td>
<td>29.28</td>
<td>75.37</td>
<td>60.22</td>
<td>43.56</td>
</tr>
<tr>
<td>Variation between existing and new populations(^d)</td>
<td>categorical</td>
<td></td>
<td>-34.12</td>
<td>-32.62</td>
<td>-24.79</td>
</tr>
<tr>
<td>Carrying capacity buffer(^f)</td>
<td>1.07</td>
<td>1.60</td>
<td>-5.44</td>
<td>-51.50</td>
<td>-52.47</td>
</tr>
<tr>
<td>Harvest efficiency(^g)</td>
<td>6.4</td>
<td>9.6</td>
<td>-3.86</td>
<td>-2.44</td>
<td>-12.65</td>
</tr>
</tbody>
</table>

\(^a\)Quasi-extinction occurs when the 8year running mean population size falls below 150 or 250. All regressions are based on 1000 scenarios derived from randomized parameter sets, with 100 replicate runs per scenario. Standardized regression coefficients (z values), created by dividing a regression coefficient by its standard error, are unitless values whose magnitude indicates the relative importance of a parameter in the model.

\(^b\)From Smith et al. (2010) for Greater Yellowstone Area wolf population.

\(^c\)Slope parameter in equation of Fredrickson et al. (2007) relating litter size to inbreeding coefficient.

\(^d\)Variation in population performance arising from contrasts between populations in initial pedigree.

\(^e\)Ratio of ecological carrying capacity to the population size threshold parameter.

\(^f\)Reciprocal of proportion of the population above the population-size threshold that is removed annually.

mortalities with known causes from 1998 to 2011, primarily due to illegal shooting (43%), vehicle collisions (14%), and lethal management removals (12%) (Turnbull et al. 2013). However, since 2009, when revised management protocols restricted management removals, the wild population has shown positive demographic trends, growing from 42 to 75 individuals (USFWS 2012). Demographic rates in the wild population, particularly survival rate, thus remain highly contingent on management policy regarding removals. Our goal here was not to review the current status of the existing wild Mexican wolf population, but to assess what conditions would allow recovery of the subspecies as a whole.

Analysis of the potential effects of stochastic factors on viability requires the assumption that demographic rates alone will not cause deterministic population decline. However, demographic data collected over the last decade for the wild Mexican wolf population imply an intrinsic population growth rate of <1 (USFWS 2012). We therefore used mortality rates from the wolf population in the Greater Yellowstone Ecosystem (GYE) because mortality rates there (24.4% and 22.9% for pups and nonpups [yearlings and adults], respectively [Smith et al. 2010]) are intermediate among the 3 NRM core populations and represent a plausible goal for mortality rates after recovery actions are implemented but before delisting (Smith et al. 2010). Our baseline demographic parameter set resulted in a deterministic lambda of 1.23, which is similar to that used in previous Mexican wolf PVAs (Seal 1990; IUCN 1996). We evaluated the effect of alternate assumptions concerning mortality rates as part of the sensitivity analysis described below.

All simulated populations were started with wolves produced from the existing Mexican wolf pedigree (Siminski 2012). Founders of the existing wild (Blue Range) population were based on the known 2013 composition of the population projected forward 9 years to a starting population of 122 wolves (Supporting Information). The 2 other simulated populations were founded by assuming 2 pairs would be released each year from 2018 through 2022 into each population. We selected individuals for release from a hypothetical new generation of captive-born wolves that were minimally related and collectively represented genetic variation in the existing captive and wild populations. Released individuals produced offspring and experienced mortality after release, and surviving founders and offspring formed new pairs such that at the start of 2022 each of the 2 new populations contained 50 wolves and 10 pairs (Supporting Information).

Sensitivity Analysis

Although wolves are among the best studied of large mammals, substantial uncertainty exists on how to appropriately parameterize demographic models. We performed a global sensitivity analysis by generating 1000 sets of parameters in which values for 9 key parameters were drawn from a random uniform distribution with a range equal to ±20% of the mean value (“relative sensitivity analysis” [Cross & Beissinger 2001]) from their best estimates (Table 1). We also varied target population size and connectivity rates across a uniform distribution spanning a range of recovery criteria values (Table 1).
Each of the 1000 parameter sets was evaluated based on 100 replicate simulations of 100 years each.

We used a relative sensitivity analysis because several parameters were either aspects of model structure for which empirical distributions do not exist (carrying-capacity buffer [i.e., the proportion by which ecological carrying capacity exceeds the population size parameter] and harvest efficiency [i.e., proportion of the population above the population size parameter that is removed in a particular year]) or would be difficult to derive from the literature (Seal 1990; IUCN 1996) (see Supporting Information for references for demographic parameters in Table 1).

We used standardized coefficients from logistic regression of parameters against extinction and quasi-extinction outcomes to rank the effect of parameters on outcomes (Cross & Beissinger 2001). Dividing a regression coefficient by its standard error results in a standardized regression coefficient or $z$ value, which expresses the unique contribution of that parameter scaled by the variability of the parameter (Cross & Beissinger 2001). The resulting $z$ values (Table 1) are unitless and interpretable only in comparison with other $z$ values in the same model. Significance tests and associated $P$ values would be uninformative because the large number of scenarios considered (1000) arbitrarily inflates sample size.

Following the global sensitivity analysis, we generated 1000 scenarios of parameters in which population size and connectivity rates were again drawn from a random uniform distribution but other parameters were fixed at their mean values (Table 1). We used locally weighted regression (loess) (Cleveland & Devlin 1988) to evaluate in more detail the relation of extinction and quasi extinction to population size and connectivity rate.

Endangered and Threatened Status under the ESA

The ESA defines an endangered species as “at risk of extinction throughout all or a significant portion of its range” (16 U.S.C. §1532[3,6]) and a threatened species as “likely to become endangered in the foreseeable future” (16 U.S.C. §1532[20]). The statute does not provide a quantitative definition of at risk of extinction. Recovery plans typically include risk thresholds of 1% to 10% over periods ranging from several decades to a century. There is less agreement over interpretation of the statute’s definition of threatened status. Angliss et al. (2002) proposed that, to be consistent with the statute, criteria for threatened status should be defined by reference to the criteria for endangered status rather than directly in terms of extinction risk. This approach was subsequently incorporated into recovery plans for species such as the fin whale (Balaenoptera physalus), which will be removed from the list of threatened species when it “has less than a 10% probability of becoming endangered (has more than a 1% chance of extinction in 100 years) in 20 years” (NMFS 2010). We used a time frame for the foreseeable future of 100 rather than 20 years because we analyzed genetic threats that require decades to accumulate to deleterious levels.

Incorporating Multiple Persistence Thresholds

To illustrate how tiered thresholds for endangered and threatened status might be informed by quasi-extinction metrics, we selected a population threshold (150 individuals) that corresponded to adequately low extinction risk (<10%) in exploratory analyses with baseline demographic rates. We then measured the proportion of simulations with a population size criteria of >150 in which, after the initial 30 years of population establishment, the 8-year (2 generation) running mean of population size drops below 150. As with extinction probability, the metrics report the mean quasi-extinction probability across the 3 populations.

Populations of most species continue to increase under state-level management after recovery and removal (delisting) from the federal list of threatened species. However, because wolves can negatively affect other resources (livestock, wild ungulates), state agencies may seek to manage delisted wolf populations at the lowest level consistent with maintaining recovered status. Due to genetic and other issues, long-term management of populations to a harvest-imposed ceiling may result in deterioration in vital rates (Mills 2012). Population thresholds implemented by the states after federal delisting are analogously related to threatened status in that they must ensure an adequately low probability of becoming threatened in the foreseeable future. This risk can be measured by a second quasi-extinction metric based on the probability of population size dropping below the threshold dividing endangered and threatened status (which was developed as described above). Under the ESA’s framework, the thresholds that distinguish extinct, endangered, threatened, and recovered species are thus interrelated and can be quantitatively assessed with a unified set of PVA-based metrics.

Feasibility of Alternative Connectivity Criteria

We assessed what rate of natural dispersal between potential core populations could be achieved given the distribution of habitat. We projected connectivity rates between primary core populations in the Mexican wolf metapopulation by relating observed connectivity rates in the NRM metapopulation (Vonholdt et al. 2010) to habitat-based effective distance between populations in both the NRM and the southwestern United States. Because published data on effective migration rate in the NRM are insufficient to build a predictive model, this extrapolation is necessarily qualitative, but nonetheless informative in this planning context. We also compared
habitat-based distances between the Mexican wolf and NRM metapopulation with the distances within those metapopulations to evaluate potential dispersal rates between the 2 metapopulations.

We compared results from 2 contrasting effective-distance metrics based on least-cost (shortest-path) distance and resistance (current flow) distance, respectively (Carroll et al. 2012) in order to assess the robustness of conclusions to choice of connectivity metric. Both least-cost distance and resistance distance have been correlated with gene flow in several species (McRae et al. 2008). Habitat suitability index values from a previously published study (Carroll et al. 2006) were assumed to be proportional to movement cost and conductance (see supplementary material S2 for description of habitat model). Least-cost distance, calculated using the Linkage Mapper software (McRae & Kavanagh 2011), represents cost of movement as distance, and identifies the single optimal path between two predetermined endpoints that has the shortest total distance (least total cost). In contrast to least-cost distance, resistance (current flow) distance integrates the contributions of all possible pathways across a landscape or network. We used Circuitscape software to calculate a resistance distance statistic that summarizes overall connectivity between each pair of core areas (McRae et al. 2008). Additionally, Circuitscape produced maps of current flow that can help planners direct conservation measures toward areas important for connectivity.

Results

Effects of Population Size and Connectivity on Extinction and Endangerment

Population size and dispersal rate interacted to influence probability of extinction and quasi extinction (Table 1, Figs. 1 & 2). Dispersal rate strongly affected extinction probability at population criteria below 200 but decreased in importance at larger population sizes (Fig. 1a). Dispersal rates of <0.5 migrants greatly increased extinction risk (Fig. 1b). Extinction risk continued to decrease at rates between 0.5 and 1 migrants for populations of <150, but there was less effect of increased dispersal on persistence for larger population sizes (Fig. 1b).

Dispersal rate had less effect on probability of endangerment (defined here by a quasi-extinction threshold of 150) than on probability of extinction (Table 1). Higher dispersal rates reduced the probability of endangerment in 2 ways. First, and most importantly, higher dispersal rates reduced the population size threshold corresponding to an extinction probability that was adequately low to merit downlisting (Fig. 1a). Second, higher dispersal rates reduced the probability of a downlisted population again dropping below that threshold and becoming endangered in the future (Fig. 2). Connectivity had less influence on persistence at the 250 quasi-extinction threshold (Table 1). Simulation results suggested that a buffer for each population of 50–100 individuals above the delisting threshold was needed to adequately reduce the risk that
Effects of Demographic Parameters on Persistence and Relisting

Results of the sensitivity analysis suggested that the most important parameters (absolute value of standardized coefficient > 100) were adult mortality, proportion of females in the breeding pool, and strength of inbreeding effects (Table 1). Parameters of intermediate importance (absolute value of standardized coefficient 70–100) were density-dependent reproduction, frequency of disease outbreaks, and pup mortality. Between-population variation was of lower importance. Carrying-capacity buffer and harvest efficiency were the least important parameters. Logistic regression of randomized parameter sets on probability of quasi extinction at either the 150 or 250 population thresholds yielded similar results, except that the effect of the carrying-capacity buffer increased and that of density-dependent reproduction decreased at these larger population thresholds (Table 1). The population-size criterion had as large an effect as the most influential demographic parameters on extinction and on quasi extinction at the 150 threshold but had lower effect at the 250 quasi-extinction threshold. The dispersal-rate criterion was of intermediate importance (Table 1). Conclusions regarding what population-size and connectivity criteria corresponded to a specific extinction risk were contingent on demographic parameters such as adult mortality, which had large $z$ values in the sensitivity analysis (Fig. 3).

Determining Anappropriate Connectivity Criterion

Linkages between primary core populations were ranked similarly (Pearson correlation = 0.85, Spearman rank correlation = 0.72, $n = 9$) under both least-cost distance and resistance distance metrics (Supporting Information). For those linkages ranked more favorably based on resistance distance than based on least-cost distance, multiple linkages may allow more dispersal between those areas than expected based on their single shortest connection (Supporting Information). Projected connectivity between the Blue Range and both the Grand Canyon and Southern Rockies primary core populations was less than that of the 2 best NRM linkages (Supporting Information) but greater than that between the Grand Canyon and
Southern Rockies populations or between Yellowstone and northwestern Montana. When considered in the context of observed NRM migration rates (Hebblewhite et al. 2010; Vonholdt et al. 2010), this comparison suggests that it may be more difficult to achieve a connectivity criterion of 1 migrant/generation for the Mexican wolf in the southwest than for wolves in the NRM.

Because both distance metrics suggest that few direct migrants would be expected between the Grand Canyon and Southern Rockies, we structured the Vortex PVA to assume dispersal would occur along a chain of 3 populations rather than directly between all pairs of populations. This metapopulation structure provides the most dispersal to the centrally located Blue Range population, which otherwise would perform poorly relative to new populations derived from less-related individuals.

Least-cost and resistance distances between the Mexican wolf and NRM metapopulation were greater than any distances within those metapopulations. Mean intermetapopulation resistance distance was 1.23 and 1.34 that of intrametapopulation resistance distance for the NRM and Mexican wolf metapopulations, respectively. Mean intermetapopulation least-cost distance was 2.59 and 1.81 that of intrametapopulation resistance distance for the NRM and Mexican wolf metapopulations, respectively. Current maps suggest that a potential core area in northern Utah could serve as a key stepping stone to enhance connectivity between metapopulations (Fig. 4).

**Discussion**

Recovery plans for endangered species frequently include either aspirational objectives for maintaining connectivity or general rules of thumb rather than specific quantitative criteria (USFWS 1987). Results from our analysis demonstrate that, where sufficient data exists, quantitative connectivity criteria based on species-specific demographic and habitat data can form an objective and measurable component of recovery plans. Use of pedigree data for the existing wild population, as well as new populations founded by hypothetical captive pairings, allowed us to realistically incorporate genetic effects on restoration success. Results from recent advances in measurement of genetically effective migration rates (Vonholdt et al. 2010) were then integrated with habitat connectivity modeling to predict migration rates and target recovery actions at specific habitat linkages. The shift from simple connectivity rules of thumb to species-specific analyses parallels the previous shift from simple rules of thumb for minimum viable population size to detailed PVA modeling in endangered species recovery planning.

**Importance of Connectivity Criteria**

Population size had among the strongest influence on population persistence of any parameter evaluated in the sensitivity analysis (Table 1). Connectivity ranked among the moderately important parameters, suggesting that it also merits attention in recovery planning. The importance of connectivity suggested by our PVA results may be most relevant to other species that have been extirpated in the wild and subsequently recovered from a limited number of captive founders or to formerly widespread species that are now limited to small isolated populations. To avoid the genetic damage that may occur during demographic downturns associated with episodic events (e.g., drought, disease), a population derived from inbred and interrelated founders generally must have a larger census population size than a population derived from outbred and unrelated individuals (Allendorf et al. 2002).
similarly, a single effective migrant is more likely to increase persistence of inbred populations (Vilá et al. 2003).

Comparing general rules of thumb on adequate rates of connectivity with results from species-specific simulations can give context to PVA results. The most commonly proposed rule of thumb for connectivity states that one genetically effective migrant per generation into a population is sufficient to minimize the loss of polymorphism and heterozygosity within populations (Allendorf 1983). Our simulation results support use of this rule of thumb because population persistence declined more rapidly at rates below one migrant for smaller populations (<150) (Fig. 1b). Our results also suggest that ensuring lower but nonzero rates of connectivity (e.g., >0.5 migrants) remains important in cases where one migrant may not be achievable. The contrast between our results and previous reviews concluding that a rate of one migrant may be less than optimal for wild populations may be because in our model inbreeding affected persistence solely via effects on litter size, whereas previous reviews considered a broader suite of potential inbreeding effects (Mills & Allendorf 1996). Additionally, we did not consider what population and connectivity criteria would ensure maintenance of adaptive potential through a long-term balance between loss of alleles via genetic drift and new alleles produced by mutation (Franklin & Frankham 1998).

Although wolves are a relatively well-studied species, our simulations necessarily involved substantial uncertainty in both model parameters and structure (e.g., density dependence). Criteria such as population size and connectivity that primarily address stochastic factors remain important even when (as here) effects of deterministic factors and parameter uncertainty are large (Fig. 3). Our baseline parameters were based on the assumption that recovery actions would be effective in reducing the Blue Range population’s currently high mortality rates. Alternate mortality-rate parameters would result in different population size and connectivity rates being required to achieve adequate population persistence (Fig. 3). Because metapopulations with adequate connectivity can better withstand less favorable demographic rates, inclusion of a connectivity criterion is precautionary and reduces uncertainty about the future status of a species.

In addition to evaluating extinction probability, we considered 2 quasi-extinction metrics related to probability of relisting as either endangered or threatened. The 2 metrics offered complementary insights regarding the resilience conferred by alternate recovery criteria. An exclusive focus on minimizing extinction might lead to criteria that result in a species persisting in a permanent state of endangerment, which is inconsistent with the intent of the ESA to recover self-sustaining populations (16 U.S.C. §1531[2][b], §1532 [3][3]). Use of multiple persistence metrics focuses attention on the often-ignored genetic and other challenges inherent in managing wildlife populations to a fixed population ceiling (Mills 2012).

Mapping and Managing Population Connectivity

Previous recovery plans for wolves and other large carnivores such as grizzly bears (Ursus arctos) noted the importance of metapopulation connectivity but did not develop objective and measurable connectivity criteria (USFWS 1982, 1987). This may have been because at the time such plans were developed, there was less recognition of the synergistic effects of dispersal on genetic diversity and demographic performance of small populations. Due to recent advances in genetic assignment tests and other techniques that allow identification of genetically effective migrants, connectivity is increasingly measurable in wild populations (Vonholdt et al. 2010). When coupled with habitat-based connectivity models, these methods allow development of quantitative connectivity criteria and their incorporation into monitoring programs. Given evidence from other species for utility of effective-distance metrics in predicting gene flow (McRae et al. 2008), they are appropriate tools for informing wolf-recovery planning and demonstrate the utility of applying such methods to data gathered in future monitoring of reintroduced populations. Our results suggest that habitat-based metrics such as least-cost and resistance distance are useful for assessing expected migration rates, but that multiple metrics should be compared to provide a more-informative ranking of alternate linkages.

Differing levels of population connectivity imply qualitatively different genetic effects on populations. We focused primarily on recovery criteria relevant to inbreeding connectivity (Lowe & Allendorf 2010). In this context, our results suggest that viability of the existing wild population is uncertain unless additional populations can be created and linked by dispersal of >0.5 migrants/generation (Fig. 1). In contrast, adaptive connectivity (sensu Lowe & Allendorf 2010) requires only low levels of dispersal (>0.1 migrants) to spread advantageous alleles between populations. Although effective distance metrics suggest that dispersal between the NRM and Mexican wolf metapopulations may be low (<0.5 migrants), this may be sufficient for maintenance of adaptive connectivity, with occasional dispersal maintaining a regional cline in genetic structure similar to historic conditions (Leonard et al. 2005). Recovery plans for formerly widely distributed species should consider how such broad-scale genetic structure can be restored via conservation of interregional linkages and stepping-stone habitat (Franklin & Frankham 1998).

An primary goal of the ESA in seeking to protect threatened and endangered species—as well as the ecosystems on which these species depend—is to recover these species to the point at which they are self-sustaining.
their natural habitat (U.S.C. §1531[2(b)]). Preservation of habitat connectivity and necessary levels of natural dispersal is analogous to preservation of the habitat that permits persistence of a wild population of any species. Absent a clear physical barrier to natural genetic exchange (such as a large urban area), achieving connectivity for highly vagile species such as the wolf via natural dispersal rather than artificial translocation is consistent with the intent of the ESA. Integrating PVA and connectivity models as we have done here allows planners to develop such criteria with species-specific PVA and to identify location-specific management actions necessary to meet these criteria and achieve recovery of self-sustaining populations.

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Supporting Information

A description of Vortex model structure and parameters (Appendix S1), description of habitat inputs and methods used in analysis of potential dispersal rates between populations (Appendix S2), plot of resistance distance versus least-cost distance between existing or potential wolf population core areas in the western United States (Appendix S3), and Vortex and connectivity analysis input files showing details of model structure used in simulations (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Cascading effects of predator activity on tick-borne disease risk

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PREDATORS AND COMPETITORS OF VERTEBRATES CAN IN THEORY REDUCE THE DENSITY OF INFECTED NYMPHS (DIN)—AN OFTEN-USED MEASURE OF TICK-BORNE DISEASE RISK—BY LOWERING THE DENSITY OF RESERVOIR-COMPETENT HOSTS AND/OR THE TICK BURDEN ON RESERVOIR-COMPETENT HOSTS. WE INVESTIGATED THIS POSSIBLE INDIRECT EFFECT OF PREDATORS BY COMPARING DATA FROM 20 FOREST PLOTS ACROSS THE NETHERLANDS THAT VARIED IN PREDATOR ABUNDANCE. IN EACH PLOT, WE MEASURED THE DENSITY OF QUESTING Ixodes ricinus nymphs (DON), DIN for three pathogens, rodent density, the tick burden on rodents and the activity of mammalian predators. WE ANALYSED WHETHER RODENT DENSITY AND TICK BURDEN ON RODENTS WERE CORRELATED WITH PREDATOR ACTIVITY, AND HOW RODENT DENSITY AND TICK BURDEN PREDICTED DON AND DIN FOR THE THREE PATHOGENS. WE FOUND THAT LARVAL BURDEN ON TWO RODENT SPECIES DECREASED WITH ACTIVITY OF TWO PREDATOR SPECIES, WHILE DON AND DIN FOR ALL THREE PATHOGENS INCREASED WITH LARVAL BURDEN ON RODENTS, AS PREDICTED. PATH ANALYSES SUPPORTED AN INDIRECT NEGATIVE CORRELATION OF ACTIVITY OF BOTH PREDATOR SPECIES WITH DON AND DIN. OUR RESULTS SUGGEST THAT PREDATORS CAN INDEED LOWER THE NUMBER OF TICKS FEEDING ON RESERVOIR-COMPETENT HOSTS, WHICH IMPLIES THAT CHANGES IN PREDATOR ABUNDANCE MAY HAVE CASCADING EFFECTS ON TICK-BORNE DISEASE RISK.

1. Introduction

The incidence of zoonotic vector-borne diseases has increased in recent decades [1]. In northwestern Europe and northeastern North America, many of these are caused by pathogens that are transmitted by ticks from the Ixodes ricinus complex: I. ricinus in Europe and Ixodes scapularis in North America [1,2]. Both species are three-host ticks that, in temperate climates, mainly feed on small rodents or birds as larvae, on multiple host species as nymphs and on deer as adults [2]. While feeding on these hosts, ticks can become infected with pathogens that are transmitted by the host [3]. Infection prevalence in ticks often increases with the number of blood meals; hence, larvae tend to have a lower infection prevalence than nymphs, and nymphs tend to have a lower infection prevalence than adults [4]. Population densities of ticks show an opposite pattern, larvae being more abundant than nymphs, which in turn are more abundant than adults [3]. Therefore, the density of infected nymphs (DIN) is often referred to as the most important ecological parameter that, together with the level of human exposure to ticks, determines tick-borne disease risk [5].
There are large differences between areas in the incidence of tick-borne diseases [6,7]. These differences are partly caused by differences in DIN, which have been attributed to differences in climate and habitat characteristics that influence tick survival [3] and to differences in host availability, which influences tick densities and infection with pathogens [8]. DIN is often estimated as the product of the density of nymphs (DON) and nymphal infection prevalence (NIP), and depends on the absolute number of larvae that get infected while feeding on reservoir-competent hosts [8,9]. This number is determined by: (i) the abundance of reservoir-competent hosts, (ii) the average number of larvae that feed on each host individual (larval burden), and (iii) the percentage of larvae that get infected while feeding on a reservoir-competent host (realized reservoir competence). The realized reservoir competence of a host species is dependent on many factors, including the infection prevalence of the host, which is again dependent on tick burden [10,11]. Therefore, DIN is mainly determined by the density of reservoir-competent hosts and their tick burden [12].

There are reasons to assume that host density and tick burden on hosts may be influenced by predators and competitors of hosts, in at least two ways [12]. First, Ostfeld & Holt [13] reasoned that predators can reduce disease transmission by lowering the density of reservoir-competent hosts. This idea was supported by a study of tick-borne pathogens in the northeastern USA, in which the incidence of Lyme borreliosis was negatively correlated with the density of red fox (Vulpes vulpes) [7]. To explain these patterns, Levi et al. [7] provided a theoretical model in which foxes decreased the density of white-footed mice (Peromyscus leucopus)—the most important reservoir-competent host for Borrelia burgdorferi, the bacteria causing Lyme borreliosis, in North America—which then led to a decrease in DIN. However, empirical data on rodent densities and DIN in this relationship were lacking.

Second, predators might reduce DIN via non-lethal effects on prey. For example, many prey species show decreased movement and increased refuge behaviour in the presence of a predator or cues of predator presence such as predator scent [14]. As movement is an important parameter determining the encounter rate of hosts with ticks, and thus tick burden [15], predators might lower disease risk by reducing tick burden on prey species. The negative correlation between fox density and Lyme borreliosis incidence in Levi et al. [7] could thus be a result of a direct effect (predation) and/or an indirect effect (changed behaviour) on white-footed mice. Changes in the presence or abundance of predators could thus have cascading effects on DIN by affecting both the density of reservoir-competent hosts and the tick burden on reservoir-competent hosts.

In this study, we empirically tested for an indirect negative correlation between the abundance of mammalian predators of rodents and DIN for three tick-borne pathogens, via rodent density and tick burden on rodents. We used a study system including two rodent species—bank vole (Myodes glareolus) and wood mouse (Apodemus sylvaticus)—and three tick-borne pathogens for which these two species are the most important reservoir-competent hosts in Europe [10,16]—Borrelia afzelii (one of the genospecies of B. burgdorferi s.l.), Borrelia miyamotoi and Candidatus Neoehrlichia mikurensis. To examine empirical evidence for a cascading effect of predator activity on DIN, we first explored the relationship between predator activity, rodent density and tick burden on rodents in 20 forest plots with differing fauna in the Netherlands. Second, we explored the relationships of rodent density and tick burden on rodents with DON and DIN for the three pathogens in the same plots. We included an analysis of DON as rodents are the most important hosts feeding I. ricinus larvae in temperate Europe, suggesting that predators might also have a cascading effect on nymphal densities [10]. As the tick burden on rodents might be dependent on rodent density and the number of ticks in the environment [17], we also included these parameters in the analyses of tick burden on rodents. Finally, we used path analysis to determine whether there was support for an indirect correlation between predator activity and both DON and DIN.

2. Material and methods

(a) Study sites

We collected data in 20 forest plots of 1 ha located within 19 forest sites in the Netherlands, with more than 5 km between sites. Sites were selected to form a large gradient in predator abundance based on distribution maps and information from the managers of the nature reserves. We assigned each plot to one of five vegetation types, based on the dominant herbaceous species (electronic supplementary material, table S1). We sampled 11 plots in 2013, and nine in 2014 (electronic supplementary material, table S1). In one site, Enkhout, we collected data in two plots 150 m apart, of which one was inside an exclosure of 3 ha. The exclosure was built to exclude large herbivores 3 years before field collection, and used by us to mimic a situation in which all larger predators were absent, which we verified with camera trapping data.

(b) Predator activity

Rodents are known to change their behaviour in response to the presence of predators or predator scent [14,18]. The likelihood that a rodent perceives a predator increases with the amount of predators passing its home range, which is determined by the local density and activity of predators in a plot [19]. This combination of local density and activity of predators can be measured using the passage rate: a photographic capture rate corrected for differences in detectability between species and habitats [20,21]. We measured passage rates of predators using camera traps (HC500; Reconyx Inc., Holmen, WI, USA) during March–November, the period in which I. ricinus is most active in the Netherlands [22]. We used the camera trap set-up described by Hofmeester et al. [21] to obtain 18 camera positions, totalling 504 camera trapping days per plot. Theft and camera malfunction caused some variation in the total number of camera trapping days per plot. To quantify effective detection distance (EDD), we placed a line of markers at distance intervals of 2.5 m in the centre of the view of each camera [21]. Then, for all animals that crossed the line of markers, we recorded the species and distance intervals. The frequency distribution of intervals was then used to estimate the EDD for each species per vegetation type (electronic supplementary material, table S2) [21].

The EDD estimates were used to determine passage rates per species per camera location as:

\[
P_i = \frac{x_i}{t \times \text{EDD}_i},
\]

where \(P_i\) is the passage rate of species \(i\) (in \(\text{m}^{-1} \text{d}^{-1}\)), \(x_i\) the number of passages of species \(i\), \(t\) the total time the camera was active (in days) and \(\text{EDD}_i\), the effective detection distance of species \(i\) in vegetation type \(v\) (in metres). This passage rate is an index of local activity, described as the number of animals passing a line in front of the camera per day standardized for differences in detectability. For each plot, we calculated the plot-specific passage rate per species as the arithmetic mean of
the passage rates for all deployments. Henceforth, we refer to passage rates as ‘activity’.

(c) Rodent density and tick burden
We quantified tick burden as: (i) larval burden, the mean number of larvae found on individual rodents at first capture per species per plot, and as (ii) nymphal burden, the mean number of nymphs found on individual rodents at first capture per species per plot. We used these measures to distinguish between the chance that individual rodents become infected by feeding an infected nymph (nymphal burden) and the chance that uninfected larvae become infected by feeding on an infected rodent (larval burden). We studied the two most important rodent species feeding *I. ricinus* in the Netherlands, bank vole (*M. glareolus*) and wood mouse (*A. sylvaticus*) [23].

Rodent density and tick burden were quantified by live trapping and screening of rodents. In each plot, we established a grid of 8 x 8 (64) longworth small-mammal live traps (Heslinga Traps, Groningen, The Netherlands) with a 12 m inter-trap distance for one week in July or August, at the peak of larval activity in the Netherlands [22]. We baited the traps with maize, wheat, mealworms and a piece of carrot, and added hay as insulating material. We pre-baited the live traps for 3 days, and then checked the traps during six consecutive trapping sessions at 12 h intervals. Captured rodents were transferred from the trap into a transparent plastic bag, from which we identified the animals to species. We handled the mice and voles with care, by holding them by the scruff of their neck and counted all the ticks on the head, ears, throat and neck of the animal. We collected a stratified random selection of ticks from rodents from each plot—approximately 10% of the counted ticks—for identification to species level in the laboratory using an established identification key [24]. All collected ticks were identified as *I. ricinus*. All rodents were individually marked by clipping some of the top fur in a unique pattern, for individual identification when recaptured [25]. We estimated the density of each rodent species using the capture–mark–recapture models for closed populations presented by Otis *et al.* [26] as implemented in MARK [27], assuming that the probability of capture (p) and the probability of recapture (c) were equal and constant during trapping sessions. As we sampled 1 ha plots, we report the abundance estimates from MARK as densities per hectare. For the six combinations of plot and species where the minimum number of animals caught per species was too low to estimate a density using MARK, we used the minimum number of individuals known alive as the density estimate.

(d) Tick density
We determined density of *I. ricinus* larvae and nymphs by collecting ticks six times in each plot, once every four weeks from April to September. Tick density was determined by blanket-dragging of six times in each plot, once every four weeks from April to September.

(e) Density of infected nymphs
To determine the DIN with tick-borne pathogens transmitted by rodents, we determined pathogen prevalence in all individual nymphs by qPCR using the methods described in Heylen *et al.* [31] (*B. miyamotoi*) and *Jahari* *et al.* [32] (*Ca. Neoehrlichia mikurensis*). There is no qPCR available for *B. afzelii* (one of the genospecies of *B. burgdorferi* s.l.), so we used a qPCR for *B. burgdorferi* s.l. as described in Heylen *et al.* [31] followed by a conventional PCR targeting the variable 59-23S intergenic spacer region on the positive samples of the qPCR according to the protocol described in Coifet *et al.* [33]. We determined the number of nymphs found with a co-infection of two pathogens and co-infection with all three pathogens, and estimated the overall prevalence of these co-infections using the measured prevalences.

Only 44% of the *B. burgdorferi* s.l. positive nymphs (as determined by qPCR) yielded a successful conventional PCR and sequence result. To be able to use the more sensitive qPCR results to obtain as good an estimate as possible for the infection prevalence with *B. afzelii*, we assumed that all genospecies of *B. burgdorferi* s.l. had an equal probability of being successfully sequenced. By doing so, we could approximate the infection prevalence of nymphs with *B. afzelii* for each plot as:

$$NIP_{ifa} = \frac{P_{ifa} \times \Pi_{ifa}}{N_i}$$

where *NIP* is the nymphal infection prevalence with *B. afzelii*, *P* is the proportion of successful sequences identified as *B. afzelii*, and *N* is the total number of nymphs infected with *B. burgdorferi* s.l. as determined by qPCR and *N* is the total number of nymphs tested in a plot.

We used the estimated infection prevalence with *B. afzelii* and the infection prevalence as determined by qPCR for *B. miyamotoi* and *Ca. N. mikurensis* to estimate the density of questing nymphs infected by these pathogens as:

$$DIN_{fi} = NIP_{fi} \times DON,$$

where *DIN* is the density of questing nymphs infected with pathogen species *i* (per 100 m²), *NIP* is the infection prevalence in questing nymphs with pathogen species *i* and DON the density of questing nymphs as determined by blanket-dragging (per 100 m²).

(f) Statistical analysis
Statistical analyses were performed in R v. 3.2.3 [34] using the nlme package [35] to fit linear mixed models (LMMs) and the glmmADMB package [36] to fit generalized LMMs (GLMMs). We first explored the data by testing for correlations between: (i) bank vole or wood mouse density, (ii) larval burden on bank voles or wood mice, (iii) nymphal burden on bank voles or wood mice (GLMMs with negative binomial distribution and log link) and the activity of the different predator species that we detected in our plots using the dredge function in the MuMln package [37]. Second, we explored correlations between rodent density, larval burden and nymphal burden (per species) with the density of questing nymphs (DON) and the DIN for all three pathogens using GLMMs with a negative binomial distribution and log link. We did not include nymphal burden in the analyses for wood mice as nymphal burden was correlated with larval burden in this species (GLMM: *β* = 0.63, *p* = 0.04). As temperature and humidity were correlated (LMM: *β* = −2.17, *p* = 0.001), we only added humidity as a covariate in all models of DON and DIN to correct for possible effects of these parameters on questing tick activity. We tested for collinearity by calculating the variance.
inflation factor [38], which was below 2 for all reported models. We allowed a random intercept per vegetation type nested within year in all models including DON or DIN to correct for possible differences in drag-sampling efficiency between vegetation types and possible differences in questing tick densities between years owing to differences in weather conditions. We allowed a random intercept per year for all other models to correct for possible differences between years.

We used confirmatory path analysis using directional separation [39], to quantify an indirect correlation of predator activity with DON and DIN via rodent density or larval burden on rodents. When data used in a path analysis have a hierarchical or multi-level structure, directional separation can be used to test causal models [39]. A causal model is rejected when variables that are only indirectly connected by a causal path are not independent from each other conditional on the variables that are direct causes of either of the variables to be tested. An example from our model is the relationship between predator activity and DIN, which would be independent conditional on rodent density and larval burden on rodents (independence claim) if a causal relationship exists. This independence can be statistically tested using a model in which all parameters in the independence claim are included. Using the example above that would be a model regressing DIN with predator activity, rodent density and larval burden, where predator activity should not be correlated with DIN when rodent density and larval burden are held constant.

We determined and tested the independence claims for the causal models (electronic supplementary material, S3) and calculated C values as described by Shipleys [39] for each of the combinations of DON and DIN for the different pathogens per rodent species. We only tested path models for predators and rodent characteristics where we found significant correlations \((\alpha = 0.05)\) for the individual tests. Causal models were rejected if the C value was unlikely to have occurred by chance \((p < 0.05)\) using a \(\chi^2\)-test [39]. We tested the path coefficients for not rejected causal models using GLMMs with a negative binomial distribution and a log link for all paths.

As larval densities, rodent densities, larval burdens and nymphal burdens were over-dispersed, we log10 transformed these parameters to approximate normality in models in which these parameters were included as explanatory variables. If the parameter included estimates of zero, we added the lowest measured positive number to circumvent problems with the transformation. We standardized all parameters, when applied after transformation, by extracting the mean and dividing by 2 s.d. [40] to obtain standardized regression coefficients.

We used a \(\chi^2\)-test to test for differences in observed prevalence of co-infections with the different pathogens in all questing nymphs, and expected prevalence of co-infections based on the infection prevalence of the separate pathogens, to test for associations between the pathogens.

3. Results

We found large variation between plots in the DIN for B. afzelii, B. miyamotoi and Ca. Neoehrlichia mikurensis, and also in the activity of mammalian predators of rodents (see [41] for full dataset). Red fox (V. vulpes) was present in most plots (18 out of 20), followed by European pine marten (Martes martes; 12 out of 20), stone marten (Martes foina; 6 out of 20) and European polecat (Mustela putorius; 5 out of 20). Where they were present, red fox also showed the highest activity (mean + standard deviation) 0.0080 ± 0.0061 m\(^{-1}\) d\(^{-1}\), followed by Pine marten 0.0041 ± 0.0037 m\(^{-1}\) d\(^{-1}\), stone marten 0.0011 ± 0.0011 m\(^{-1}\) d\(^{-1}\) and polecat 0.0011 ± 0.0006 m\(^{-1}\) d\(^{-1}\).

Figure 1. Correlations between the mean larval burden on bank voles and (a) red fox and (b) stone marten activity, and correlation between the mean larval burden on wood mice and (c) red fox and (d) stone marten activity. Points show the raw data, solid lines show the model predictions for a model including both predator species.
the activity of any of the predators, although there was a negative trend for polecat (β = 1.22, p = 0.06; electronic supplementary material, S4). Wood mouse (A. sylvaticus) density was not correlated with the activity of any of the other predators (electronic supplementary material, S4). Larval burden on bank voles (β_{fox} = −0.99, p_{fox} = 0.004; β_{marten} = −0.91, p_{marten} = 0.02) and wood mice (β_{fox} = −1.60, p_{fox} < 0.001; β_{marten} = −1.32, p_{marten} < 0.001) decreased with the activity of red fox and stone marten (figure 1; electronic supplementary material, S4). Nymphal burden on bank voles and wood mice was not correlated with predator activity (electronic supplementary material, S4), although there was a negative trend of nymphal burden on wood mice with red fox activity (β = −1.29, p = 0.11). Further exploration showed that both DON and DIN for all three pathogens increased with larval burden on both bank voles and wood mice (figure 2; electronic supplementary material, S5).

Path analyses supported an indirect correlation of both red fox and stone marten activity with DON (electronic supplementary material, figure S6) and DIN for B. afzelii, B. miyamotoi and Ca. N. mikurensis via mean larval burden on both bank voles and wood mice (figure 3). One of the independence claims for the path concerning DON was not met (electronic supplementary material, S3), so this path was added to the path diagram, after which both the path models for bank vole (C = 4.8, p = 0.60) and for wood mouse (C = 5.8, p = 0.47) were not rejected (electronic supplementary material, figure S6). None of the tested path models for DIN for bank vole (B. afzelii: C = 5.3, p = 0.72; B. miyamotoi: C = 3.7, p = 0.88; Ca. N. mikurensis: C = 3.4, p = 0.90) and for wood mouse (B. afzelii: C = 9.4, p = 0.31; B. miyamotoi: C = 7.2, p = 0.52; Ca. N. mikurensis: C = 7.9, p = 0.45) were rejected. Consistent with the previous analyses, not all path coefficients were significantly different from zero: there was no correlation of red fox and stone marten activity with either bank vole or wood mouse density, no correlation between bank vole density and mean larval burden on bank voles, no correlation between wood mouse density and mean larval burden on wood mice and no correlation between bank vole or wood mouse density and DIN for any of the pathogens (figure 3). Larval burden on bank voles and wood mice increased with larval density, and decreased with red fox and stone marten activity, as expected (figure 3). For each of the pathogens, DIN increased with larval burden in rodents also after correcting for differences in bank vole or wood mouse density (figure 3).

Among 16,617 questing nymphs that we screened, we found very low co-infection percentages with an over-representation of all four possible co-infections: B. afzelii and B. miyamotoi (observed % = 0.084, expected % = 0.045, χ²-value = 4.3, p = 0.038), B. afzelii and Ca. N. mikurensis (observed % = 0.54, expected % = 0.13, χ²-value = 168.1, p < 0.001), B. miyamotoi and Ca. N. mikurensis (observed % = 0.18, expected % = 0.12, χ²-value = 4.0, p = 0.047) and the
rodent density and larval burden on rodents. We found that was explained by variation in predator activity via both variation in the density of questing nymphs (DON) and DIN disease risk. We carried out a field study to determine whether presence and activity might thus have cascading effects on ticks and reservoir-competent hosts [7,13]. Changes in predator activity is needed to test these hypotheses.

4. Discussion

Theory predicts that predators can reduce the DIN by suppressing reservoir-competent hosts and the encounter rate between ticks and reservoir-competent hosts [7,13]. Changes in predator presence and activity might thus have cascading effects on disease risk. We carried out a field study to determine whether variation in the density of questing nymphs (DON) and DIN was explained by variation in predator activity via both rodent density and larval burden on rodents. We found that larval burden on two important reservoir-competent hosts, bank vole (M. glareolus) and wood mouse (A. sylvaticus), decreased with activity of two predators: red fox (V. vulpes) and stone marten (Martes foina). Overall DON as well as DIN for three tick-borne pathogens—B. afzelii, B. miyamotoi, and Ca. Neoehrlichia mikurensis—increased with larval burden on these rodents. Path analyses supported an indirect (negative) correlation between both predator species and DON, and DIN for all three pathogens, which is in agreement with theory.

Path analyses revealed an indirect negative correlation of both red fox and stone marten activity with DON and DIN for all three tick-borne pathogens via differences in the mean larval burden on rodents, even after correcting for an indirect correlation with questing larval density (figure 3; electronic supplementary material, figure S6). Red foxes and stone martens generally carry few I. ricinus [42–44]. Therefore, we conclude that it is unlikely that the negative correlation between predator activity and larval burden on bank voles and wood mice is caused by a dilution effect where foxes and martens divert ticks that would otherwise feed on rodents [12]. We suggest two other mechanisms that might explain the negative correlation between predator activity and larval burden on bank voles and wood mice. First, bank voles and wood mice can become less active in areas with more cues of predator presence [18], reducing their encounter rate with ticks and therefore tick burden [15]. Second, those animals that do move more and therefore acquire more ticks [15] might also have a higher risk of being predated, leading to a selective predation on highly infested animals [45]. Further research estimating the day range of rodents in relation to predation risk and tick burden in areas differing in predator activity is needed to test these hypotheses.

Our analyses focused on the determinants of DON and DIN. The reason that we did not do the same for NIP is that we lacked data on one of the main determinants: the number of larvae feeding on non-rodent hosts [9]. There is certainly a potential for predators to influence NIP, namely by changing the number of larvae feeding on rodents and possibly also the number of larvae feeding on non-rodent hosts that are prey to the same predators. An analysis of the entire host assemblage is needed to fully understand how predators influence NIP, and thereby one of the parameters determining tick-borne disease risk.

We sampled predators, rodents and questing ticks in each plot in the same year. However, where there is a time lag between these factors, we might have missed correlations. By measuring all variables in the same year, we assumed that densities were constant between years, but this assumption is probably invalid, especially for rodents [46]. Ostfeld et al. [47] found a positive correlation between rodent density in year \( t - 1 \) and the density of I. scapularis nymphs in year \( t \). Similarly, there might be a time lag on potential effects of predators on rodent density [13]. This is further complicated by the fact that on different spatial scales (i) predator activity might reduce rodent population densities (negative correlation) [46], while at the same time, (ii) patches with high rodent density might attract predators from the surrounding area (positive correlation) [48]. We mainly found support for the second relationship as all correlations between predator activity and rodent density in our study were positive (electronic supplementary material, S4). Therefore, correlational studies on a small spatial scale (less than or equal to 1 ha) might not be able to show regulation of rodents by predators. Studies that
span multiple years on several spatial scales are thus needed to better understand the correlations between predator activity and rodent and tick density.

We found a strong identity effect of red fox and stone marten compared with the other mammalian predators of rodents (electronic supplementary material, S4). All predators were generalist foragers that feed on a large variety of food items, but red fox has the highest proportion of small rodent biomass in its diet [49–51], which might explain the strong identity effect. Second, the identity effect might relate to predator size as red fox and stone marten were the two largest predators that we recorded [52]. Reducing movement and increasing refuging behaviour may be more effective as strategy to avoid a larger predator than as strategy to avoid a smaller predator that can also hunt in dense vegetation or enter rodent burrows.

We found further support for a reservoir role of bank vole and wood mouse for B. miyamotoi and Ca. N. mikurensis as co-infections of these pathogens with B. afzelii in questing nymphs occurred more than expected by chance. This suggests that larvae get infected with these three pathogens while feeding on the same host species, suggesting that the same host species that maintain B. afzelii also maintain B. miyamotoi and Ca. N. mikurensis. This is further supported by the higher standardized correlation coefficients for larval burden in correlation with DIN for these pathogens compared with the results for DON. Overall, the patterns were less strong for B. miyamotoi, probably because infection by larvae and transovarial transmission also play a role in the maintenance of this pathogen, but not for the others [53].

This study is, to our knowledge, the first to find empirical support for a negative correlation between the activity of predators, the density of questing nymphs and DIN for tick-borne pathogens. Our study also highlights the importance of differences in larval burden between sites as these were correlated with differences in nymphal densities and DIN between sites. The results suggest that predators can indeed lower the number of ticks feeding on reservoir-compotent hosts, which implies that changes in predator abundance may have cascading effects on tick-borne disease risk.

The emergence of cascading effects of predator activity on tick-borne disease risk calls for the appreciation and protection of predator species such as red fox, many of which are persecuted across Europe [54].

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MEXICAN GRAY WOLVES AND THE ECOLOGY OF FEAR: A COMPARATIVE
ASSESSMENT OF COMMUNITY ASSEMBLAGES IN ARIZONA

by

JOSHUA SCOTT HOSKINSON

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STATEMENT BY AUTHOR

The thesis titled *Mexican Gray Wolves and the Ecology of Fear: A Comparative Assessment of Community Assemblages in Arizona* prepared by Joshua Scott Hoskinson has been submitted in partial fulfillment of requirements for a master's degree at the University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

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April 10, 2018
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DEDICATION

This master’s thesis is dedicated to two species in particular – the Mexican gray wolf (Canis lupus baileyi), and the coyote (Canis latrans). These two species have been subjugated to the intense pressure of environmental anthropocentrism, in which the wishes of humans were violently placed onto them and other predators. This anthropocentrism continues, although not as violently, and thus hopefully one day wolves, coyotes, humans, and other predators will be able to live in ecological balance.
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ABSTRACT

The dramatic ecological influence of northwestern gray wolves (*Canis lupus occidentalis*) on the landscape of Yellowstone National Park, termed a trophic cascade, has been well-documented and a marvel of reintroduction efforts of apex predators in the United States. These wolves have initiated both a traditional trophic cascade, which spans across trophic levels (predator-prey-vegetation), and a carnivore cascade, which spans across a predator guild (wolf-coyote-fox). The present study asks whether or not the Mexican gray wolf (*Canis lupus baileyi*) can influence the distribution of coyotes, gray foxes, elk, and mule deer in the Blue Range Wolf Recovery Area (BRWRA). This was completed through means of a camera trap survey, with two experimental plots within the core home range of Mexican gray wolves in the BRWRA (i.e. the “north” and “south” plots) and one plot west of the BRWRA (i.e. the “west” plot) without sustained Mexican gray wolf activity. After the camera survey, detection rates for the coyotes, gray foxes, elk, and mule deer were calculated. Through both a generalized linear mixed modelling (GLMM) approach, and a Kruskal-Wallis analysis, detection rates were compared across the north, south, and west plots. No statistically significant differences were found in detection rates between the plots, which means there is no indication that the Mexican wolves are influencing the distribution of coyotes, gray foxes, elk, or mule deer in the region. However, since the Mexican wolf population in Arizona is heavily managed, as well as issues with missing data in the camera survey itself, it would be unwise to make broad claims about the ecological implications of Mexican gray wolf reintroduction from this study.
INTRODUCTION

Apex Predators, Trophic Cascades, and Non-Trophic Cascades

Apex predators, or those species that occupy the highest trophic level in a given environment, have been repeatedly shown to have strong effects upon their respective communities and ecosystems (Ripple et al. 2014b). Attributes that are frequently ascribed to these apex predators are: body size of larger than 18-34 kg, K-selected reproductive strategy, cooperative social behaviors, “family planning” (e.g. female reproductive suppression and infanticide), and territoriality; these characteristics facilitate apex predators to intrinsically regulate their own population sizes (Wallach et al. 2015). Whilst having this ability, apex predators also hold a keystone role in communities and ecosystems by extrinsically regulating the population sizes and densities of prey species as well as other species within the predator guild; this property can influence the occurrence of an ecological phenomenon known as an ecological cascade.

Ecological cascades are defined as reciprocal effects that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in a food web (Pace et al. 1999). Two broad categories of ecological cascades occur – trophic cascades and non-trophic cascades. Trophic cascades are those ecological cascades that occur across trophic interactions, or those interactions that involve the consumption of one species by another (i.e. predator-prey, plant-herbivore, etc), whereas non-trophic cascades would be defined as ecological cascades that occur across other types of species interactions, such as mutualism and competition (O’Connor et al. 2012, Sanders et al. 2013). For this discussion, it is important to note the different types of ecological cascades, as apex predators have the propensity to initiate ecological cascades across trophic levels (e.g. predator-herbivore-vegetation) or across non-trophic levels, such as within a predator guild (e.g. wolf-coyote-fox).

Ecological cascades have two mechanisms of operation, both integral to the overall cascade effect: N-driven cascades and μ-driven cascades. In N-driven ecological cascades the apex predator can directly influence the census population size of organisms. In μ-driven ecological cascades the apex predators can influence the foraging behavior of either prey species or other carnivores within their guild and thus more
indirectly influence the population density and distribution across a landscape (Brown, Laundre, and Gurung 1999). It is namely this last mechanism that can be more important in terms of optimal foraging strategy of either other carnivores or prey species, and this instills a “landscape of fear” for these species in which these species incorporate predation risk into their optimal foraging strategies (Brown, Laundre and Gurung 1999; Ripple and Beschta 2004a). Both of these mechanisms have been demonstrated to be equally important, with the µ-driven mechanism perhaps being stronger due to predation risk factor being incorporated into the optimal foraging strategy with the presence of an apex predator (Lima and Dill 1990; Schmitz, Beckerman, and O’Brien 1997).

When these apex predators are missing from their communities or ecosystems, either through natural extinction or anthropogenic local extirpation, irruptions of herbivores likely result, which would increase browsing rates and cause trophic downgrading of local environments (Estes et al 2011). This would also cause the release of mesopredators to potentially assume an “apex predator-like” role in the environment, although in some cases the mesopredator cannot attain the apex predator ecological niche (Ritchie et. al 2009; Ripple et. al 2013; Wallach et al 2015; Jones et. al 2016). Thus, the importance of maintaining the presence of apex predators within communities and ecosystems is to keep the ecosystems stable and prevent trophic downgrading.

**Case Study: Gray Wolves (*Canis lupus occidentalis*) and Yellowstone National Park**

Perhaps one of the most well-known apex predators in the United States is the gray wolf (*Canis lupus sbsp*.*). The gray wolf was persecuted during the early 1900s due to ubiquitous misunderstanding and fear of the wolf, as well as the perceived threat of livestock depredation. Following this fear, misunderstanding, and anthropocentrism, the United States Congress established the United States Bureau of Biological Survey with the Division of Predator and Rodent Control (PARC) in 1915 which had expressed the purpose of eliminating the wolves and other large predators from the United States (Brown 1983; Mech and Boitani 2003).
As a result, not only was trophic downgrading caused due to increased browsing rate by elk (Cervus canadensis) and deer (Odocoileus virginianus and Odocoileus hemionius), but the tide was turning as American culture gained a more favorable opinion of wolves (Mech and Boitani 2003). As such, wolf conservation programs were initiated and wolves (Canis lupus occidentalis) were captured in Canada (Chambers et al 2012) and released into Yellowstone National Park in 1995 and 1996 (Merkle et al 2009). Research following the reintroduction of gray wolves into Yellowstone National Park studied how the wolves affected lower trophic levels and the abiotic environment (i.e. trophic cascade), and also included carnivore cascades (i.e. non-trophic cascade).

Researchers attempted to find evidence for occurrence of a trophic cascade in Yellowstone National Park resulting from wolf reintroduction. Ripple and Larsen(2000) documented a historic trend of aspen (Populus tremuloides) recruitment in Yellowstone National Park and found that aspen recruitment was diminished during the years of wolf extirpation from Yellowstone National Park, and the age class that would have been recruited during this time was missing (Larsen and Ripple 2003). Following the wolf reintroduction, studies found that reintroduction of the gray wolf contributed to increased recruitment of aspen (Ripple et al 2001), cottonwoods (Populus spp.) (Beschta 2003), willow (Salix spp.) (Ripple and Beschta 2004b), and alders (Alnus incana tenuifolii) (Ripple, Beschta, and Painter 2015). This trend of increased recruitment is still maintained15 years after the initial wolf reintroduction into Yellowstone National Park (Ripple and Beschta 2012). In addition, studies have found that due to the increase tree recruitment the morphology of Yellowstone rivers have changed (Beschta and Ripple 2006; Beschta and Ripple 2012), leading to the inference that wolves had an effect on the abiotic environment of Yellowstone National Park. Thus, in terms of trophic cascades, the northwestern gray wolf effect on the Yellowstone National Park ecosystem has been quite remarkable.

This trophic cascade in Yellowstone National Park resulting from wolf reintroduction was primarily a µ-driven cascade; that is to say, it was primarily behavior-driven. Through reintroducing the wolf back into the environment, the elk (Cervus canadensis) changed its optimal foraging strategy by
incorporating the risk of predation and thus leaving “plant refugia” in locales that have high predation risk (Ripple and Beschta 2004a). It is these “plant refugia” locales where the greatest amount of tree recruitment (aspen, cottonwood, willow, and alder) occurred within Yellowstone National Park. Therefore, the major mechanism of trophic cascade occurrence was not through population reduction, but rather through behavior modifications that redistributed the density of elk post-reintroduction (Ripple and Beschta 2004a).

**Carnivore Cascades**

In addition to the remarkable trophic cascades, carnivore cascades occur within the carnivore guild that lives in sympatry with the apex predator (e.g. wolf-coyote-fox). Studies have shown that the mechanisms are the same except behavior modification is achieved by competitors of the same guild rather than at different trophic levels. For example, in Yellowstone National Park as a result of the wolf reintroduction, interference competition between coyotes (*Canis latrans*) and the northwestern gray wolves (*Canis lupus occidentalis*) causes a change, not necessarily in the population sizes of the coyotes, but in the population density and abundance of coyotes in a particular locale (Berger and Gese 2007; Berger, Gese, and Berger 2008; Merkel et al 2009).

These systems influence the distribution and abundance of coyotes, but the wolves can also extend their influence to other systems. For instance, by influencing the distribution and abundance of coyotes, wolves can affect pronghorn distributions (Berger, Gese, and Berger 2008), allow for irruptions in small mammal populations such as rodents (Miller et al 2012), and influence the distribution of foxes (*Vulpes spp.* and *Urocyon cineroargenteus*) at the local scale (Levi and Wilmers 2012) and the continental scale (Newsome and Ripple 2014). Wolves can also allow recovery of grizzly bear (*Ursus arctos*) populations by limiting browsing of berry plants by elk (Ripple et al 2014a). Therefore, wolf reintroduction could assist in the recovery and conservation of other predator species by proxy. It is important to note that wolves involved in the carnivore cascades discussed here were *Canis lupus occidentalis*, one of the larger wolf subspecies.
Mexican Gray Wolves in Arizona and New Mexico

Mexican gray wolves (*Canis lupus baileyi*), the smallest subspecies of gray wolf, was historically distributed in the American Southwest and Mexico (Brown 1983; Beschta and Ripple 2010; Hendricks et al 2016). Beschta and Ripple (2010) was the only study to examine whether or not Mexican gray wolves initiated a trophic cascade after their reintroduction to the Apache-Sitgreaves National Forest in 1998. They analyzed aspen recruitment in the BRWRA in the Apache National Forest near Alpine, Arizona in three locales: a refugium site inaccessible to both elk and cattle, an old growth site accessible to elk, and a thinned site accessible to elk. They found aspen in the refugium site was consistent with climactic variation, and no significant difference from what aspen recruitment was expected from climactic variation post-reintroduction of the Mexican gray wolf. As this was contradictory to what Ripple and Beschta observed in previous studies with wolves in Yellowstone National Park, they concluded there was no trophic cascade occurring in the BRWRA of 2010.

Curiously, there have been no studies of whether or not N-driven or μ-driven cascades have occurred with regard to the Mexican gray wolf. In other words, there have been no studies on whether Mexican gray wolves have influenced either the population size or population density of other sympatric carnivores such as coyote or fox. In addition, there have been no studies on the interactive behavior between Mexican gray wolf and these sympatric canids. If the Mexican gray wolf can influence the population size and/or distribution of coyote and fox, it would be important to estimate whether or not Mexican gray wolves have established an ecologically effective density to initiate a carnivore cascade (Soulé et al 1999). In addition, data used in the Beschta and Ripple (2010) study is approaching 10 years old, and updated information to reassess the question of Mexican gray wolf involvement in any ecological cascades would be useful.
The Present Study

For the present study, the primary objective is to estimate whether or not the Mexican gray wolf is influencing the distribution of prey species, such as Rocky Mountain Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), as well as competitor species, specifically coyote (*Canis latrans*) and gray fox (*Urocyon cinereoargenteus*) in the BRWRA. In concordance with previous studies, the hypothesis of this study is that Mexican wolves have influenced the distribution of both prey and competitor species, and therefore we predict that areas without Mexican gray wolves would have a higher abundance of prey and competitor species than areas with Mexican gray wolves.
METHODS

Study Site Description

The present study was conducted within the confines of the BRWRA and adjacent areas, which are all within the larger Mexican Wolf Experimental Population Area (MWEPA). The MWEPA is defined by the geographical area that encompasses the states of Arizona and New Mexico, bounded by Interstate 40 (I-40) to the north and the international United States-Mexico border to the south (US Fish and Wildlife Service, 2017). The MWEPA itself contains a variety of biotic communities as defined by Brown and Lowe (1994), ranging from Subalpine Grassland in the White Mountains of Arizona, to the Sonoran Desertsrub that is characteristic of Southern Arizona.

This study primarily dealt with the Rocky Mountain (Petran) Montane Conifer Forest and all cameras are at elevations between 1900m-2900m. This biotic community is semi-ubiquitous across the Mogollon Rim of Arizona – this is a major biotic community that is found within the BRWRA, and as such a majority (sixteen) of camera sites are within this biotic community, specifically located in pure stands of Ponderosa Pine (*Pinus ponderosa*). Other adjacent biotic communities present in the BRWRA are Rocky Mountain (Petran) Subalpine Conifer Forest, a mixed conifer forest including aspen (*Populus tremuloides*), and Subalpine Grassland, and two cameras are placed within these biotic communities (Figure 1). It is useful to mention that not only wolves, but Rocky Mountain Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), coyotes (*Canis latrans*), and gray foxes (*Urocyon cinereoargenteus*) are ubiquitous throughout this area (Anderson and Wallmo 1984, Bekoff 1977, Fritzell and Haroldson 1982, Nowak 1999).

Wildlife Camera Experimental Design

The present study consisted of three plots (two experimental plots with high wolf activity and one control plot with no wolf activity), with six (6) cameras per plot for a total of eighteen (18) camera sites. The experimental plots, hereafter referred to as “north” and “south” plots and within the boundaries of the BRWRA, were in areas of sustained Mexican wolf activity across multiple years. The “north” experimental
plot consisted of: Burro Mountain, Mamie Creek, Roger’s Marsh, Rudd Creek, Sherlock Draw, and Sizer Knoll camera sites. The “south” experimental plot consisted of: Crow Poison, Double Cienega, Foote Creek, Highline Trail, Reservation Creek, and Tenney Mountain camera sites. The control plot, hereafter referred to as the “west” plot, was located west of the experimental plots in an area of no Mexican wolf activity. The “west” control plot consisted of: Canyon Creek, Hess Draw, Hog Wash, Potato Field Draw, Upper Cherry Creek, and Willow Creek camera sites. All three plots were within the Apache Sitgreaves National Forest in Arizona, and in the same habitat type (Figure 1).

Remote digital wildlife trail cameras (Covert Deuce) were placed within experimental plots based on Mexican wolf pack home range data for 2014, 2015, and 2016 provided by wolf biologists with the Mexican Wolf Interagency Field Team (IFT). The home ranges included 90% kernels, which represented areas Mexican wolves occupied 90% of the time, and 50% kernels, which represented areas Mexican wolves occupied 50% of the time (50% kernels represent the “core” home range of each pack and were always within the boundaries of the 90% kernels for a given wolf pack). Home range maps across years were compared, and locations where the 50% kernel for a given pack overlapped across multiple years were candidates for camera placements for the experimental plots. The same home range maps were referred to when deciding the camera locations for the control plot. Areas that were excluded from any 90% kernel of any given Mexican wolf pack over multiple years were candidates for the control plot. Once candidate locations were identified, and since the wolf biologists of the Mexican Wolf IFT knew each of the locations with certainty, the wolf biologists decided on exact locations for wildlife cameras in all three plots and provided GPS coordinates for each camera.

Camera settings were: 1 photo per event, 5MP photo size, 1 minute interval between photos, normal PIR sensitivity, xenon flash for night photos, and normal range for flash unless a particular camera site required adjustment in PIR sensitivity or flash range.
Each of these cameras were baited by placing scent lure (Mark June Cherry Red commercial bait) approximately 5m from the camera at ground height each time the camera was checked. This was done to maximize the number of carnivores that walked in front of the camera. Each camera was checked by the wolf biologists of the Mexican wolf IFT approximately every 2-2.5 months, for a total of one year, starting approximately December 1, 2016, and ending by November 30, 2017. In this way, data was collected for each off our seasons and for one full year.

Data Analyses

Analyses of this data was performed in two parts. First, the photos downloaded from each camera were sorted using a hierarchical method as described in Sanderson and Harris (2013). This hierarchical method involved sorting photos by plot (i.e. north, south, or west), and within each of these plots into location folders. There was a location folder for each camera, and within each location folder was a folder for each species photographed. Following photo sorting, the total number of photographs captured at each location, trap-nights (i.e. camera trap effort) for each camera location, number of independent photos of each species captured, and detection rates of each species captured were calculated with an algorithm in the program (Sanderson and Harris 2013). Photographs were considered independent if 60 minutes passed without the camera capturing another photograph of the same species – if there was another photo of the same species within that 60 minute interval, it was discounted. For further analyses, photographs that contained no species (i.e. “ghost” photographs), or photographs that contained domestic species (e.g. domestic dog *Canis lupus familiaris*, domestic cow *Bos taurus*, or humans *Homo sapiens*), were discounted. In this way, the number of independent photographs of wildlife was calculated. The independent photographs of all wildlife species, which included the independent photographs of the species of interest (i.e. coyotes, gray foxes, elk, and mule deer), were used for further statistical analyses, which consisted of analyzing differences in detection rates for species of interest between plots.
Statistical analyses were performed in two ways to provide multiple measures to determine significance for detection rates between plots. First, generalized linear mixed modelling analyses were completed using a GLMM package in the statistical program R (Knudson 2017). Secondary analyses were the Shapiro-Wilk normality test, the Kruskal-Wallis test, and Conover’s test of multiple comparisons with a Holm-Bonferroni correction using the PMCMR package in the statistical program R (Thompson et al 2010; Bates et al 2011; Pohlert 2014; Li et al 2014; Gustavo Pinoargote, personal communications).
RESULTS

Results of Camera Trap Analysis

In the north plot, there were a total of 10,034 photographs captured, 313 of which were independent photographs of wildlife species, across a total of 1,679 trap nights. In the south plot, there were a total of 7,342 photographs captured, 295 of which were independent photographs of wildlife species, across a total of 1056 trap nights. Lastly, in the west (control) plot, there were a total of 21,444 photographs captured, 616 of which were independent photographs of wildlife species, across a total of 1,782 trap nights. This results in a total of 38,820 total photographs captured across all 18 camera locations, 1,224 of which were independent photographs of wildlife species, across a total of 4,517 trap nights (Table 1, Table 2, Table 3).

Further analyses were completed by the software program in Sanderson and Harris (2013). These analyses calculated detection rates of each species (i.e. coyotes, gray fox, elk, and mule deer) by dividing species abundance (i.e. the number of photos of that species) by camera trap effort (i.e. trap-nights). In this way, we are able to analyze the abundance of each species per unit camera effort. In the north plot, the average detection rate was 1.44 coyotes/unit effort for coyotes, 0.05 gray foxes/unit effort, 12.52 elk/unit effort, and 3.16 mule deer/unit effort. In the south plot, the average detection rate was 0.788 coyotes/unit effort, 0.16 gray foxes/unit effort, 24.03 elk/unit effort, and 5.05 mule deer/unit effort. Lastly, for the west (control) plot, the average detection rate was 5.38 coyotes/unit effort, 0.97 gray foxes/unit effort, 14.01 elk/unit effort, and 8.95 mule deer/unit effort (Table 4). These detection rates were then statistically analyzed.

Results of Statistical Analysis

Statistical analyses consisted of first using a generalized linear mixed modelling (GLMM) approach to test for significant differences in the detection rates amongst the north, south, and west plots. The GLMM analyses for coyotes (p = 0.604), gray foxes (p = 0.259), elk (p = 0.480), and mule deer (p = 0.270) all resulted in non-significant differences between the three plots for any species of interest.
Supplementary statistical analyses were performed to provide additional measures for significant differences between the three plots. A Shapiro-Wilk normality test was performed to see if the distribution of detection rates was normally or non-normally distributed, and the distributions of detection rates for coyotes ($p = 1.402e-07$), gray foxes ($p = 2.33e-07$), elk ($p = 0.0002399$), and mule deer ($p = 0.002226$) were all determined to be non-normal due to all $p$-values being below the threshold of 0.05. Next, a Kruskal-Wallis test was performed for each species, and the differences between plots for coyote ($p = 0.2686$), gray fox ($p = 0.2668$), elk ($p = 0.8948$), and mule deer ($p = 0.1923$) were all determined to be non-significant. Lastly, a Conover’s test for multiple comparisons, with Holm-Bonferroni corrections, was performed between each plot for each species of interest to provide a post-hoc analysis of each pairwise comparison. For coyote, the north-west ($p = 0.64$), south-west ($p = 0.37$), and north-south ($p = 0.64$) pairwise comparisons all resulted in non-significant differences between plots. For gray fox, the north-west ($p = 0.36$), south-west ($p = 0.65$), and north-south ($p = 0.65$) pairwise comparisons all resulted in non-significant differences between plots. For elk, the north-west ($p = 1.00$), south-west ($p = 1.00$), and north-south ($p = 1.00$) pairwise comparisons all resulted in non-significant differences between plots. Lastly, for mule deer, the north-west ($p = 0.24$), south-west ($p = 0.50$), and north-south ($p = 0.51$) pairwise comparisons all resulted in non-significant differences between plots.
DISCUSSION

According to these analyses, it is a reasonable suggestion that Mexican gray wolves have yet to be successful in achieving their ecological role as top predator in the BRWRA. This conclusion is reached by the lack of significant difference of detection rates between plots with Mexican gray wolves (as measured by overlap of 50% kernels, which represent the sustained presence of a core home range for one or multiple packs of Mexican gray wolves) compared to plots without Mexican gray wolves. These non-significant differences were also true for coyotes, gray foxes, elk, and mule deer. From statistical analyses, another reasonable suggestion is that Mexican gray wolves do not affect the distribution of coyotes, elk, or mule deer. Given that the Mexican gray wolves have been consistently been in the area for 20 years, there is some question of why they have not yet achieved their ecological role as top predator. This result is contradictory to the patterns observed in Yellowstone National Park and other areas of wolf reintroduction, yet the Mexican wolves not having an effect on ecological cascades was observed with prior data collected for trophic cascade (Beschta and Ripple 2010). Though, this relationship between the north, south, and west plots only implies a correlation, not a causation, between wolf presence/absence and detection rates of elk, mule deer, coyote, and gray fox. From this study, we can say that there is no relationship between wolf presence/absence and the detection rates of the species of interest, but we cannot say that the lack of significant difference in detection rates between the plots was because of wolf presence/absence. This lack of significant difference between the plots may be due to a variety of factors.

One plausible explanation for the lack of significance may be due to the Mexican gray wolf population size and range. In 2016, the Mexican gray wolf population was estimated to be around 113 wolves occupying 41,735 km², primarily in New Mexico (US Fish and Wildlife Service, 2016) whereas the wolf population of approximately the same size in Yellowstone National Park occupied 8989 km² (Smith et al 2017). For a landscape of fear to be instituted in coyotes, gray foxes, elk, and mule deer, these species would have to encounter the Mexican wolves, in either a competitive or preyed upon manner, often enough for the Mexican wolves to be incorporated into each species’ optimal foraging strategy (Lima and Dill 1990,
Brown, Laundré, and Gurung 1999) as happened in the Yellowstone National Park system (Ripple and Beschta 2004a). If these species were to encounter the Mexican gray wolf on a consistent basis, it would be reasonable to assume a modified distribution of these species, as measured by detection rate, such that a lower detection rate is observed for coyotes, elk, and mule deer, but a higher detection rate for gray foxes, in areas consistently occupied by Mexican wolves. If, however, a Mexican gray wolf is encountered only occasionally, not consistently, then the risk of predation/competition by the Mexican gray wolf would not be incorporated into the species’ optimal foraging strategy. Therefore, in this case, we should not see differences in distribution of these species as measured by detection rate. According to our analyses there is no statistically significant difference in detection rate between plots with Mexican wolves and plots without, thus we suggest that a landscape of fear has not been instituted in the Blue Range Wolf Recovery Area.

Another reasonable explanation for the lack of significance is the reintroduced habitat itself. Brown (1983) states that the Mexican gray wolves historically have been associated with montane forests and woodlands within vegetation such as oak woodlands, pinyon-juniper forests, and adjacent grasslands while avoiding the Mohave, Sonoran, and Chihuahuan deserts and adjacent semi-desert grasslands. These habitats would be consistent with the habitats of Madrean Evergreen Woodland, Interior Chaparral and Montane Grasslands of Brown and Lowe (1994), which are found in the Sky Islands of Southern Arizona and New Mexico and extends well into the Sierra Madre Occidental and Sierra Madre Oriental mountain ranges of Mexico. Historically, there was perhaps another subspecies of wolf (Canis lupus youngi or Canis lupus mogollonesis) that occupied Petran Montane Conifer Forests of the Blue Range Wolf Recovery Area (Brown 1983). Both Brown (1983) and Hendricks (2016) support the notion that current territory occupied by the reintroduced Mexican gray wolves would have been the extreme farthest north of the historical distribution. In addition, according to Brown (1983) the presumed main prey item of the Mexican wolf would have been Coues’ White-tailed deer (Odocoileus virginianus couesi) and possibly the mule deer (Odocoileus hemonius), not elk (Cervus canadensis). Thus, the lack of significance could be partially due
to the reintroduction effort being in non-historical habitat, which may affect hunting behavior, as well as presumably a non-historical prey base.

It is also worth mentioning that as part of the management plan of the Mexican wolf, supplementary food caches (i.e. road-killed native prey carcasses provided to wolf packs to assist in feeding young) and diversionary food caches (i.e. road-killed native prey carcasses provided to wolf packs to reduce potential conflicts with livestock) are provided to aid the Mexican wolves (US Fish and Wildlife Service, 2016). This provision of food caches may affect the hunting behavior of the wolves, and thus may have some effect on the ecological implications of the reintroduction effort. Though, this has not been directly studied, and so an ecological study needs to be done to assess the ecological implications of these food caches.

In any case, the Mexican gray wolf could be argued to have no significant effect on coyotes, gray foxes, elk, or mule deer for any of these reasons, or for reasons that we have not considered here. Though, due to these concerns, one should be cautious about making such claims, as this study only indicates that Mexican gray wolves have yet to achieve their top predator status. The present study is not complete in its assessment of the ecological implications of the reintroduction efforts of the Mexican wolves and further examination of a variety of questions need to be addressed before making any kind of claim as to the ecological implications of the Mexican wolf.

These further examinations of effects could take a variety of forms. First, there could be further analyses on the effects across the prey guild, which would include the prey base of not only the Mexican wolves (e.g. ungulates), but also the prey base of competitors (e.g. coyotes, pumas), as well as a vegetation assessment to analyze bottom-up trophic effects. Second, there should be a more complete analysis on other potential prey items of Mexican wolves, rather than solely focusing on elk and mule deer. One notable instance that would be necessary to look at would be the effects that Mexican gray wolves have on pronghorn (*Antilocapra americana*), as they were detected at three cameras: Hess Draw (1.32 pronghorn/unit effort), Potato Field Draw (3.21 pronghorn/unit effort), and Willow Creek (0.36 pronghorn/unit effort), which results in an average detection rate of 0.79 pronghorn/unit effort. Pronghorn
were only found in the west plot, and thus were not able to be analyzed in the present study. Though, pronghorn are known to be ubiquitous both historically and currently (Hall and Kelson 1959; Nowak 1999), and so it would be interesting to look at potential reasons as to why no pronghorn were detected at all within the 50% kernels of the Mexican gray wolf home range.

In addition to these assessments, it would be ideal to compare the results of this study to that of historical records and other Mexican gray wolf reintroduction efforts. For the historical assessment, it would be crucial to know how the Mexican wolf has historically affected the distribution of coyotes, gray foxes, mule deer, and white-tailed deer (*Odocoileus virginianus*) through trapping records (Brown 1983) in the American Southwest and Mexico. In this way, we would develop a metric by which to compare current distributions of these species of interest to their historical distributions. As for other Mexican gray wolf reintroduction sites, through a binational effort there were Mexican wolves reintroduced in the northern Sierra Madre Occidental of Chihuahua and Sonora in Mexico, and 41 wolves have been reintroduced in this area. As of 2017, these wolves are still in the establishment phase and approximately 31 wolves inhabit the northern Sierra Madre Occidental (US Fish and Wildlife, 2017). With this particular reintroduction site being in historical Mexican wolf territory (Brown 1983, Hendricks et al 2016), this would be perhaps a more suitable location for studies into the ecological effects of Mexican wolves. After all, this is the similar habitat that Roy T. McBride trapped the seven Mexican wolves in 1980 which founded the captive breeding program the ancestors to all modern Mexican wolves (Brown 1983).

In any case, whether it’s continuing this study in the northern Sierra Madre Occidental in Mexico, to analyzing historical records in both Mexico and the American Southwest, to broadening the scope and looking at other competitors, prey bases, and vegetation assessments, there are far more questions to pursue before a proper conclusion on the ecological impact of the Mexican wolf reintroduction can be obtained.
Figure 1. Map of camera locations overlaid onto the biotic communities map from Brown and Lowe (1994). The study area in relation to the entire state of Arizona is depicted in the insert map in the bottom left hand corner. Legend includes the biotic communities, camera locations for the no wolves plot (i.e. west plot) labeled in green, the north plot labeled in blue, and the south plot labeled in red.
Table 1. North study plot wildlife pictures. Description of the start/end dates, number of trap-nights, the total number of pictures, and the total number of independent pictures of wildlife for the north plot. Four of the six cameras were down for a period of time, and so each start/end date for each period that the camera was actively capturing photographs is described. Trap-nights, or camera effort, are the number of 24 hour periods that the camera was actively capturing photographs. Total number of pictures includes all of the photographs obtained by that particular camera. The total number of independent pictures of wildlife excludes multiple photographs of the same species taken within a 60-minute period, photographs with no species (i.e. “ghost” photos), and photos of domesticated species (e.g. domestic dogs, domestic cows, and humans). This column includes, but isn’t limited to, the species of interest.

<table>
<thead>
<tr>
<th>Location</th>
<th>Start Date</th>
<th>End Date</th>
<th>Trap Nights</th>
<th>Total Number of Pictures</th>
<th>Total Number of Independent Pictures of Wildlife</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burro Mountain</td>
<td>1. 11/6/2016 2. 7/5/2017</td>
<td>1. 4/19/2017 2. 8/10/2017</td>
<td>268</td>
<td>908</td>
<td>22</td>
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<tr>
<td>Mamie Creek</td>
<td>1. 11/15/2016 2. 6/8/2017</td>
<td>1. 5/15/2017 2. 10/12/2017</td>
<td>332</td>
<td>3155</td>
<td>43</td>
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<tr>
<td>Roger’s Marsh</td>
<td>1. 11/5/2016 2. 7/3/2017</td>
<td>1. 3/28/2017 2. 10/26/2017</td>
<td>349</td>
<td>2539</td>
<td>49</td>
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<tr>
<td>Rudd Creek</td>
<td>11/25/2016 6/24/2017</td>
<td></td>
<td>97</td>
<td>113</td>
<td>46</td>
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<td>Sherlock Draw</td>
<td>11/6/2016 10/16/2016</td>
<td></td>
<td>344</td>
<td>1688</td>
<td>91</td>
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<tr>
<td>Sizer Knoll</td>
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<td>1. 4/15/2017 2. 8/18/2017</td>
<td>289</td>
<td>1634</td>
<td>62</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>-</td>
<td>-</td>
<td>1679</td>
<td>10034</td>
<td>313</td>
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Table 2. South study plot wildlife pictures. Description of the start/end dates, number of trap-nights, the total number of pictures, and the total number of independent pictures of wildlife for the south plot. Two of the six cameras were down for a period of time, and so each start/end date for each period that the camera was actively capturing photographs is described. Trap-nights, or camera effort, are the number of 24 hour periods that the camera was actively capturing photographs. Total number of pictures includes all of the photographs obtained by that particular camera. The total number of independent pictures of wildlife excludes multiple photographs of the same species taken within a 60-minute period, photographs with no species (i.e. “ghost” photos), and photos of domesticated species (e.g. domestic dogs, domestic cows, and humans). This column includes all wildlife photos, not just the species of interest.

<table>
<thead>
<tr>
<th>Location</th>
<th>Start Date</th>
<th>End Date</th>
<th>Trap Nights</th>
<th>Total Number of Pictures</th>
<th>Total Number of Independent Pictures of Wildlife</th>
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<tr>
<td>Crow Poison</td>
<td>1. 1/13/2017</td>
<td>2. 7/26/2017</td>
<td>178</td>
<td>215</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>1. 3/1/2017</td>
<td>2. 8/27/2017</td>
<td></td>
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<tr>
<td>Double Cienega</td>
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<td>167</td>
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<td>Highline Trail</td>
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<td>Reservation Creek</td>
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<td>2. 7/26/2017</td>
<td>282</td>
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<tr>
<td></td>
<td>1. 3/24/2017</td>
<td>2. 9/9/2017</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tenney Mountain</td>
<td>11/30/2016</td>
<td>1/13/2017</td>
<td>3†</td>
<td>52</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>1056</td>
<td>7384</td>
<td>295</td>
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</table>

† There was a malfunction in the camera at Tenney Mountain, South Plot. Thus, even though it was out longer than three nights, it only had pictures for three nights.
Table 3. West study plot wildlife pictures. Description of the start/end dates, number of trap-nights, the total number of pictures, and the total number of independent pictures of wildlife for the west plot. Three of the six cameras were down for a period of time, and so each start/end date for each period that the camera was actively capturing photographs is described. Trap-nights, or camera effort, are the number of 24 hour periods that the camera was actively capturing photographs. Total number of pictures includes all of the photographs obtained by that particular camera. The total number of independent pictures of wildlife excludes multiple photographs of the same species taken within a 60-minute period, photographs with no species (i.e. “ghost” photos), and photos of domesticated species (e.g. domestic dogs, domestic cows, and humans). This column includes all wildlife photos, not just the species of interest.

<table>
<thead>
<tr>
<th>Location</th>
<th>Start Date</th>
<th>End Date</th>
<th>Trap Nights</th>
<th>Total Number of Pictures</th>
<th>Total Number of Independent Pictures of Wildlife</th>
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<td>Canyon Creek</td>
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<td>1. 5/23/2017 2. 10/5/2017</td>
<td>232</td>
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<td>Hess Draw</td>
<td>1. 11/27/16 2. 6/8/2017</td>
<td>1. 5/18/2017 2. 10/13/2017</td>
<td>303</td>
<td>2149</td>
<td>102</td>
</tr>
<tr>
<td>Hog Wash</td>
<td>1. 11/30/2016 2. 6/8/2017</td>
<td>1. 5/15/2017 2. 11/2/2017</td>
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<td>3159</td>
<td>101</td>
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<td>Potato Field Draw</td>
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<td>Willow Creek</td>
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<tr>
<td>Total</td>
<td>11/26/2016</td>
<td>9/23/2017</td>
<td>1782</td>
<td>21444</td>
<td>616</td>
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Table 4. Description of the camera effort and the detection rates for coyotes, gray foxes, elk, and mule deer for each of the locations at each of the study plots. Camera effort, or trap-nights, is the number of 24 hour periods that the camera was actively capturing photographs. Detection rate is the number of photographs of that species, at that location, per unit camera effort.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Location</th>
<th>Camera Effort</th>
<th>Coyote Detection Rate</th>
<th>Gray Fox Detection Rate</th>
<th>Elk Detection Rate</th>
<th>Mule Deer Detection Rate</th>
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<tr>
<td>North</td>
<td>Burro Mountain</td>
<td>268</td>
<td>0.00</td>
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<td>7.46</td>
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<tr>
<td></td>
<td>Mamie Creek</td>
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<td>0.90</td>
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<td></td>
<td>Roger’s Marsh</td>
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<td>12.61</td>
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<tr>
<td></td>
<td>Rudd Creek</td>
<td>97</td>
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<td>0.00</td>
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<td></td>
<td>Sherlock Draw</td>
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<td>0.00</td>
<td>10.76</td>
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<td>Sizer Knoll</td>
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<td>0.69</td>
<td>0.00</td>
<td>15.92</td>
<td>3.81</td>
</tr>
<tr>
<td>South</td>
<td>Crow Poison</td>
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<td>0.00</td>
<td>3.93</td>
<td>0.00</td>
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<td></td>
<td>Double Cienega</td>
<td>257</td>
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LITERATURE CITED


Miller, Brian J., Henry J. Harlow, Tyler S. Harlow, Dean Biggins, and William J. Ripple. 2012. Trophic cascades linking wolves (Canis lupus), coyotes (Canis latrans), and small mammals. Canadian Journal of Zoology 90: 70-78.


Letter to the editor

Genetic rescue, not genetic swamping, is important for Mexican wolves

ARTICLE INFO

Keywords:
Adaptive introgression
Genetic rescue
Inbreeding depression
Standing genetic variation

The recent article by Odell, Heffelfinger et al. (2018) (hereafter OH) is another effort to limit and stymie Mexican wolf recovery by state game and fish ungulate biologists and their allies. OH advocate relying substantially on Mexico for recovery, a possibility that is very uncertain due to a largely unquantified but limited natural prey base and widespread killing of predators in the Mexican areas suggested for recovery. On the other hand, the reintroduced Mexican wolf population in Arizona and New Mexico, outside what OH state is historical range, now numbers over 100, and preys primarily on elk despite the availability of white-tailed deer. Further, it is unlikely that there will be effective natural interchange between Mexican and USA populations because of the proposed construction of a border wall and inhospitable habitat between the two countries.

A new aspect of the anti-wolf arguments in OH is that if Mexican wolves are successful in expanding their range northward they would be in danger from “genetic swamping” by northern gray wolves. However, such contact would actually reinstate the historical situation where wolves once occupied the geographic range in the western United States from Mexico to Canada and formed a continuous population where wolves once occupied the geographic range in the western United States from Mexico to Canada and formed a continuous population. Wolves in the reintroduced Mexican wolf population, descended quite unequally from three lineages (0.78 McBride, 0.07 Aragon, 0.15 Ghost Ranch) with seven total founders, have an average pedigree inbreeding coefficient of 0.20 and the estimated number of remaining founder genome equivalents is only 2.0 (Siminski and Spevak, 2017). Fredrickson et al. (2007) found that there was inbreeding depression for litter size in both captive and wild Mexican wolves and also found that crosses between the three lineages showed an increased fitness, resulting in temporary genetic rescue.

Since 2009, there has been artificial supplemental feeding of wild denning Mexican wolves that has greatly increased the survival of pups. It is probable that this supplemental feeding masks some of the detrimental effects of inbreeding, an impact that would be evident if feeding is discontinued. The present-day descendants, three generations later than examined by Fredrickson et al. (2007), are in need of genetic rescue again and crosses with northern gray wolves would provide an appropriate cross to increase fitness.

OH suggested that the somewhat smaller body size and smaller pack size in Mexican wolves than in other wolves would make Mexican wolves at a disadvantage when interacting with northern gray wolves. However, the smaller body size and smaller pack size might actually be adaptive characteristics that allowed Mexican wolves to survive where there was more limited and smaller prey, and where larger body size might be disadvantageous. Because of their predatory flexibility, Mexican wolves can use larger prey, such as elk, where the current wild population exists, and potentially other areas.

Eight Texas cougar females were translocated to Florida to breed with Florida panthers because Florida panther numbers were very low and they showed several traits indicating inbreeding depression. There was concern that adaptive traits that allowed Florida panthers to successfully survive in the Florida environment would be eliminated by this translocation. As a result, the number of animals translocated were at a level such that expectations were that detrimental traits accumulated by inbreeding would be eliminated but traits adaptive to Florida would be retained (Hedrick, 1995), a prediction that has generally been proven correct (Johnson et al., 2010). As precedent, descendants of Texas cougars and Florida panthers are considered Florida panthers and are therefore protected as endangered species.

Using genomic analysis, Mexican wolves have the lowest genetic variation of any wolves (vonHoldt et al., 2011), indicating that there is limited standing variation for future adaptation to environmental challenges, such as new diseases and climate change. Two other sources of adaptive variation are from mutation and from crosses with related subspecies or species, called adaptive introgression. Generating adaptive variation from mutation generally takes very many generations and often has negative pleiotropic effects. On the other hand, variants present in other related subspecies or species should be adaptive in those species and are more likely to be adaptive when introgressed.

There are a number of examples, including humans, in which genetic variation that has been naturally introduced from other animal subspecies or species has been adaptive (Hedrick, 2013). For a genetically depauperate subspecies such as Mexican wolves, crosses with another subspecies, such as northern gray wolves, might restore variation and provide a source of genetic variants that would allow future adaptation.

Overall, given the discussion of the relevant evolutionary biology principles here, genetic rescue from crossing with northern gray wolves would likely facilitate Mexican wolf recovery. Unfortunately, the goal of OH appears to be to put as many roadblocks in the way of Mexican wolf recovery as possible, including now the specier of genetic
swamping, because of their short-sighted view that fewer wolves will provide more ungulates for hunters.

References


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⁎⁎ Department of Ecology and Evolutionary Biology, 610 Charles E. Young Dr. South, University of California, Los Angeles, CA 90095, USA

⁎ Missoula, MT, USA

E-mail address: philip.hedrick@asu.edu
James’s alumroot, *Telesonix jamesii* (Saxifragaceae). James’s alumroot—or brookfoam—was first collected by Edwin James on Pikes Peak in 1820. It is usually found in the cracks of granite outcrops at 8,700-13,050 ft elevation, although the plant can also be found on scree slopes. While it seems to prefer east and north exposures on these surfaces, it can be found growing in full sun to full shade and in variable levels of moisture. Most populations are found on Pikes Peak granite, but there are a few outlier populations in Rocky Mountain National Park, which are on Precambrian gneiss and schist. *T. jamesii* is 60-180 mm tall, with glandular-pubescent stems and leaves.

Alumroots (*Heuchera spp.*) are often found nearby *Telesonix*. Be careful not to confuse the plants when they are not in bloom. *Telesonix heucheriformis*, which has a wider distribution, was once considered a variety of *T. jamesii*, but is now categorized as its own species.

The name *Telesonix* is derived from Greek; “tele” translates as “perfect” and “onyx” translates as “claws.” *T. jamesii* has been reported to be used medicinally by the Cheyenne. KA

*Botanicum absurdum* by Rob Pudim


*Aquilegia* uses Jennifer Ackerfield’s *Flora of Colorado* (2018, second printing) as its preferred guide to plant naming conventions. Readers may also want to familiarize themselves with other guides such as *Colorado Flora*, Eastern and Western editions, by William A. Weber and Ronald C. Wittmann (2012), as well as The Biota of North America Program online guide to North American Vascular Flora (http://www.bonap.org/), and other resources.
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17th Annual Colorado Rare Plant Symposium
“Globally Imperiled Plants Found on the Front Range and Central Rockies”

Friday September 18
8:30 AM to 2:30 PM

Registration is $10 per person at https://conps.org. The Colorado Rare Plant Symposium is held each fall in conjunction with the Colorado Native Plant Society’s annual conference. Hosted by the Colorado Natural Heritage Program, the symposium is an annual meeting to address current status and conservation needs of rare plants in Colorado.

This year the symposium is going virtual and consists of three short sessions. Topics will include:

• A progress report on the conservation actions needed for the Tier 1 and Tier 2 plant species included in the 2015 State Wildlife Action Plan;
• An update to the Floristic Quality Assessment revision; and
• A photo review of the rare plants found on the Front Range and Central Rockies in Colorado.

The 2015 State Wildlife Action Plan included plants for the first time and identifies conservation needs and actions for 120 of Colorado’s rarest plant species including federally-listed species such as Astragalus osterhoutii, and endemic species like Aliciella sedifolia. Jessica Smith of CNHP will provide a review of the conservation needs of these species and the actions that have been taken to date to meet those needs. The Rare Plant Addendum to the SWAP can be viewed at https://cpw.state.co.us/aboutus/Pages/StateWildlifeActionPlan.aspx

In 2007, CNHP published Colorado’s initial FQA report that included Coefficient of Conservation or C-values for the Colorado flora for 80% of the known taxa at that time (Rocchio et al. 2007 https://cnhp.colostate.edu/download/documents/2007/FQAFinalReport.pdf). However, since 2007 there have been numerous taxonomic changes to the Colorado flora—with new species added to the flora, and other species dropped. During 2019 and 2020, CNHP updated the C-values for the 20% of the flora that did not yet have values. C-values are assigned to each plant taxa based on its affinity for natural habitats (for example, those not affected by human disturbance). Land managers can apply the C-values to a plant list for an area, which can then be used to help quantify the quality of that site. Many of the new C-values were evaluated using habitat quality information collected from nearly 3,000 wetland and riparian plot locations (see https://cn.colostate.edu/cwic/tools/plot-database/).

At the 2020 meeting, Pamela Smith of CNHP will present the new C-values calculated for the 20% of the flora that did not have values. She will also discuss how the new online calculator works and how the values were evaluated for the update. In addition, through this effort a number of sources of taxonomic information have been cross-walked for the entire Colorado plant list including the USDA PLANTS database, Weber and Wittmann (2012), and Ackerfield (2015).

In the afternoon session, CNHP botanists will provide a photo review of the rare plants of the Front Range and Central Rockies in Colorado. This will include several species of Aletes, Potentilla, Penstemon, and local favorite Physaria bellii.

CNHP tracks the location and condition of over 500 imperiled plants. Tracking and monitoring efforts guide effective management and protection of those species and thereby prevent extinctions or statewide extirpations of Colorado’s native plant species. ➤
CNHP conducts field surveys for rare native plants; designs and implements monitoring studies; produces models, best management practices, and conservation strategies; and develops detailed maps for rare plants as well as noxious weeds. The CNHP team has active members on the Colorado Rare Plant Technical Committee, the Colorado Weed Advisory Committee, the Colorado Native Plant Society, and NatureServe. Colorado Natural Heritage Program staff works closely with botanists and land managers across Colorado to develop the state’s most comprehensive and accurate dataset of Colorado’s rare flora.

Annual presentations and species-specific meeting notes are available for past years at https://cnhp.colostate.edu/projects/colorado-rare-plant-symposia/

View the Colorado rare plant guide at https://cnhp.colostate.edu/library/field-guides

Past presentations and species-specific meeting notes are available on the CNHP website for 2004-2019. View or download copies of past symposia presentations at https://cnhp.colostate.edu/projects/colorado-rare-plant-symposia/ or view the Colorado rare plant guide here: https://cnhp.colostate.edu/library/field-guides/

Contact Jill Handwerk for more information at (970)491-5857 or jill.handwerk@colostate.edu

**Member Input Needed for Virtual Social**

**Peaks to Prairies: CoNPS Members in the Field!**

By Lenore Mitchell

**Share your summer activities!**

Eventually we’ll be able to hike together again, attend in-person meetings and workshops, and give and receive hugs. In the meantime, we can still share.

Whatever you’re doing this summer, wherever you are from—Durango to Denver, La Junta to Grand Junction—if it involves native plants, tell us about it! Whether you’re doing research, sleuthing around for rare plants, taking fun hikes to worship the blooms, or working away at native plant garden projects, please snap a few pics and jot down a few notes.

Send a few photos and your brief notes to Tom Schweich (tomas@scheich.com) no later than August 25 so we can include you and your activities in the member slide show during the virtual social at this year’s annual conference. Include a photo of yourself, preferably in the midst of your activity.

Here is the agenda for the Virtual Social on Friday, September 18. The following is included with your paid conference registration:

- Welcome to the conference and announcements;
- Narrated presentation about a July 2020 hike to Pikes Peak to commemorate the 1820 Long’s Expedition to Colorado;
- Narrated presentation of slide show with photo contest finalists and first place winners;
- Narrated presentation of slide show depicting statewide member projects, including research, hikes, and gardening related to native plants; and
- Brief narrated slide show to introduce key people who keep CoNPS running, including board members, chapter presidents, and others.
Friday through Sunday, September 18-20
Four sessions over three days

Welcome to the 2020 Annual CoNPS Conference, hosted by the Metro-Denver Chapter, which now has 420 members. State-wide membership totals more than 1100 members in six chapters and includes everyone from professional botanists to beginning plant enthusiasts.

This year’s Annual Conference is brought to you in a webinar format that allows participants to join in from the comfort of their own homes.

We look forward to having as many as 500 native plant lovers gathering virtually to hear and watch this year’s expert speakers.

Daily schedules contain ample break times and a lengthy lunch time on Saturday. In addition, recordings of select presentations may be available for viewing by registered participants for a limited time after the conference—in case you either missed a presentation or wish to repeat it. Audience questions may be submitted via chat boxes during live presentations.

Thanks not only to all conference committee members whose efforts have made this year’s conference possible, but also to the many other volunteers who’ve offered their assistance. Kudos to everyone for making the best of a challenging situation. We give a very special note of gratitude to each of our speakers.

State-wide leadership of CoNPS begins with the operating committee comprised of: Ginger Baer, Deryn Davidson, Mo Ewing, Ann Grant, Irene Weber and Amy Yarger. In addition to the OC, CoNPS board of directors includes chapter presidents and members-at-large. CoNPS staff includes Linda Smith, who keeps us all organized as administrative coordinator, Denise Wilson as marketing and events coordinator, and Kathy Okon as the workshop coordinator. Volunteers from all over the state contribute in various ways to CoNPS success and new volunteers are always welcome.

Thanks to this year’s conference committee members: Kelly Ambler, Courtney Cowgill, Sue Dingwell, Mo Ewing, Lenore Mitchell, Tom Schweich, Bruce Tohill, John Vickery, and Denise Wilson. Special thanks to Aquilegia managing editor Mary Menz and associate/design editor Kelly Ambler.

Registration
See page 11 for registration information. Registrants will receive an email with details for accessing all webinar events. There will be a instructional materials available for those unfamiliar with webinar formats.

Speakers and Presentations
(arranged in order of presentations)

Heidi Steltzer
“The richness of plants in the mountains benefits people”

Mountain regions are home to 25% of the earth’s biodiversity, provide water to billions of people, and sustain us by providing refuge. The Colorado mountains are a unique place for plant life, and one that is changing quickly due to the warming of our planet and a changing snow pack. Heidi will provide insights into the benefits that mountain plants provide for people to inform why we should conserve these incredible species. They are resilient, and this contributes resilience to each of us.

Heidi Steltzer, PhD, is professor of environment and sustainability at Fort Lewis College in Durango. Heidi is a mountain scientist, explorer, and science storyteller. She has spent 25 years conducting field studies in remote regions of Colorado, Alaska, Greenland, and China to understand how mountain ecosystems are unique and valued regions of our world. She is a lead author on high mountain areas in a recent intergovernmental panel on climate change report and has testified before US Congress on climate change. Find her on social media @heidimountains
Mike Kintgen
“Circumborial Alpine Plants and Biogeography”

Mike will share some of the circumborial element in our flora—species found both in Colorado and in places as diverse as Newfoundland, Kamchatka, Norway, Iceland, and Switzerland. Colorado’s flora share diverse links with mountainous and high latitude regions around the world. Mike will show how Colorado flora is linked to that of Eurasia and South America. He will also dip into the Asiatic element in Colorado’s high elevation flora, as well as links with the flora in places as far away as Patagonia. Lastly, he will brush on the rich, endemic North American influence on our flora which includes genera such as Penstemon, Eriogonum, Calochortus, and Heuchera.

Mike Kintgen is the curator of alpine collections at Denver Botanic Gardens, where he has been a formal part of the staff since 2004. He has played an informal role since 1992, having started as a volunteer at age eleven. His botanical travels have taken him to most of Western Europe, European Russia, Morocco, and Argentine Patagonia.

Jennifer Bousselot
“Colorado Native Plant Availability in the Green Industry”

Native plant aficionados often struggle to find Colorado native plants available in the green industry. Often that is due to two things: lack of demand so most producers do not grow them, and the fact that many Colorado native plants are not as attractive in containers so most gardeners don’t buy them. Because of this, Jen and others have acquired USDA funding and have begun plant finishing protocol research on several of the species in Plant Select® that are native to Colorado. Jen will talk about one of her greatest passions—how to ensure that our beloved Colorado native plants become more available in the green industry.

Jennifer Bousselot, PhD, is an assistant professor in the department of horticulture and landscape Architecture at Colorado State University. Jen completed her doctorate research studying green roof species selection, including Colorado native plants, at Colorado State University in 2010. Jen also does research ensuring that Colorado native plants are marketable in the green industry. She is a previous marketing and events coordinator for CoNPS and is co-author of the CoNPS-published 3rd edition of Common Southwestern Native Plants.

Jennifer Ackerfield
“Thistle Be Fun: Untangling Taxonomy and New Species Discoveries”

Have you ever wondered what defines a species, or how new species are discovered and named? Well, wonder no longer! Join Jennifer as she talks about the process of defining a species and all the lines of evidence that scientists use to inform this decision. After laying the groundwork for how species are named, she will discuss an exciting development in her alpine thistle research.

Many members of CoNPS participated in Team Thistle, a citizen science initiative in which Jennifer asked members to “get high on alpine thistles” with her. Through this initiative, approximately 50 collections of alpine thistle were made and observations recorded on iNaturalist. She used several of these collections and observations in her research and discovered an unnamed species hidden right under our noses! This exciting discovery also highlights the need and importance of field studies, iNaturalist observations, archives, and natural history collections.

Jennifer Ackerfield, PhD, is the head curator of natural history collections at Denver Botanic Gardens. She was previously a curator at the Colorado State University herbarium and also taught plant identification at CSU. Most notably, she is the author of the Flora of Colorado. She has been studying the flora of Colorado for 25 years and has traveled extensively across the state documenting its rich floristic diversity. She received her master’s in botany with a concentration in taxonomy and systematics in 2001 and is currently working on her PhD in botany, studying the taxonomy and evolution of the genus Cirsium (thistles) in North America. Jennifer has worked with the Colorado Native Plant Society, Colorado Natural Heritage Program, US Forest Service, Colorado BLM, Rocky Mountain National Park, and Mesa Verde National Park.
Shannon Murphy
“Light Pollution Affects Invasive & Native Plant Traits Important to Plant Competition & Herbivorous Insects”

Many exotic invasive species have traits that allow them to outcompete native species when there have been changes in the environment relative to conditions under which the native plants have evolved. However, invasions in urban settings have been insufficiently studied, including exploring the impacts of the uniquely urban stressors of streetlights.

Plant physiology and phenology are impacted by Artificial-Light-at-Night, but no studies have yet examined if light pollution differentially affects native versus invasive plant species. We tested the hypothesis that ALAN affects plant traits important to plant fitness and susceptibility to herbivory and found that these effects differ between some invasive and native grass species. As urbanization increases, its role in understanding invasion biology becomes more important, especially when an urban disturbance such as ALAN benefits the growth of invasive species.

Dr. Shannon Murphy is associate professor of biology at the University of Denver. She graduated from the University of Colorado at Boulder in ecology and evolutionary biology. She received her PhD in ecology and evolutionary biology from Cornell University and completed two post doctorates, one at the University of Maryland in entomology and the other at the George Washington University in biology.

Steve Yarbrough
“Fen Ecosystems of Colorado”

Finns? Or Fins? No....Fens! Fens are groundwater-fed, peat-forming wetland ecosystems. Where exactly are they hiding out and why the heck are they so interesting for native plant enthusiasts?

Fens contain a great number of Colorado rare plant species and even a few globally rare species. They occur in a variety of landscapes and boast some interesting chemistries. What conservation measures and strategies are being used with fens and what difference will it make in the long run? Steve will provide some insights from 22 years of balancing through, plunging in, and rescuing himself from a variety of fens across Colorado.

Steve Yarbrough is a senior ecologist and professional wetland scientist working for Tetra Tech, Inc., in Golden, Colorado. He has enjoyed a 36-year career in the environmental consulting field. His job assignments typically involve siting studies for renewable energy projects, assessing impacts, obtaining required permits, and monitoring the recovery of damaged resources, including wetlands and native prairie. He has previously served on the CoNPS board of directors and served stints as field trip coordinator and workshop coordinator for the society. He is currently a member of the conservation committee.

Tim Seastedt
“Climate Change Effects on Herbaceous Plant Community Composition in the Colorado Front Range”

The high elevation ecosystems of the Colorado Front Range have been under study by CU researchers for 70 years, a time period sufficient to study impacts of climatic changes. Climate and atmospheric inputs are the dominant change factors of high elevation ecosystems, but these drivers influence a complex terrain that is impacted unevenly by local growing season length, moisture, and nutrient limitations. These differential outcomes produce differential changes in vegetation composition across the landscape that benefit components of the alpine flora while penalizing others. Willow invasions into herbaceous areas have, perhaps, been the most dominant change to date. The entire alpine zone is undergoing elevation changes, but these changes are controlled by the interaction of climate changes with local abiotic and biotic factors.

Tim Seastedt is professor emeritus for the department of ecology and evolutionary biology and is a fellow, Institute of Arctic and Alpine Research, University of Colorado, Boulder. Seastedt spent a decade studying grasslands in Kansas prior to coming to Colorado in 1990. He became the principal investigator of the Niwot Ridge long-term ecological research program in 1992 and has continued studies to date on plant and soil interactions in herbaceous ecosystems on both at the top and bottom of the Front Range.
## “Peaks to Prairies—Plants in the Land of Extremes”

### Conference Schedule

#### Friday Virtual Social Event: Highlights from 2020

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<th>Time</th>
<th>Description</th>
<th>Speaker</th>
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| 6:30 PM to 9:00 PM | Introduction  
Pikes Peak commemorative hike  
Photo contest winners  
Break  
Peaks to Prairies: CoNPS Members in the Field  
Break  
Key people who keep CoNPS running | Denise Wilson  
Kelly Ambler  
Bruce Tohill  
Tom Schweich  
Moderator(s) |

#### Session 1: Saturday morning

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<td>9:10 AM</td>
<td>The Richness of Plants in the Mountains Benefits People</td>
<td>Heidi Steltzer</td>
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<td>9:55 AM</td>
<td>Break</td>
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<tr>
<td>10:05 AM</td>
<td>Circumboreal Alpine Plants and Biogeography</td>
<td>Mike Kintgen</td>
</tr>
<tr>
<td>10:55 AM</td>
<td>Break</td>
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<tr>
<td>11:10 AM</td>
<td>Colorado Native Plant Availability in the Green Industry</td>
<td>Jennifer Bousselot</td>
</tr>
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#### Session 2: Saturday afternoon

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<td>Thistle be Fun: New Species Discoveries</td>
<td>Jennifer Ackerfield</td>
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<td>2:25 PM</td>
<td>Break</td>
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<td>2:35 PM</td>
<td>Light Pollution Affects Invasive &amp; Native Plant Traits Important to Plant Competition &amp; Herbivorous Insects</td>
<td>Shannon Murphy</td>
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#### Session 3: Sunday afternoon

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<tr>
<td>1:10 PM</td>
<td>Fen Ecosystems of Colorado</td>
<td>Steve Yarbrough</td>
</tr>
<tr>
<td>1:55 PM</td>
<td>Break</td>
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<tr>
<td>2:10 PM</td>
<td>Climate Change Effects on Herbaceous Plant Community Composition in the Colorado Front Range</td>
<td>Tim Seastedt</td>
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Annual Silent Auction Benefits CoNPS Activities

The Annual Conference traditionally hosts a silent auction to benefit CoNPS. This year the auction will be online! Proceeds support the Colorado Native Plant Society’s wide-ranging projects including education, conservation, native plant gardening, botanical and horticultural publications, and activities.

Denise Wilson and the silent auction committee seek your donations for this event. We are accepting only small, mailable, above $20 value items, and requesting that donors hang on to them and mail them to the winning bidder afterward. Donors can bill CoNPS for shipping cost reimbursement, but we also appreciate the donation of your time and shipping cost, if you are able to do so. To submit an item, email to Denise 1) 2-3 good quality photos showing different angles (one picture of the cover is good for a book), 2) a short description, 3) and the value.

Denise suggests donations might include—
- Sample of a member artist’s painting, photography, or other work; flat, small and no glass;
- Greeting cards, stationary, markers, pens, stickers, and so on;
- Tee shirts, hats, gloves, raingear, gaiters, UPF clothing, technical fabric clothing;
- Water bottles;
- Lightly used backpacks, items to fill a backpack, other outdoor gear;
- An unopened bottle of wine or liquor;
- SMALL garden tools, art, statuary, wind chimes in “like new” condition;
- Gift cards;
- Any unused SMALL gift you’ve received and would like to find a home for; and
- Money that the committee can use to make a great gift basket.

We are asking donors who are able to donate their time and shipping cost to hang onto the item until the end of the auction, and then mail it to the winning bidder for us.

If you or your business are interested in donating an item for the silent auction, please contact Denise at deniseclairewilson@gmail.com Likewise, if you’d like to volunteer to help with the silent auction, contact Denise.

Auction preview will be available September 1-11. Bidding on silent auction items will be open September 12-20.

Annual Photo Contest—Call for Entries

Have you taken some spectacular photos of native plants this summer or in years past? If so, consider entering the CoNPS annual photo contest. Photos may only be submitted electronically with a completed entry form. You must be a CoNPS member to participate.

Entries can be made in any of five categories including:
- Colorado Native Plant Landscapes;
- Colorado Native Plants;
- Artistic (of Colorado Native Plants or Native Plant Landscaping);
- Colorado Native Plants & Wildlife (including native insects/polliinators); and
- Native Plant Gardens.

Contest rules and agreements are posted on the CoNPS website. Photos may be submitted to the contest August 1-31. Photos will be displayed on the CoNPS website and judged by CoNPS members prior to the conference (September 1-15). Winners will be announced on September 18 during the Friday night social.

Entries must be a single work of original material taken by the contest entrant. No more than one photo per category may be submitted. Photos may be from previous years (for example, you may submit a photo that you took in 2013). A $50 prize will be awarded to the first place winner of each category.

Contest is open to CoNPS members only. Please see the CoNPS website for entry forms:
https://conps.org/xxyyzz-2020-photo-contest/

Questions? Contact Bruce Tohill at tohillb@msn.com

Reporters Needed for the Annual Conference

Are you willing to write a summary of one or two of the presentations from the Annual Conference? If so, please contact Mary Menz (Mary.T.Menz@gmail.com) or Kelly Ambler (alpineflowerchild@gmail.com)
Registration

Registration is available online at http://conps.org. Please log in if you are a CoNPS member, then proceed to the Calendar of Events to register. Online registration ends September 15.

If registering by mail, please complete the following registration form for each person attending and submit by September 7.

Mail registration form and payment to: CoNPS, c/o Linda Smith, 4057 Cottonwood Dr., Loveland, CO 80538

Name (first, last) ____________________________________________________________
Phone ______________________ Email ___________________________________________
Mailing address ____________________________________________________________
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The registration fees include attendance to the Annual Conference webinars on Saturday and Sunday, September 19 and 20 plus the Friday night virtual social on September 18. A separate fee is charged for attending the Rare Plant Symposium. An optional practice webinar is also included in the registration.

Member registration*

The 17TH Annual Rare Plant Symposium @ $10 __________
The 44TH Annual Conference @ $30 __________
Optional donation __________
Membership Renewal (if necessary) __________
Individual @ $25 __________
Family/Dual @ $35 __________
Senior or Student @ $17 __________
Plant Lover @ $50 __________
Supporting @ $100 __________
Patron @ $250 __________
Benefactor @ $500 __________
Lifetime @ $800 __________
Aquilegia print subscription @ $20/year __________

Total enclosed $ __________

Non-member registration. Consider becoming a member! See page 26.

The 17TH Annual Rare Plant Symposium @ $10 __________
The 44TH Annual Conference @ $35 __________
Optional donation __________

Total enclosed $ __________

* A limited number of scholarships are available. See CoNPS.org for details.

The Annual Conference Committee appreciates all businesses and individuals who have contributed gift certificates or merchandise to our online auction to help defray cost of this year’s event. Business logos are displayed online at CoNPS.org and will be displayed in Aquilegia beginning Fall, 2020.
Celebrating the Bicentennial of Stephen H. Long’s Expedition
Part 3 of 4: The Ascent of Pikes Peak and Noteworthy Species Found

By Mike Kintgen and Jen Toews

This is the third in a series of four articles about the Long Expedition to the Rocky Mountains.

On July 14, 1820, Edwin James and two other men trudged slowly up what would later be named Pikes Peak. Without today’s well-maintained trail system, the ascent would have been especially grueling. It would first have been a long bushwhack through the forest and then a tedious scramble through the talus. It is also easy to imagine that James, the first American botanist of European descent to see the alpine tundra of Colorado, would have been distracted by the flora. Indeed, in his diary and Account James lists many species he encountered on this excursion, from the charismatic sky-blue alpine forget-me-not (Eritrichium nanum var. elongatum) to the circumboreal mountain dryad (Dryas octopetala) to the narrowly endemic James’s alumroot (Telesonix jamesii), which Torrey would later describe.

By 2:00 PM that day, the trio was so exhausted that they stopped for food and rest at a stream about one mile above tree line. That is when they realized that if they continued, it would be impossible to return to camp by nightfall where they had stashed their food and shelter. However, the prospect of summiting the mountain was irresistible and they hiked on.

Just one day prior, James and four others had begun their ascent of the Pikes Peak massif. The plan was for two men to accompany James to the summit, while the other two would attend to the horses at a camp on Boiling Springs near present-day Manitou Springs. Initially, Lieutenant Swift and his guide Bijou were also in the party. Their duty was to obtain observations for measuring the height of the peak. Having completed this task, they returned to base camp on Fountain Creek where Stephen Long and the rest of the party waited.

Twenty-five miles from Long’s base camp and higher up Fountain Creek, James and the others set up a horse camp. Around 3:00 PM and after breaking for lunch and a quick rest, James, Verplank, and Wilson left the horsemen behind and pressed toward the summit. They traveled all of two miles before setting up a precarious camp for the night (their camp would have been on Ruxton Creek). Apparently, “[b]ecause of the steep sides of the ravine, the men placed a pole on the ground between two trees; by laying their beds on the uphill side, they were thus prevented from rolling down into the creek during the night.” Before falling asleep, James wrote a somewhat discouraged note in his diary: “[W]e laid down to rest for the night, having found few plants or anything else to reward us for our toils.”

On the 14th, James and his two companions hung their camping supplies and food in a tree near their campsite. They planned to return before nightfall. By daybreak they were once again bound for the
summit. Interestingly, the route they took up the mountain is nearly the same as the route of the Pikes Peak Cog Railway today.

At around 4:00 PM, James, Verplank, and Wilson reached the 14,115 ft. summit of what would become known as America’s mountain. They were the first Americans of European descent to have done so. It must be mentioned that Native Americans had undoubtedly already climbed the mountain during their long history in the region.

Meanwhile, back at base camp, Major Long and Lieutenant Swift had mathematically calculated the height of the mountain to be 11,507.5 feet. They arrived at this figure because they had calculated the elevation at their base camp along Fountain Creek to be 3,000 feet. They surmised that Pikes Peak was another 8,507.5 feet above them. In reality, their base camp was closer to 5,600 feet in elevation.

The short time James and the others spent on the summit was both literally and metaphorically the high point of the Long Expedition of 1820. The alpine was not what James expected. Instead of a barren wasteland, the men were greeted by a multitude of dwarf alpine plant species with showy, colorful flowers in full bloom. A quote from James sums up his surprise and delight with this biome:

“...a region of astonishing beauty, and of great interest on account of its productions; the intervals of soil are sometimes extensive, and are covered with a carpet of low but brilliantly flowering alpine plants. Most of these have either matted procumbent stems, or such as including the flower, rarely rise more than an inch in height. In many of them, the flower is the most conspicuous and the largest part of the plant, and in all, the coloring is astonishingly brilliant."

...We met, as we proceeded, such numbers of unknown and interesting plants, as to occasion much delay in collecting, and were under the disagreeable necessity of passing by numbers which we saw in situations difficult of access. As we approached the summit, these became less frequent and at length ceased entirely.”

It was late in the day, and after spending less than an hour on the summit, James and his party began their long descent. By sunset they reached timber line. Realizing they had lost the route back to their camp, they had no other choice but to spend the night with just a campfire and no food.

At first light on July 15, James and his companions were on the move back to the previous camp of July 13. Three hours later, as they neared their camp, they were greeted with a dense column of smoke. Apparently, they had failed to completely extinguish their campfire. The fire had burned their blankets, clothes, and most of their provisions. They were able, however, to salvage some fragments of charred buffalo meat for breakfast. Curiously, no other mention was made of what became of the fire. (Ironically, the Pikes Peak region has been the site of two of the...
most costly forest fires in Colorado’s history, both since 2012.

James, Verplank, and Wilson reached the horse camp shortly after NOON where the other two men awaited with a meal of fresh venison. At 7:00 PM, they arrived on horseback at their base camp farther down Fountain Creek, where the entire Long’s party was once again reunited.

During this three-day trip into the alpine world of the Southern Rockies, Edwin James observed and documented many alpine species, some of which had already been described from other regions of the country and world. Examples of previously described species include: alpine avens (Geum rossii var. turbinatum), alpine lily (Lloydia serotina), shrubby cinquefoil, (Dasiphora fruticosa ssp. floribunda, now Potentilla fruticosa), mountain sorrel (Oxyria digyna), mountain death camas (Anticlea elegans, now Zigadenus elegans), elephant’s head (Pedicularis groenlandica), alpine bistort (Bistorta vivipara), Whipple’s penstemon (Penstemon whippleanus), snowball or diamondleaf saxifrage (Micranthes rhomboidea), moss campion (Silene acaulis), and marsh marigold (Caltha leptosepala, now Caltha chionophila).

In addition, James collected fifteen new species during these three days, which would be described from the Long Expedition of 1820:

- Boreal rockjasmine (Androsace chamaejasme Wulfen subsp. carinata (Torr.) Hultén);
- Western Indian paintbrush (Castilleja occidentalis Torr.);
- Rocky Mountain snowlover (Chionophila jamesii Benth), described July 14 in James’s diary as “a small plant somewhat resembling Penstemon with erect flowers;”
- Pikes Peak alpine parsley (Cymopterus humilis (Raf.) Tidestr.), a rare plant endemic to Pikes Peak;
- Alpine bluebells (Mertensia alpina (Torr.) G. Don);
- Streamside bluebells (Mertensia ciliata (E. James ex Torr.) G. Don.), though there is no record of this species in James’ diary or the Account and it was likely collected between Denver and Cañon.
City in July, but certainly could have been collected during their Pikes Peak excursion;
- Alpine sandwort (Minuartia obtusiloba (Rydb.) House);
- Rocky Mountain nailwort (Paronychia pulvinata A.Gray);
- Alpine sawsedge penstemon (Penstemon glaber var. alpinus (Torr.) A. Gray);
- Limber pine (Pinus flexilis E. James,) that James described in his diary as having “leaves 5 in a fascicle, branches remarkably flexible;”
- Alpine primrose (Primula angustifolia Torr.);
- James’s telesonix (Telesonix jamesii (Torr.) Raf.) of which the type collection was made on Pikes Peak probably near Windy Point;
- Pygmy goldenweed (Tonestus pygmaeus (Torr. & A. Gray) A. Nelson);
- Alpine clover (Trifolium dasphyllum Torr. & A. Gray); and
- Dwarf clover (Trifolium nanum Torr.).

Thus, as the first scientifically-trained botanist to venture to the alpine biome of Colorado and the southern Rocky Mountains, Edwin James left an indelible mark on the alpine flora of this region.

A few days after James’s ascent of Pikes Peak, Long commemorated the accomplishment by naming the mountain James Peak. Later the peak would be christened Pikes Peak after Zebulon Pike. Pike had spotted the mountain fourteen years earlier in November 1806, had attempted to climb it (wrong time of year), and had declared it to be unclimbable. However, the name Pikes Peak would stick. James’s name would be moved to a somewhat prominent mountain and the high point of the 17,015-acre James Peak Wilderness, which is nestled between Rollinsville, Central City, and Winter Park.

Since James climbed Pikes Peak in 1820, much has changed. Instead of bushwhacking their way up, hikers can now choose between a well-maintained 28-mile, class-1 hike up the mountain or a slightly more technical, but shorter, 14-mile hike. However, more people opt for the Pikes Peak Cog Railway (currently closed for improvements, but reopening in 2021). Still more opt to drive their vehicles up a curvy paved road followed by a shuttle ride to the summit. At the top, hikers, tourists, and their dogs, are greeted with a visitor center and gift shop serving warm food and beverages. James probably would have appreciated this. Also available for purchase is an assortment of tchotchkes and souvenirs stating the height of the peak.

On a clear day, visitors to America’s mountain are rewarded with a 360-degree view. To the east, the plains with their “amber waves of grain” gradually decrease in elevation until they are swallowed up by the horizon; the prominent Spanish Peaks tower to the south; and to the north and west the “purple mountains majesty” of the Rockies extend as far as the eye can see. In the foreground, colorful alpine plants abound and a small herd of bighorn sheep can be seen grazing. Two-hundred years later, it is safe to say that the Pikes Peak area remains “a region of astonishing beauty.”

References
Mike Kintgen is the curator of Alpine Collection at Denver Botanic Gardens. His work has taken him across the globe to biomes similar to the Rocky Mountains and steppes of Western North America. He greatly enjoys working with regionally native flora and learning the botanical history of Colorado. Jen Toews works in the Plant Records department at the Denver Botanic Gardens and is a Colorado Native Plant Master® who advocates for native plants at every opportunity. In her free time, she enjoys expanding her native plants garden, hiking to see native flora, photographing native flora, and writing. 🌿

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Diné Bih Naniseh Bah Haneeh: Navajo Ethnobotanical Teachings

By Arnold Clifford

Editor’s note: Approximately half of Colorado’s Western Slope is part of the Colorado Plateau, an area that encompasses large portions of Colorado, Utah, Arizona, and Nevada. The 130,000 square-mile region is rich in geologic and floristic diversity. Arnold Clifford is a botanist, a geologist, and a Navajo elder. He is co-author of The Flora of the Four Corners (2013) and is working on a complete Diné Bih Naniseh: Flora of the Navajo Indian Reservation. The following article is reprinted with permission from the Winter 2016 issue of The Plant Press, (Vol 38, No 2), the newsletter of the Arizona Native Plant Society.

Navajo Culturally Significant Plant Species

Navajo people have lived within the physiographic boundaries of the Colorado Plateau for thousands of years before the arrival of the first European settlers. Their extensive understanding of plants and uses of plants were derived from knowledge passed down through Divine intervention of the Navajo Holy People into the lives of the early predecessors of the Navajo people. As a result of species range expansion, travel during herbal pilgrimages, experimentation, and trial and error, other new plant species were incorporated within the vast knowledge of plants.

Various Navajo deities have also instructed the people on uses of native plants and the importance of plants for the well being of the Navajo people.

Navajo Ethnobotany

Plants are sacred, alive, and dynamic, and Navajos refer to them as “Holy Plant People.” Knowledge of plant use is interwoven with traditional religious contexts, cultural oral tales, and history. Navajos have their own plant classification systems, just as the Europeans have in the sciences of systematic botany and plant taxonomy. Navajo herbalists recognize different individual plant species, including grouping together closely related species by generic Navajo names, similar in some respects to Western botanical scientists’ use of Latin binomial scientific names for individual plant species. Navajo plant names are very descriptive names that may refer to the morphology of the plant, leaf color, medicinal connotations, ceremonial associations, tobacco types, and animals based on their morphological similarities.

Navajo Philosophy Relating to Plants

In the process of developing intimate relations with all plants, Navajo have drawn similarities between plants and their own bodies. Teachings include how plants are decorations, garlands, and jewelry of Changing Woman, Mother Earth. Plants also play roles in the human anatomy where our blood, arteries, and veins were modeled after the divaricated, branching nature of plant roots. That is how our arteries and veins began branching out of our hearts, the center of the body. The arteries branching into smaller vessels cover the whole human body, providing warmth, oxygen, and other life-giving minerals and elements to the body.

Plant roots function in a similar way as they break down and draw up vital nutrients, minerals, elements from the soil to distribute into all parts of the plant, to give plants life. The Navajo “Holy Plant and People”

Golden Mariposa (Calochortus aureus). © Arnold Clifford

Navajo Tea (Thelesperma megapotamicum). © Arnold Clifford
are treated with respect, holiness, and reverence. When plants are collected for ceremonial use, or for medicinal healing properties, Navajo herbalists talk to the plants they need. Herbalists introduce themselves, stating their reason for collecting each plant, describing the ailment of patients in need of treatment, and calling out sacred plant names. Herbalists offer prayers and make offerings to plants that are gathered for use. This ensures the curative healing powers of the plant will be invoked, as well as extends protection to the herbalist gathering the plants.

**Navajo Classification of Plants**

Navajos have several classifications of plants. One simple Navajo classification is based on its intended use in ceremonies: as tobaccos, as food items, or in everyday utilitarian usage. Navajo plant classification is a primitive, systematic approach to better understanding the flora of the diversified habitats the Navajo people occupied. Classifying also provided a better understanding of different groups of closely related plant species. Navajo plant classification was partly based on floral morphology or physical similarities of natural families. One basic Navajo botanical classification of plants includes the identification of Life Way, Evil Way, and Beauty Way plant groups. These plants are associated with various ceremonial rites. Most plants have more than one use and can be classified under several different categories. A basic way Navajos classify plants is based on its uses: edible plants, medicinal plants, ceremonial plants, tobacco plants, utilitarian plants, dye plants, and plants for protection and for talismans.

**Edible Plants**

Native plant species are utilized for supplemental food, food additives, seasoning, spices, and sweet treats from flower nectars. Hundreds of plants are used as foods, with different plant parts such as roots, stems, leaves, flower petals, flower nectar, assorted berries, tasty fruits, and grass seeds all providing valuable nutrients and sustenance for surviving in the desert wilderness environment.

**Medicinal Plants**

Medicinal plants constitute a large group known as the Life Way medicines. These plants are intended to sustain good health and mental wellness and they help to improve the lives of Navajos who reverently partake of them. Life Way plant knowledge was acquired from supernatural events involving the Holy People. The body of Rainboy was dismembered by lightning bolts sent by Big Thunder as punishment for being promiscuous. A restoration rite was held for Rainboy by the Holy People. Before the rite, insects, animals, and other holy deities were instructed to gather Rainboy’s dismembered remains. Rainboy’s remains were collected with different herbs that grew nearby. The dismembered remains and sacred herbs were brought back together, so a restoration rite could be performed. The holy plants were applied to different body parts of Rainboy, and each body part began to heal and was restored to health. From that time forward, these plants were considered plants that would heal that particular part of the human anatomy. The healing powers of these holy plants were “life-giving” and therefore, considered Life Way medicinal plants. There are about three hundred Life Way medicines available for Navajos to rely on for curative remedies.

**Ceremonial Plants**

Numerous species of trees, shrubs, grasses, and flowering, herbaceous forbs are used for different aspects and rites of Navajo ceremonials and chants. Plants designated for ceremonial use are employed to make ceremonial implements and paraphernalia,

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Morning Lily (*Oenothera caespitosa* var. *navajoensis*). © Arnold Clifford

Broadleaf Cattail (*Typha latifolia*). © Arnold Clifford
such as prayer sticks, prayer wands, cigarettes for offerings to various deities, ceremonial masks, dry paint material, incense for fumigants, and for medicines administered during ceremonial rituals. Plants used in ceremonial rites are considered sacred and are therefore reserved for chanters and medicine people who perform these chants.

**Tobacco Plants**

Tobacco plants are utilized reverently. Most tobacco plants are used as offerings for various deities and sacred ceremonial animals. Tobaccos are smoked during ceremonial rites, ritual baths, sweat lodge cleansing rites, as well as during personal meditation and prayer sessions. Tobacco smoke helps to clear the mind and blesses the body and soul. Tobacco smoke also carries a person’s prayer to the holy deities. Tobaccos utilized in Navajo society are not for pleasure, relaxation, or for recreational smoking.

**Utilitarian Plants**

Many plants are used to make everyday utensils and household objects for domestic use, such as hair brushes for grooming, floor brooms, kitchen utensils, digging tools, farming tools, weaving looms, weaving tools, carding combs and spinning spindles, weaving dowels, bows, and arrows. Trees and larger shrubs are prepared for hogans, shade houses, sheep corrals, sweat lodges, fencing material, and firewood for heating, cooking, and ceremonial fires.

**Native Dye Plants**

Numerous plants are used by Navajo weavers for dying wool. Various plant parts provide natural dyes. The bark of some shrubs and trees yield red, reddish brown, and brown dye hues. The roots of canaigre dock can produce yellow, yellow-orange, and yellow-brown colors. Flowers and seeds of many plant species are also used to create many unique dye hues. Plants are normally boiled in an acidic solution containing a mordant, which helps the dye color to turn a richer hue and also helps the dye to fix to the wool fibers.

These are specialized plants used to ward off evil influences and also for the protection of individuals. Most of these plants are known by very few people, some are known only by certain clan or family groups. These plants are carried on a person for protection while they are at public functions where many people are in attendance, such as fairs, ceremonial gatherings, rodeos, and other public gatherings.

The Navajo Gods of Botany: The Humpback Gods

The Navajo Gods of Botany, Ah Ghaah Dah Hiskid Dih (Humpback Gods) are fertility gods and are of the utmost importance to the Navajo ceremonial system. Humpback Gods are sacred, powerful deities of native plants and seasonal weather, especially precipitation. They include the god of harvest, of abundance, and the fruits of the fields as well as a polymorphic deity incorporating desert bighorn and Rocky Mountain bighorn sheep, holy people, and humans. They are responsible for revegetation and reseeding the Earth with grasses, flowering plants, shrubs, and trees. In the process of reseeding, they bless each seed with all kinds of precipitation. During the coldest part of winter, when extensive stands of fog cover the desert southwest, the Humpback Gods come out in large numbers, walking amid fog, each burdened and hunched over, carrying bags of seeds and precipitation. The humpbacks utter “Ah Woo” as they walk about in the cold, frosty fog, often stopping to shake their backs to release native plant seeds and precipitation. They do circular dances to poke each seed into the ground with their planting stick-cane. During the spring and early summer, the whole southwest is blessed with new flowering plants, grasses, and shrubs.

The Humpback God wears an inverted Navajo basket with an opening at the top to help secure it to the top of the impersonator’s head. The basket is painted black with a white zigzag all the way around the rim. The black represents night time clouds, with the white zigzag depicting lightning strikes between adjacent dark clouds. Standing upright around the rim of the basket are numerous red flicker or red woodpecker feathers. The feathers represent sunbeams shining through clouds immediately after rain. On top of the basket are two bluish horns that represent dark clouds before and during rain. The whole head piece is a crown of thunder, lightning, and rain. Along the back is a rainbow with feathers attached along the crest. The feathers indicate sun rays radiating from the eastern horizon, and the rainbow indicates the presence of holy people and the blessings of rain. Under the rainbow is a dark, black sack with white bars. The hump contains mist, dew, frost, female rain, male rain, snow, all aspects of precipitation, and vegetation seeds of all types. Humpback Gods carry and walk with planting-stick canes.
A Note from the Author

These stories of the Navajo Gods of Botany, Ah Ghaah Dah Hiskid Dih (Humpback God), the Navajo classification system, the sacred Navajo plant names and its uses were bestowed and blessed upon me from my late maternal grandmother Sarah Charley of Beclahbito, New Mexico.

This ancient, sacred, Navajo ethnobotanical knowledge comes from seven or more generations of my family. Sarah was taught by her late mother Irene Bennallie of Beclahbito, New Mexico. Both Sarah and Irene were instructed by Sarah’s paternal grandfather, and both collected ceremonial herbs, medicines, and tobaccos for him. Sarah’s grandfather was Tsao Lao Alth Tsosii (police slender, or slim police), who practiced the Shooting Way, Wind Way, and Beauty Way chants. He also specialized in Navajo herbal and medicinal application. I possess a small portion of this once vast family knowledge, and I feel it is time to pass this knowledge onto other Navajos.

This knowledge, I believe, belongs to the collective Navajo people as a whole. It belongs to Navajos willing to learn, willing to keeping an open heart to our traditions, our culture and our religious beliefs. If we horde such sacred knowledge, no one benefits; it all becomes lost. We have already lost over half of our ceremonial systems, including unmatched plant knowledge acquired by our ancestors who never had a chance to pass on their infinite knowledge of all aspects of Navajo teachings.

Examples of Navajo Plant Uses

Navajos still utilize 1,500 or more native plant species; however, plant knowledge is declining. In the past Navajos had a vault of plant knowledge that included more than 3,000 to 4,000 plant species occurring within the Colorado Plateau. Six different plants are presented here to give an example of the diversity of plants available.

*Aliciella cliffordii* (Clifford’s Diné Star, or Clifford’s Gilia), a member of Beauty Way tobacco. They are essential plants required in a mixture of several plants that constitute the Beauty Way tobacco mixture. Different species of the genus *Aliciella* are called by the generic Navajo name Hozho Nah Toh (beauty tobacco) and are classified as Beauty Way plants. Clifford’s Diné Star is a rare plant known only from the north foothills of the Lukachukai Mountains and the foothills of Mexican Cry Mesa, Arizona. Named after Arnold Clifford of Beclahbito, New Mexico.

*Calochortus aureus* (golden mariposa), a showy yellow-flowered member of the Lily family. The white bulbs below the ground are edible when fresh. They taste similar to peanuts. Its Navajo name is Alth Chiin Daah, which means children’s food. Found south of Sheep Springs to Window Rock regions.

*Oenothera caespitosa* var. *navajoensis* (morning lily), a plant called Kleeh Yih Ghaii, meaning night time turning white, or night bloomer. A plant used as a medicine to heal body sores. Found on weathered, grayish white-colored Mancos Shale surrounding the Shiprock region to the Four Corners. The papery, white flowers are very large.

*Rumex hymenosepalus* (canaigre dock), a plant of sandy places. Easily identified by its large wavy leaves and light reddish flowering stems. Its large, bunch root tubers are about a foot and half or more below the basal leaves. The tuber roots are boiled to produce various colors of orange-brown to brownish dyes. Thick lower stems are used to make Navajo pie fillings. In some species, the seeds are used medicinally. Its Navajo name, Chaa Ha Tiin Ni, refers to darkness dweller.

*Thelesperma megapotamicum* (Navajo tea, greenthread), a plant gathered to make Navajo tea, a mild stimulant, served as a beverage during meals or during social greetings. During illness, Navajo tea helps to reduce fevers, helping the body feel better. Boiling the plant produces different shades of a yellowish-orange dye that is used by weavers to dye sheep wool. Chiil Ah Whee (plant coffee) is the Navajo name. Found throughout the desert southwest.

*Typha latifolia* (broadleaf cattail), a multi-use plant growing in wetlands. Its fleshy roots are edible. Its long, broad leaves were used to make mats, skirts, and other useful items. Flower stalks provided ceremonial pollen and the fresh green flower stalks are also edible. When the flower stalks matured and were dry, they were collected for stuffing in pillows, pads, kid’s toys and other items. The Navajo name, Ethel Nigh Teel, means cattail wide. The generic Navajo name is Ethel.
All Life Depends on Plants
By Deryn Davidson

Do you know that a large percentage of our population is afflicted with something known as plant blindness? It’s true. By definition, these poor people have “the inability to see or notice the plants in one’s own environment,” which leads to “the inability to recognize the importance of plants in the biosphere and in human affairs.” It seems that most people favor animals over plants. Sure, animals might seem more charismatic and dynamic, but come on now! We would be nothing without plants.

All joking aside, plant blindness actually has some pretty big implications. The term was coined in 1998 by botanists James Wandersee of Louisiana State University and Elisabeth Schussler of the Ruth Patrick Science Education Center. It’s quite a fascinating topic. The average person truly just doesn’t process that there are plants in their view. Because plants grow close to one another, are a similar color, and don’t move (much), humans tend to clump them together as “non-threatening things” and filter them out of the many, many other bits of visual data the eyes receive.

"There is a kaleidoscopic array of visual information bombarding our retinas every waking second, and plants are so easy to ignore unless they are in bloom," Wandersee says. "Plant blindness is the human default condition."

If people don’t pay attention to plants, they won’t place much importance on them and the role they play in our daily lives. They are, of course, not only food—they are medicine, they are fiber, they are fuel, they are beauty, and so on.

What can we do about this?? We can be plant advocates! I have no doubt that most, if not all, of the people reading this are already in that camp. Anytime there is an opportunity to tell our family, friends, neighbors, and even complete strangers about the wonders of plants, we should seize that moment. Stimulate their imagination with stories of your favorite plants and gardening moments.

Exposing younger generations to plants is key, too. I’m realizing that my 2.5-year-old has tons of books about animals, but very few about plants. Okay, he does have “Botany for Babies,” but he also has two parents who are plant nerds. Perhaps if there were board books with photos of different plants, he would be able to identify penstemons and prickly pears just as quickly as he identifies horses and pigs.

Wandersee recommends having a plant mentor in your life, or you can be the mentor. I am encouraged by the huge uptick in interest around houseplants. Apparently, houseplants are super hip right now. Surely that will have an impact on combating plant blindness and will extend beyond the walls of their homes as people come to appreciate the positive affects those plants have on them.

The work of volunteer programs like CoNPS, CSU Extension Native Plant Master® and Master Gardener programs, along with public botanic gardens, are doing a lot to help educate the public about the importance of plants.

So, if you’re going on hikes with friends who don’t understand why you stop every 10 feet to point out a plant, or if you have been putting a lot of time and effort into your garden and people aren’t knocking down your door to compliment you, it’s probably because they just don’t see the plants. Keep up the good work and little by little we’ll help combat plant blindness together!

I do have to share that my 2.5-year-old is doing pretty well with his plant ID skills. So far on his list are yucca, ponderosa, pinon, juniper, cactus, oak, mint, dandelion, and daffodil.

Deryn has been a native plant enthusiast since her time as a horticulturist at the Lady Bird Johnson Wildflower Center. She is now the CSU horticulture extension agent in Boulder County and co-runs the Native Plant Master® program there. She is passionate about helping people understand the importance of native plants in our open spaces and natural areas and also in incorporating them into our urban landscapes.
This November, Coloradans will have the opportunity to vote on Proposition 114 to restore gray wolves to Colorado. Wolves were deliberately extirpated from Colorado during the first half of the 20th century. The last wolf in the state was killed in 1945. Since then a few wolves have wandered into Colorado, but most have been killed; there is no sustained population. If Proposition 114 passes, it would mandate the development of a scientifically-based wolf management plan; after which, wolves would be reintroduced to a small number of public land sites on Colorado’s western slope.

Those of us who are passionate about our native plant species and plant communities, and who have spent considerable time on our public lands, have undoubtedly observed widespread degradation to these communities by wildlife and livestock grazing. In places of heavy grazing, plant community diversity is low and the composition of introduced plant species is often high. Add the potential impacts of climate change and the degradation is liable to worsen. A fair question, then, is whether wolf reintroduction might have a beneficial effect on our native plant communities.

Wolves are a keystone species. Their activities as ungulate predators produce trophic cascades affecting plant survival, pollinators, birds, mesopredators such as foxes and weasels, and smaller herbivores such as rabbits and various rodents. It is difficult to estimate what the disappearance of wolves has meant to the structure of our native ecosystems.

Elk are the primary prey of Rocky Mountain populations of wolves. In Colorado, there are more than 280,000 elk, the largest population of any state. There are also 430,000 mule deer, mostly concentrated in western Colorado. However, there are also approximately 500,000 cattle and 175,000 sheep that also are grazed on public lands west of Interstate 25. Grazing by these ungulates has a significant impact on our plant communities.

To assess the potential impact of wolves on Colorado’s landscapes, it is useful to examine the effect that wolves have had on Yellowstone National Park. Wolves were reintroduced to Yellowstone National Park beginning in 1995. That was also about the time when elk populations were at all-time highs in both Yellowstone and Rocky Mountain National Parks, and much has been written about resource damage due to elk in both places.

The most noticeable damage occurs in aspen groves and in riparian willow carrs, particularly if elk use these resources year-round or if unmanaged livestock overgraze these systems. When healthy, both ecosystems support a high diversity of sub-dominant plant species, as well as diverse animal communities including mammals, birds, and invertebrates. This diversity declines with prolonged heavy grazing. In Rocky Mountain National Park, excessive grazing of alpine tundra plants by elk may have contributed to the decline of ptarmigan numbers.

Aspen groves—typically clones in which the trees are interconnected by a common root system—produce shoots, or suckers, from the root system to expand the grove or to replace ageing or diseased trees. When the shoots are heavily browsed by elk and other herbivores, the groves fail to mature. Elk also gnaw the bark of aspen trees during late winter and early spring, and that can lead to infection of the tree by various diseases. Both situations in concert can eventually lead to the death of the entire clone.

Forty-one gray wolves were introduced to Yellowstone National Park from 1995 to 1997. Their numbers tripled during the first few years, then settled to about 100 wolves in the park since 2009. If Proposition 114 is passed, wolves would be reintroduced to Colorado by the end of 2023 with the numbers of introduced wolves yet to be determined. Photo © National Park Service, Yellowstone National Park.
Riparian willow carrs, particularly those in broader valley bottoms, are commonly occupied by beavers. Willows and beavers are codependent. Beavers use the willows for food and building materials for their dams and lodges. Beaver dams raise the water table, providing shallow ground water that willows need. When willows are browsed heavily by elk, beavers leave due to over-competition with elk, beaver dams are no longer maintained, and streams and rivers begin to run straight and fast. This results in downcutting of the channel, a drop in the water table, and further demise of the willows. Sedges, grasses, and smaller shrubs that help to maintain channel stability are also affected by heavy elk browsing.

Many observations from Yellowstone National Park show that the presence of wolves keep elk moving, preventing them from yarding in riparian willows and aspen groves for long periods of time. There are both diurnal and seasonal movements of elk to avoid areas where wolves are active.

Despite many articles claiming that elk decline and ecosystem recovery in Yellowstone is due to wolf reintroduction, more recent investigations have shown that the situation is much more complicated. For example, cougar and grizzly numbers were also on the increase, which increased elk mortality, and there was a high volume of elk hunting outside of the Park. Beaver populations began to rise in some areas due to declining elk populations, benefitting riparian plant and animal diversity. While there certainly has been ecosystem recovery in some areas, there is little improvement in others. It is worth noting that as elk populations declined, bison numbers increased. Also, since wolves suppress coyote numbers, this could have led to increases in the numbers of mule deer and pronghorn, two important prey species for coyotes.

The reintroduction of wolves to Colorado is likely to have mostly subtle and indirect effects on our native plant communities. Those effects will probably not occur after until wolf populations increase to ecologically effective numbers and stabilize. Some over-browsed ecosystems might benefit through a wolf-elk-plant trophic cascade as has been documented in Yellowstone and Banff National Parks. However, Colorado has experienced almost a century without a full suite of large predators at a time when elk and livestock populations have been climbing on our public lands. The effects of overgrazing on some of these lands will not be reversed by wolves alone; that will also require a public commitment for effective wildlife and grazing management.

Certainly, there is concern from the ranching community about potential livestock depredation by wolves. This is to be expected. However, studies have shown that when wild prey is abundant, wolves will select those animals even when livestock are abundant. In the five states of the northern Rocky Mountains (Washington, Oregon, Idaho, Montana, Wyoming) there were in 2015 a total of 1,980,600 cattle in counties that also had wolves. In those same counties of that year, confirmed depredation of cattle by wolves was 148, or 0.007 percent. It has also been shown that the use of range riders and other predator coexistence strategies can drastically reduce livestock losses to wolves.

Proposition 114 is likely to succeed. According to a recent statewide survey completed earlier this year,
84% of respondents favored the measure. While most ranching and hunting organizations oppose wolf reintroduction, there is high consistency between urban and rural communities, as well as between eastern slope and western slope communities in support of the proposition. Some have suggested that the popularity of the measure is driven by younger Coloradans who are more interested in ecology and conservation than their parents or grandparents.

Perhaps the reintroduction of wolves to Colorado—if it occurs—will be a catalyst for a larger, more holistic movement in which Coloradans will press for:

- Better scientifically-based wildlife management, including non-lethal predator control;
- More responsible livestock management, including predator coexistence strategies and cessation of over-grazing on public lands; and
- Programs to restore plant and animal diversity to our public lands where it has been lost due to excessive livestock grazing and large elk populations.

Native plants matter for ecological sustainability, for aesthetics, and for maintaining the integrity of the natural world. In the face of changing climate, we need to do as much as possible to conserve and restore our native plant communities. Wolves may be part of that equation.

References


John Emerick, PhD, is on the emeritus faculty of the department of environmental science and engineering, Colorado School of Mines. In addition to his academic career, John has taught numerous field seminars on various aspects of Colorado’s ecology for over 40 years, mostly in Rocky Mountain National Park. He has hiked extensively throughout the state. Nowadays, he spends part of his summers conducting field surveys for the Colorado Natural Heritage Program.

Basal Rosettes
By Arthur Clifford

I have lust
For the living
The Holy Earth
And its giving
Many are such
Common things
The petals on sunflowers
Rayed sparrow’s wings
In rapture joined
I am with these
We upward gaze
From our knees

Alpine spring beauty (*Claytonia megarhiza*) on Pikes Peak. © Kelly Ambler
Aspen for the Landscape
By Jim Borland

Not very long ago, every aspen planted in the landscape was collected from the wild. Collected with it was the possibility that any of a myriad of diseases and damage from over 300 insects, if not the insects themselves, came with it, too. These factors, combined with the difficulty of collecting sufficient supporting roots from a species whose root system meanders, non-tapered through the soil, result in losses commonly exceeding 50 percent.

The better aspen for your landscape is the one grown from seed. Yes, seed. Regardless of what you may have heard, aspen do, indeed, produce great quantities of viable seed. Small and losing viability rapidly after shed from the tree, aspen seed rarely finds natural conditions conducive to germination and early seedling success. Instead, the vast quantity of annually-shed seed is simply lost. A successful germination event in the wild is cause for celebration and papers written.

Yet when collected, cleaned, and sown under ideal nursery conditions, aspen seed quickly produces fast-growing, healthy, and strong trees free of diseases and insects. The seed-grown aspen is a tree far superior to those collected from the wild. When properly grown, pruned, and dug, a much higher percentage of the root system goes with the seed grown tree to the landscape and local establishment is virtually 100% assured.

Through progressive nursery techniques that involve greenhouse sowings, specialized soils, carbon dioxide enrichment of the atmosphere, fertilization with every watering, and 24-hour-per day lighting, 12 feet of growth during the first season is common.

Why, then, are aspens still being dug and sold? They are cheap. And, as one coffee magnate once said, “You get what you pay for.” Insist on seed-grown aspen for your landscape. Only when enough of us do this will the nursery industry make the appropriate changes and give us what we insist upon.

Jim has been fooling around with native plants for more than 40 years in private, commercial, and public venues. His home garden contains 1000s of native plants, most grown from seed at home and now not supplementally watered for 20 years. Jim has written hundreds of articles, given talks too numerous to count, and continues to grow and plant the two or three native plants not yet in his garden.
If you planted a garden two to three years ago and you still see lots of wood mulch, then you need more plants. You’re probably still seeing a decent number of weeds at this point, too (mulch isn’t a magic weed bullet and, if too thick, often creates an ideal seed bed). So, you know, more plants. More layers. More density.

And if you are planting a garden today think about where you do and don’t want to be in two- to three years:

1. Only put down 1” of mulch if you are using it. More mulch = less plant sowing while generally inhibiting forb and grass growth.
2. Put plants on 12” centers (12” apart) and no more.
3. Consider mixing potted plants and seeds to increase coverage. In spring, sow grasses and annuals among what you planted. In mid-to-late fall, consider a dormant seeding of perennial forbs among what you planted. (Maybe what you plant is the highly designed part, or plants that need a head start because they work on roots first like baptisia and amorpha and silphium, [or other plants suited to Colorado]).

What do you do if you are on a constrained budget?

1. See #3 above. The best advice is to plant the architectural plants—trees, shrubs, and perennial flowers—that take longer to establish and serve as the backbone for the design. You may also want to plant aggressive species and let them start to self-sow or run asap.
2. Get plugs. Most landscapers and nurseries get their plant material from wholesalers, and that requires a business license. But you can also get them (if you're east of the Great Plains) via Izel Native Plants (https://www.izelplants.com/), which works as a middleman for wholesalers to sell to the public. That means if you need plants in quantities of 32 and 50 you can get them for a much better per-plant cost.

My new book will attempt to better align these two perspectives, as both are critical for the success of urban gardens that both appeal to and involve people and wildlife together. It is critical that people find nature-inspired gardens beautiful, while it is just as critical that wildlife find them beautiful as well. Just because one has host plants does not mean the garden is beautiful to wildlife, and just because one has a diversity of flowers doesn’t mean the garden is beautiful to wildlife.

Benjamin Vogt is the author of A New Garden Ethic: Cultivating Defiant Compassion for an Uncertain Future. His prairie-inspired design firm, Monarch Gardens, is based out of Nebraska. https://www.monarchgard.com/thedeepmiddle/still-seeing-mulch-years-later-plant-more
Please check the Calendar of Events online at https://conps.org/mfm-event-calendar/#/calendar for chapter meetings, garden tours, and other events. With the evolving COVID-19 situation, CoNPS is not hosting any in-person events. The status of future CoNPS events might also change.

CoNPS may offer some chapter meetings, workshops, and lectures as webinars or other online meetings. Others might be postponed or canceled. Field trips are also being scheduled, but may be canceled or postponed. These will be posted online and will be promoted via the CoNPS E-News.

Plateau Chapter

Help with Native Vegetation Efforts
Grand Junction
Wednesday mornings
Colorado West Land Trust and the City of Grand Junction are looking for volunteers for the ecological restoration of the Three Sisters/Lunch Loops recreational area south of Grand Junction. Legacy land uses and last year’s development of a recreational pathway through the area have impacted soils and native vegetation.

The revegetation project aims to restore native vegetation and establish sustainable community stewardship of the resources. The properties are owned by City of Grand Junction and protected by conservation easements held by the land trust. A grant awarded from Colorado Youth Corps Association (and GoCO) enabled the project to use crews from Western Colorado Conservation Corps to do some of the heavy lifting, but the rest is being done by land trust employees and volunteers.

Volunteers meet Wednesday mornings to do the work. With the pandemic, it has been tricky to engage many volunteers, but social distancing and mask wearing practices are in use. The public, and especially CoNPS members, are invited to participate in the revegetation effort. For more information, contact monument.stewards@gmail.com

Learn About Plants Used by the Utes on the Western Slope
Montrose
Thursday, August 20 10:00–11:00 AM
The Plateau Chapter invites CoNPS members on the Western Slope to learn more about Ute ethnobotany at the Ute Indian Museum in Montrose. After the short program, attendees may want to stay for an hour to help weed a section of the garden in preparation for fall mulching. Bring gloves and a trowel.

The Ute Indian Museum is in the final stages of a complete restoration of its native plant garden. The new Ethnobotany Garden is the result of a two-year makeover of an existing garden space. Chinese willow have been replaced with coyote willow; Shasta daisies have been replaced with Rocky Mountain penstemon, scarlet gilia, and more; and nearly all non-native plants have been removed and replaced with native plants.

Plant stakes paid for by a generous CoNPS Mission Grant have been installed to inform visitors about the names of plants in the garden.

Interpretive signage is currently being designed and will be installed this fall. Curriculum is also being developed to educate school children and museum visitors about Ute ethnobotany. For more information and to RSVP, contact mary.t.menz@gmail.com

Southeast Chapter

Watershed Restoration in Action!
Colorado Springs
Saturday, August 15 8:30–10:00 AM
Join local citizen scientist and CoNPS member Gary Rapp for an engaging discussion and demonstration of how riparian forests can be restored to protect us from stormwater damage and enhance native pollinator and songbird habitat.

Please meet at the Shooks Run Agroforestry Project terrace garden at the north end of North Shooks Run Park, about a 200-yard walk north from on-street parking near 653 N. Franklin St. (just west of its intersection with N. Prospect St.). Please observe City Park and Recreation rules for COVID-19 posted at: https://coloradosprings.gov/parks

October 1-November 3
Colorado Parks & Recreation Annual Conference
https://www.cpra-web.org/page/SessionProposals

October 6-8
Sustaining Colorado Watersheds Conference
Avon, CO
https://www.watereducationcolorado.org/programs-events/conferences/
CoNPS offers webinars on a variety of native plant topics. Sign up for these webinars on the CoNPS website (https://conps.org/mfm-event-calendar/#/calendar). New webinars are constantly being added to the calendar.

**Ecosystems in Colorado’s Southeast Prairie**
**Saturday, August 15; 9:00 AM–NOON**
**Presenter: Carol English, MS**

This workshop focuses on several ecosystems within the Western Great Plains Ecoregion including the shortgrass prairie, shale barrens, sandhill shrubland, playas, and southwestern great plains canyon areas. Carol will cover the native plants and animals that are dependent on plant species in this region. Participants will also learn about the different types of rare plant communities that occur in these areas.

Carol English has been involved in the field of natural resources and education for more than 30 years. She holds a BS in earth science, teaching certificate, and MS in biology. Carol has presented natural resource classes and programs at Yosemite Institute, Outward Bound, and Jefferson County Open Space. She is a certified Native Plant Master® and taught Native Plant Master courses for nine years. In addition, Carol has worked as a botanist for the Colorado Natural Heritage Program, Yosemite National Park, and Colorado State Land Board. She has owned her natural-resource based business for seven years.

**Learn How to Use iNaturalist**
**Tuesday, August 25, 2020 9:30–11:00 AM**
**Presenter: Audrey Spencer**

Looking to contribute to citizen science? Or maybe you just want to share your observations and connect with scientists who can identify the plants, animals and other organisms you observe? Learn how to use this dynamic tool at a free webinar sponsored by the CoNPS education and outreach committee. Sign up at CoNPS.org. A link will be sent to registrants by or before Monday, August 24.

**Wildscaping 101—Native Plants for Birds**
**Sunday, August 30; 1:00–3:30 PM**
**Presenter: Kate Hogan, MS**

Are you passionate about native plants and want to learn more about the ecological connections between our natives and our Colorado bird life? Join Kate for an engaging and exciting webinar on ways to diversify the birds found in your own yard, using a variety of food groups provided by our native plants. Participants will review the newly created Native Plants for Birds handout designed in partnership with Denver Audubon, CoNPS, Audubon Rockies, and CSU Extension. This webinar is designed for all skill levels of native plant enthusiasts. Kate will review some of the science behind the essential need for native plants in our landscape, and some of the native plants that can be planted in the fall.

Kate Hogan has worked in the field of ecology for more than 20 years. She holds a BS in natural science and biology from the University of Puget Sound and an MS in nonprofit management from Regis University. For the last five years, Kate has worked at Denver Audubon as the community outreach coordinator, where she presents outreach programs throughout the Denver metro area and manages the Audubon Center at Chatfield.
Amateur Botanist, Friend, and Mentor
By Denise C. Wilson

I first met Stan in 2006, when I was looking for a local expert on the plants of Golden Gate Canyon State Park. The Chicago Botanic Garden had hired me to collect native, wild seed for the Kew Gardens Millennium Seed Bank. GGCSP had recommended I contact Stan, because he had established an herbarium starting in 1991. In it was more than 600 voucher specimens; and boy, he knew the plants of that park!

On one of our forays near a trailhead at the southern end of the park, Stan found a substantial population of early cinquefoil (Potentilla concinna). It’s a relatively small plant, so we were on hands and knees with noses to the ground, when a hiker came up and asked, “Did you lose a contact lens?” Stan replied, “No, we’re collecting seeds of Potentilla concinna!” The man replied, “Oh yeah, I thought that!”

Stan had been working with long-time companion Linda Senser and Steve Austin on the GGCSP identification and voucher project for some time. Still, he liked to tell me that the seed collection work was his first paid botany gig. I remember him calling out the species name as we found them. Sure enough, when we ran the plant through the key, he’d be right. When he wasn’t, he would sulk like Walter Matthau in the movie “Grumpy Old Men.” He thought he should be right all the time.

SEINet has 805 voucher collections by Stan and those do not include vouchers from the GGCSP herbarium, because it hasn’t digitized them. Stan took it upon himself to make a list of local plants that the Denver Botanic Gardens Kathryn Kalmbach Herbarium did not yet have. He then worked with Linda Senser for fifteen years collecting those vouchers.

The GGCSP herbarium collection eventually topped 800 voucher specimens. Throughout the years, Stan and Linda maintained a species list with all the locations and descriptions.

Stan was a patient mentor, always sharing his knowledge. Together we eventually collected more than 100 seed accessions within GGCSP for the original seed bank, the Seeds of Success Program, and the Dixon National Tallgrass Prairie Seed Bank.

Panayoti Kelaidis once verified that Stan had found alpine aster (Aster alpinus), not in its typical location, which is the tundra, but at GGCSP! This plant is native to the mountains of Europe (including the Alps) with a subspecies in Canada and Alaska.

However, Stan’s greatest find was in 1982. It was the Ute lady’s tresses (Spiranthes diluvialis), which is now a US Fish & Wildlife threatened species. He alerted Dr. Bill Weber, who called in Charles Sheviak, a prominent native orchid specialist from New York. Charles subsequently described this species with the type locality from the area where Stan had found the plants.

Stan passed away March 28 in Boulder. He loved to encourage people to study plants and to share knowledge.

I will always be grateful and carry the memories of our fieldwork. I owe him a great debt, but Stan would never want to be paid back.

Denise is the CoNPS marketing and events coordinator, in addition to running Wilson Associates, Inc., a botanical contracting firm specializing in native seed collection for the National Park Service. She worked for Chicago Botanic Gardens for twelve years, contributing to three of their seed banks while taking seasonal positions in plant vegetation. Her botany master’s degree was completed May 2009 from the University of Colorado, Denver, with a geographic information systems certificate.
Colorado's Go-to Botanist Steve Olson Sets Sights on Retirement
By Seth Bolster

Editor's note: the following is reprinted with permission from the June 24, 2020, edition of The Gazette. Steve Olson is a long-time CoNPS member, chair of the field studies committee, and a member of the Aquilegia review board.

Steve Olson stops along the Pikes Peak Highway and enters a spruce forest to see what he can find. "Let's see what this is," he says, crossing his long, skinny legs and folding downward to the ground. His arms are gangly, like branches, his fingers spindly, and they gently inspect this green patch. It's not an inch away from his glasses, which rest at the crook of his nose. He sits as if in communion, or like a kindergartner at story time. "A-ha," he softly remarks. It's Pikes Peak parsley. One of a kind, Olson explains, found only around this summit and the neighboring slopes of Almagre. It's something about this particular soil, Olson says, this crumbly granite. "It's been suspected in a few other places," he says, "but nothing definitive."

It would be easy to confuse. Pikes Peak parsley looks like some clump you might find in your backyard. That is if you're someone without the analytical eye of Olson. He's the US Forest Service botanist assigned to the 3 million acres defining the Pike and San Isabel national forests and Cimarron and Comanche grasslands. You can find Pikes Peak parsley—its scientific name is Oreoxis humilis—within a database of some 2,200 other hard-to-pronounce plant names that Olson has compiled. This has been a project of his for the nearly 20 years he's spent at his Forest Service post in Pueblo.

Efficiency has been key to his job. A permit request comes, and "the ultimate goal is to look at every single site," Olson says. "But also it’s a labor-saving device," he says. He might train the binoculars on a distant ridge and decide he need not go there. Efficiency has been key to his job. A permit request comes, and “the ultimate goal is to look at every single site,” Olson says. “But also it’s a labor-saving device,” he says. He might train the binoculars on a distant ridge and decide he need not go there.

Here on the side of the Pikes Peak Highway, it’s easy to imagine a cement drainage — built as part of the mountain’s long history of development and commercialism — consuming ground where Pikes Peak parsley might have once sprouted. True, Olson says. Pikes Peak parsley was probably impacted. But for as globally rare as it is, “within this place, it’s clearly not hard to find,” Olson says, “and it seems to be fairly happy.” Here in early June, he’s pleasantly surprised to see some yellow already bursting forth, not long after snow melted from these high elevations. “It’s just getting started,” he says.

Olson, however, is wrapping up. He’s looking to retire in the coming months. He’ll leave behind that database for his successor — assuming there will one. It's hard to know for sure amid ongoing uncertainties with the Forest Service’s budget, which has been increasingly consumed by wildfire management. For fiscal year 2021, the agency’s proposed cuts were described as “an improvement over past years’ recommendations” by the National Association of State Foresters, “but nearly all of those proposed cuts would be made to state and private forestry programs.”

Olson has been the lone botanist assigned to the entire PSICC. He concedes those 2,200 plant entries hardly scratch the surface of the vast and varied beauty and mystery of his assigned “unit,” covering the Kansas prairie, the canyonlands of southern Colorado, the famed rivers of Chaffee and Fremont counties, the foothills of America’s Mountain and other 14,000-foot peaks spread across the Sangre de Cristo, Sawatch and Mosquito ranges. Olson’s database “is one of those things that’ll never be complete,” he says. "Because there’s always something new showing up.”

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In the broader management of the PSICC, his duty is to protect rare life that grows from the earth. Permit renewals will reach his desk. A continued request for an overhead power line, for example. Or a new permit proposing construction, or logging, or mining, or gas and oil exploration. Olson will turn to his database to see what flora might be harmed.
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Plants in the Land of Extremes”
Evaluating how lethal management affects poaching of Mexican wolves

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Despite illegal killing (poaching) being the major cause of death among large carnivores globally, little is known about the effect of implementing lethal management policies on poaching. Two opposing hypotheses have been proposed in the literature: implementing lethal management may decrease poaching incidence (killing for tolerance) or increase it (facilitated illegal killing). Here, we report a test of the two opposed hypotheses that poaching (reported and unreported) of Mexican grey wolves (Canis lupus baileyi) in Arizona and New Mexico, USA, responded to changes in policy that reduced protections to allow more wolf-killing. We employ advanced biostatistical survival and competing risk methods to data on individual resightings, mortality and disappearances of collared Mexican wolves, supplemented with Bayes factors to assess the strength of evidence. We find inconclusive evidence for any decreases in reported poaching. We also find strong evidence that Mexican wolves were 121% more likely to disappear during periods of reduced protections than during periods of stricter protections, with only slight changes in legal removals by the agency. Therefore, we find strong support for the ‘facilitated illegal killing’ hypothesis and none for the ‘killing for tolerance’ hypothesis. We provide recommendations for improving the effectiveness of US policy on environmental crimes, endangered species and protections for wild animals. Our results have implications beyond the USA or wolves because the results suggest transformations of decades-old management interventions against human-caused mortality among wild animals subject to high rates of poaching.

1. Background

Human-caused mortality is the major cause of death among large, terrestrial, mammalian carnivores worldwide [1], including the
Anthropogenic mortality has precipitated the decline and extirpation of carnivore populations worldwide both indirectly and directly through the often coinciding threats of habitat loss and degradation, prey depletion and killing [6]. Indeed, reported and unreported poaching is the major form of human-caused mortality for large carnivore populations in several regions [7,8], including five US wolf populations [4]. Such mortality raises individual and societal concerns because poaching is an environmental crime, harms individual animals, and undermines restoration and conservation efforts.

Identifying and estimating poaching is hindered by concealment of evidence. Estimating concealed, illicit killing rates has recently been transformed by two analyses that used data that had previously been ignored. Liberg et al. [7] estimated the hazard rate of cryptic (i.e. unreported or concealed) poaching by considering slow-downs in population growth and accounting for the disappearances of marked grey wolves in Scandinavia. Similarly, Treves et al. [5] re-calculated the risk of poaching relative to other causes of death by considering missing, marked animals, which had previously been excluded from analyses under an erroneous assumption that marked animals that disappeared would have died of similar causes as those marked animals found dead. Therefore, investigators can now better estimate heretofore under-appreciated variables that are essential to understanding population dynamics and individual animal life histories. However, the latter study admittedly did not directly estimate poaching, instead using estimates from other populations (Scandinavia and Wisconsin) as multipliers to indirectly quantify cryptic poaching, and did not measure policy effects on poaching or consider time to exposure of wolves to policies. Its objective was strictly to estimate the risk of poaching in a population regardless of policy period. Therefore, here, we propose an important advance to estimate the relationships between policy interventions and fates of marked carnivores, while controlling for spatio-temporal covariates. We test opposed hypotheses from the literature explained next.

The scientific literature has recently addressed the question of if and how policies may influence the hazard and incidence of poaching. The usual assumption (despite lack of empirical evidence) is that some predator-killing (e.g. government permits for killing or public hunting seasons) might increase tolerance for a species (and thus reduce poaching); an argument first articulated in federal court in 2006 [9] and summarized more generally in [10]. We call this first hypothesis ‘killing for tolerance’, which predicts legal killing will reduce poaching through the following mechanism: legalizing or liberalizing killing of controversial species will lead would-be perpetrators to desist from poaching because of increased tolerance for the species or approval for protectionist policies. Early tests of this notion of ‘killing for tolerance’ include [11–17]. Olson et al. [11] examined correlations between documented (i.e. reported) poaching of Wisconsin’s wolves and management policies between 2003 and 2011. They suggested that the incidence of known poaching events was inversely related to the proportion of each year with state management associated with liberalized killing periods, and hypothesized that frustration with protections for wolves led to increased poaching. Studying the same population, albeit with more sophisticated modelling of demographic processes, Stenglein et al. [18] estimated an additional mortality of 4% was necessary to explain the observed slow-down in the population’s annual growth rate within that same time period. These early tests of the killing for tolerance hypothesis attribute rates of poaching and population dynamic changes to illegal actions motivated by inconsistent management and protections for controversial wolves. By contrast, Chapron & Treves [15] reported serial slow-downs of wolf population growth during six non-consecutive policy periods in Wisconsin and Michigan from 1995 to 2012, which seemed attributable to unreported wolf-killing. They proposed an explanation we refer to as ‘facilitated illegal killing’. Three social scientific studies published between 2013 and 2015 [12–14] examined attitudes towards wolves in Wisconsin and found that tolerance decreased as wolf-killing was progressively liberalized, or intention to poach wolves increased as wolf-killing was progressively liberalized from 2003 to 2013. Considering such evidence, the alternative hypothesis of ‘facilitated illegal killing’ suggests that liberalized killing might decrease the value of wolves to would-be perpetrators of poaching, or decreasing the risk of being caught [15]. A 2019 re-analysis using the methods proposed below found liberalized killing policy periods in Wisconsin, USA (1979–2012), were associated with increases in hazard and incidence of wolf disappearances that outweighed by fivefold any decreases in reported poaching, undercutting the ‘killing for tolerance’ hypothesis [19]. Despite the lack of a clear causal connection between attitudes and poaching, the study described here tries to establish a closer mechanistic link between policies and poaching behaviour. In sum, two published hypotheses make opposed predictions about the rates of poaching in relation to policies for liberalizing legal killing of controversial species.

Other research linking wolf mortality to population growth rates in a hunted Finnish population found increases in population size were positively associated with increases in poaching [8]. Using generalized linear models focused on predictors of poaching, the same team later found the number
of legally hunted wolves both across the country and at the local scale was associated with a decrease in the probability of poaching, while increases in the number of wolves that could be legally killed (the ‘bag limit’) were associated with increases in the probability of poaching [20]. Additionally, the authors suggest that declines in poaching following higher levels of legal hunting might be an artefact of a decrease in the individual wolves exposed to poaching [20, p. 7]. They concluded that ‘tolerance for carnivores cannot be promoted by legal hunting alone, so more comprehensive conservation efforts are needed’ [8,20].

The most recent publication on this topic for grey wolves in Scandinavia [21] suggested that when more territorial breeding individuals were removed legally, fewer such animals disappeared (presumably poached), but their analysis has been questioned on the grounds of inappropriate statistical analyses and incomplete treatment of the apparent rise in disappearances during years with legal wolf-killing [22].

However, there remain unresolved concerns about omitted methods and the statistical approaches and assumptions made in all three studies from the US upper Midwest and Nordic countries [19,23]. None of the studies [8,15,16,18] explicitly modelled survival in relation to the amount of time wolves were exposed to liberalized killing policies that changed 12 times between 1995 and 2012 in the USA and several times in the Nordic countries [15,24]. Here, we build on these analyses by including the amount of time that radio-collared wolves were exposed to liberalized killing policies to re-estimate hazard and incidence of poaching.

Indeed, a simple reduction in poaching may not be equivalent to ‘tolerance’; that is, greater acceptance of wolves on the landscape. The ‘killing for tolerance’ hypothesis suggests a cognitive mechanism that implies something broader than a reduction in poaching, which is only one anthropogenic endpoint affected by tolerance. However, poaching is not the only human behaviour affected by tolerance causing wolf mortality. Human tolerance would arguably affect other anthropogenic endpoints such as legal killings or (in this particular population) final removals (e.g. through increased legal killings by citizens or requests for action to government agents leading to increased mortality, similar to that found in Scandinavia [20]). Thus, any comprehensive exploration of ‘tolerance’ affecting wolf mortality should examine the interactions between the different anthropogenic endpoints and their resulting incidences.

Opposing views of the relationship between legal killing and poaching of wolves can be tested if we analyse individual wolf survival in relation to the timing and duration of their exposure to periods with different policies for legal killing. Here, we will test the specific hypothesis that rates of hazard and incidence of mortality or disappearance of wild Mexican grey wolves (*Canis lupus baileyi*) in Arizona and New Mexico, USA, changed after policies altered the legality of killing or harassment of Mexican wolves by the public and government agencies. Table 1 provides predictions for the two response variables of hazard ratios (HRs) and competing risk subhazard ratios (SHRs). There has been no research on the opposing hypotheses of ‘killing for tolerance’ or ‘facilitated illegal killing’, within this population. Such a test is particularly important as Mexican wolves are a highly endangered subspecies of grey wolves. Previous estimates [4] indicate poaching rates in this population have been high and underestimated by traditional methods.

The subspecies was functionally extinct in the USA by the 1970s due to extermination efforts by state, federal, tribal and private actors [25]. A captive breeding programme began in 1977, and the US government began releasing Mexican wolves to the Blue Range Wolf Recovery Area in southern Arizona and New Mexico in 1998. From 1998 to 2016, all Mexican wolves released to the recovery area were fitted with a radio collar and were closely monitored (n = 279 radio-collared). Here, we examine the survival and disappearances of adult marked Mexican wolves before, during and after two policy periods, one in 2005–2009 and another starting in 2015, that liberalized killing or removal of wolves by government or private actors.

We examine data on radio-collared animals using competing risk analyses that allow the modelling of hazards and incidences of multiple fates (i.e. various causes of death or lost to monitoring; endpoints, hereafter) while controlling for multiple covariates. We model exposure time to policy changes. This analysis allows us to make inferences beyond the cursory examination of compensatory mortality caused due to changes in policy, to examine how policies might affect an individual wolf’s probability of succumbing to a cause of death. Furthermore, using a competing risks analysis allows us to include disappearance as an endpoint which is crucial, given that prior work shows that censoring lost to follow-up (LTF) led to systematic underestimates of poaching in other grey wolf populations [4,19]. The results of this analysis can provide recommendations for improving the effectiveness of US policy on environmental crimes, endangered species and protections for wild animals. Therefore, our analyses have implications beyond the USA or wolves because the methods promise to transform
Table 1. Relationship between our hypotheses, proposed analyses and interpretation of outcomes (including contingent interpretation and synthesis of model results). HR_{poa} refers to the HR of the poaching endpoint, while HR_{ltf} refers to the HR of the lost to follow-up endpoint.

<table>
<thead>
<tr>
<th>question</th>
<th>hypotheses</th>
<th>sampling plan (e.g. power analysis)</th>
<th>analysis plan</th>
<th>interpretation given different outcomes (see note and main text for Bayes factor specifications*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Do hazard rates or cumulative incidence of death by poaching or disappearance (DV) of wild, collared adult Mexican grey wolves change after policies change (IV) from strict protection to liberalized killing and back again?</td>
<td>'Killing for tolerance' predicts the hazard and incidence decline for the endpoint 'poached' (poa) or the endpoint LTF when the IV of policy period liberalizes wolf-killing.</td>
<td>All collared wild Mexican grey wolves from MWRP and OLE 1998–2016 (n = 279). A diagnostic test is run on the samples with four endpoints (human, natural, removal, LTF) before proceeding to the analysis plan (see Diagnostic step). See tables 3 and 4 for endpoint-specific sample sizes split by the IV of policy period.</td>
<td>For MWRP and OLE datasets: Endpoint-specific Cox multiple regression models (for each endpoint) on the IV of policy period and other covariates. Competing risk Fine and Gray multiple regression models (for each endpoint) on the IV of policy period and other covariates. CIFs allow for analysis of population effects (incidence) while considering the prevalence of each endpoint in the population.</td>
<td>HR_{poa} and HR_{ltf} are &lt;1 or (HR_{poa} has to be &lt;1 and greater in magnitude than any increase in HR_{ltf} or HR_{ltf} has to be &lt;1 and greater in magnitude than any increase in HR_{poa}) and endpoint-specific CIFs estimate which endpoint has a greater effect on the population (from Fine–Gray models of competing risks). The criterion for determining if 'TOTAL potential poached' probability f declined is a decline in the combined incidence of LTF and POA.</td>
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Table 1. (Continued.)

<table>
<thead>
<tr>
<th>question</th>
<th>hypotheses</th>
<th>sampling plan (e.g. power analysis)</th>
<th>analysis plan</th>
<th>interpretation given different outcomes (see note and main text for Bayes factor specifications(^a))</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Facilitated illegal killing' predicts the hazard and incidence increase</td>
<td>All collared wild Mexican gray wolves from MWRP and OLE 1998–2016 ((n = 279)).</td>
<td>For MWRP and OLE datasets: Endpoint-specific Cox multiple regression models (for each endpoint) on the IV of policy period and other covariates.</td>
<td>HR(<em>{poa}) and HR(</em>{ref}) are &gt;1 OR (HR(<em>{poa}) has to be &gt;1 and greater than any decrease in HR(</em>{ref}) OR HR(<em>{ref}) has to be &gt;1 and greater than any decrease in HR(</em>{poa})) AND endpoint-specific CIFs estimate which endpoint has a greater effect on the population (from Fine–Gray models of competing risks). The criterion for determining if 'TOTAL potential poached' probability for wolves declined is a decline in the combined incidence of LTF and POA.</td>
<td></td>
</tr>
<tr>
<td>for the endpoint 'poached' (poa) or the endpoint LTF when the IV of policy period liberalizes wolf-killing.</td>
<td>A diagnostic test is run on the samples with four endpoints (human, natural, removal, LTF) first before proceeding to the analysis plan (see Diagnostic step). See tables 3 and 4 for endpoint-specific sample sizes split by the IV of policy period.</td>
<td>Competing risk Fine and Gray multiple regression models (for each endpoint) on the IV of policy period and other covariates. CIFs allow for analysis of population effects (incidence) while considering the prevalence of each endpoint in the population.</td>
<td></td>
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</table>

\(^a\)Following reviewer recommendations, we will use BF using three specifications. BF estimates the strength for our alternative and null hypotheses for particular endpoints, and allows us to assess insensitivity of the data to resolve differences between hypotheses. For purposes of comparison, and to provide estimates of policy effects on 'total potential (cryptic+reported) poaching', we proceed to aggregate poaching endpoints and run all analysis on the new endpoint LTF + POA (including BF\(_{s}\)) (see Statistical methods).
2. Methods

2.1. Data collection and preparation

We analysed data acquired from the Department of Interior US Fish and Wildlife service (USFWS) Mexican Wolf Recovery Program (MWRP) and their Office of Law Enforcement (OLE) in separate but overlapping datasets on marked (hereafter collared), monitored Mexican wolves in the wild. The MWRP survival data include the monitoring history for all collared and monitored adult Mexican wolves in the wild since the beginning of the recovery programme, 29 March 1998–31 December 2016; n = 279 (monitored wolf pups were excluded from this dataset).

Because of the small wild population size and the captive breeding programme, the majority of wolves in the Mexican wolf recovery area were collared for monitoring. Only wild-born individuals that eluded capture remained unmonitored. Therefore, our analysis has the benefit of reducing (but not completely eliminating) a common bias in monitored animal studies when the marked subsamples are non-random, unrepresentative samples of the wild population and may not have the same mortality risk as unmarked individuals [26–30].

The MWRP survival data contain the following individual covariates we used in our statistical analysis: monitoring start date, sex and endpoint (i.e. end of monitoring time by: cause of death, lost to follow-up (LTF) or removal by agency action). The endpoint ‘removal’ by agency action typically involved USFWS live-capture of a wolf from the wild followed by either placement in captivity or killing. The endpoint of LTF occurred when the telemetry equipment affixed to a wolf in the wild stopped functioning and the collar was never recovered. This could happen from mechanical/battery failure or destruction by external causes such as humans. Some wolves had multiple collars during their monitoring history as a result of recapture and recollaring. The vast majority of monitored time intervals (87.6%) were obtained using VHF collars, while the remaining 13% of monitored intervals were obtained with GPS collars. In our data, the average amount of time to LTF for wolves wearing VHF collars was 621 days, with a range of 7–3079 days. The average battery life of a VHF radio collar is about 1095 days, but wolves were often recollared. Only one individual disappeared while wearing a GPS collar, and this individual went LTF after 169 days. For recovered collars, the cause of death was estimated by USFWS using standard methods following necropsy and radiography.

For each of the 279 wolves in the MWRP survival data (1998–2016), we estimated the time between collaring (monitoring start date) and endpoint in days (t), but we did so differently for surviving, dead and LTF endpoints. We censored surviving, monitored wolves at the end of our study period. For LTF endpoints, we used the date of last telemetry contact. The inclusion of LTF as a separate, explicitly modelled endpoint was crucial for our inferences because of the prior work showing that censoring LTF led to systematic underestimates of the proportion and hazard of poaching in other grey wolves [4,19]. Some wolves might have lived on for a time after their telemetry contact was lost, so LTF led to systematic underestimates of the proportion and hazard of poaching in other grey wolves modelled endpoint was crucial for our inferences because of the prior work showing that censoring endpoints, we used the date of final telemetry contact. The inclusion of LTF as a separate, explicitly modelled endpoint was crucial for our inferences because of the prior work showing that censoring LTF led to systematic underestimates of the proportion and hazard of poaching in other grey wolves [4,19]. Some wolves might have lived on for a time after their telemetry contact was lost, so LTF represents a systematic underestimate of survival and hence of our parameter, t. We address the consequences and magnitudes of that bias in Results. For our ‘mortality’ and ‘agency removal’ endpoints, we estimated t for wolves monitored by telemetry until death and the date of final removal to captivity by agency action, respectively.

Mortality endpoints obtained from the MWRP survival data were classified only as ‘human’ or ‘natural’ in our first analysis step. Natural used by both MWRP and OLE presumably meant non-human cause of death. The human-caused endpoint was identified in the MWRP data as mortality with ‘likely and known human causes’, without a more specific cause of death (e.g. vehicle collision, poaching). In the second analysis step, we turned to the OLE data, which categorized human-caused mortality by the following causes of death: vehicle collisions, trap, gunshot, blunt force trauma, ‘unknown’ or ‘other’. Using these data, we classified human-caused deaths as either poached (trap, gunshot, blunt force trauma) or non-criminal (vehicle collisions, ‘unknown’, ‘other’ with no evidence of human intent). We used all human-caused deaths recorded up to and including 31 December 2016.

We focused our analysis on a time-varying covariate for policy period (the policy intervention or IV in table 1). Policy period was binary for period of liberalized wolf-killing (1) or stricter protections (0) following exact policy change dates. Our policy covariate changed from 0 to 1 on 10 October 2005 when Standard Operating Procedure 13.0 (SOP 13) ‘Control of Mexican wolves’ was implemented by
the Mexican Wolf Blue Range Reintroduction Project Adaptive Management Oversight Committee (AMOC) and changed back to 0 on 2 December 2009 (table 2). SOP 13 liberalized wolf-killing (1) by establishing a ‘three-strikes’ policy requiring the permanent removal of wolves implicated in three instances of predation on domestic ungulates during a 1-year period. During SOP 13, removals of wolves more than doubled relative to the previous 7 years [31]. The policy was challenged in court and terminated by a federal judge on 2 December 2009. However, a subsequent change in policy would again liberalize the killing of wolves. Thus, our policy covariate changed from 0 to 1 again from 16 January 2015 to 31 December 2016, which is the last date of our Freedom of Information Act data request (and the end of our study period). On 16 January 2015, the USFWS implemented a modification to the 1998 Endangered Species Act (ESA) 10(j) rule that expands the area where Mexican wolves can be released, allows permitted private entities to kill wolves on non-federal land if wolves are deemed to be a danger to domestic animals and allows killing by government agents on private and state lands if wolves cause unacceptable predation on big game animals.

We also modelled season as a time-dependent covariate using an October–March (winter) and April–September (summer) split, because elsewhere season is known to mediate mortality in wolves [8,19,32,33]. For example, preliminary analysis of a population of Wisconsin wolves revealed winter periods were associated with increases in the hazard and incidence of various endpoints (LTF, poaching, natural death) and at different rates [19]. To model both time-dependent covariates (policy and season), we created splits in each collared wolf’s monitoring history. We refer to these splits as ‘spells’ given they refer to briefer periods within an individual’s monitoring time (table 2). In selecting the covariates of interest, we are following best practices of having at least 10 endpoint events per covariate [34–36]. We have, therefore, excluded from our multivariate models any covariates unless they are essential to control.

Nuisance variables are unlikely to confound our analyses as we discuss next. A hypothetical nuisance variable would have to not only correspond to the various changes in policy (2–3) but also be widespread across both NM and AZ across multiple jurisdictions (tribal, state, federal, county lands), and affect multiple independent adult wolves in packs occupying virtually exclusive home ranges. That leaves a climatic event or other widespread biotic event such as a disease with more than one change (to correspond with the policy changes of interest). We have searched both USFWS programme documents and the scientific literature and have found no evidence of changes in environmental events or onsets of disease. Moreover, the covariates that may impact our hypotheses would need to affect the poaching, LTF and legal killing risks. Instead, environmental changes that may covary with the policy may, in fact, show changes to the ‘natural’ endpoint hazard and incidence, while perhaps affecting the changes in the incidence of our anthropogenic endpoints (through endpoint interactions, see below) but not their hazards.

Table 2. Example of monitoring history of a hypothetical wolf ID, broken up into spells for the integration of time-dependent covariates. We use ‘analysis time’ for the time intervals and order of spells, as covariates change (either policy or season). The endpoint categorical variable is only reflected for the last spell, which corresponds to when monitoring ended (at \( t = 250 \) in this hypothetical case).

<table>
<thead>
<tr>
<th>wolf ID</th>
<th>analysis time when spell begins</th>
<th>analysis time when spell ends</th>
<th>policy</th>
<th>season</th>
<th>endpoint</th>
</tr>
</thead>
<tbody>
<tr>
<td>MX1209</td>
<td>0</td>
<td>57</td>
<td>1</td>
<td>1</td>
<td></td>
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<tr>
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<tr>
<td>MX1209</td>
<td>140</td>
<td>350</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

2.2. Statistical methods

We employed endpoint-specific hazard and subhazard models in a competing risk framework, which are extensions of survival (or ‘time-to-event’) analyses, and a special case of multi-state models [37]. Survival analyses estimate the probability of observing a time interval from the start of monitoring (in our case, release to the wild with a functioning transmitter) to an endpoint, \( T \), greater than some stated value \( t \), \( S(t) = P(T > t) \) within a specified analysis time (our study period above). These techniques allow for calculating the (endpoint-specific) hazard function, \( h_k(t) \), or the instantaneous rate of occurrence of a particular endpoint \( k \) conditional on not experiencing any endpoint until that time [38–41]. We used the
hazard function to estimate the relative hazard of a collared wolf reaching an endpoint such as LTF, given its survival to a particular date. We used the semi-parametric Cox proportional hazard models to estimate covariate HRs to model how endpoint-specific $h_k(t)$ changes as a function of survival time and model covariates. The estimation of covariate effects on the endpoint-specific hazard is modelled as $h_k(t) = h_{0k}(t) \exp(\beta_1 x_1 + \ldots + \beta_j x_j)$, where $h_{0k}(t)$ is an unestimated baseline hazard function (i.e. semi-parametric) and $\beta_j$ represent the estimates of HRs for each covariate $x_j$ (HR < 1 represents a reduction in hazard and HR > 1 an increase in hazard).

However, hazard rates do not consider competing risks. Competing risk analyses go beyond standard survival analyses by considering multiple endpoints simultaneously (e.g. multiple causes of death, agency removal or LTF). These models are useful for estimating the relative incidence of a particular endpoint, while accounting for other competing endpoints (e.g. the occurrence of human-caused death in the presence of a risk of natural-caused death and LTF). In a competing risk framework, individuals can potentially experience the event of interest (i.e. end of monitoring time) by multiple, mutually exclusive endpoints, although only one is observed. Because the event of interest can only occur due to one endpoint, we refer to the endpoints as ‘competing’ to bring about that event, and to the respective probabilities over time of that occurring as ‘competing risks’.

Competing risk techniques estimate the cumulative incidence (CIF) curve for each endpoint, defined by the failure probability Prob($T < t, D = k$); that is, the cumulative probability of endpoint $k$ having occurred first (element $D$ is an index variable that specifies which endpoint occurred) at time $T$, which specifies when the event happened within the study period interval defined over time $t$ in the presence of other competing endpoints (i.e. subjects experiencing other endpoints are still considered at risk as individual wolves entered and left the risk set throughout the study period) [37,41,42].

Within the competing risks framework, Fine–Gray (FG) subhazard models estimate differences in CIFs for a given endpoint conditional on covariates [42,43]. FG models use regression techniques similar to the Cox model, except parameter interpretation changes as follows: estimates are interpreted as SHRs or relative incidence (rather than HRs) in the presence of other endpoints (i.e. for each covariate $x_j$: SHR < 1 represents a reduction in incidence and SHR > 1 an increase in incidence). Although both hazard and competing risk models are informative, the competing risk models consider more information and provide greater predictive power [41,42,44].

Hence, while endpoint-specific Cox models and their HRs allowed us to test the hypothesis that liberalized wolf-killing affected the rate of occurrence (i.e. hazard) of any endpoint relative to policy periods, the FG models and their SHRs allowed us to test if and how much liberalized killing affected the probability and incidence of endpoints, in addition to the potential simultaneous effects of other covariates. CIFs allowed us to visualize those effects on incidence while considering the prevalence of each endpoint in the population. Therefore, we used both hazard and incidence to infer the changes due to policy period and test the opposed hypotheses (table 1).

Our Cox proportional hazards and FG subhazard models comply with the appropriate number of events per variable recommended in the scientific literature to ensure the accurate estimation of regression coefficients and their associated quantities for the endpoints of interest (poached, agency removals, LTF) (see tables 3 and 4) [34,35,45].

Following recommendations for rigorous competing risk analysis [41,42,44,46], we reported results on all endpoint-specific hazards and CIFs to elucidate how hazards and incidences of multiple endpoints interact. For example, analysis of Wisconsin wolves suggested the increases in both the hazard and incidence of LTF during liberalized killing periods offset and potentially overcompensated for the smaller decreases in hazard and incidence of reported wolf-poaching estimated during those same periods [19].

Finally, we used Bayes’ factor (BF) [47] to assess the strength of evidence for each of our alternative hypotheses and the null hypothesis for each poaching endpoint. We used the free BF online calculator found at http://www.lifesci.sussex.ac.uk/home/Zoltan_Dienes/inference/Bayes.htm, which assumes parameter estimates are normally distributed with known variance. The parameters used for each endpoint will be its point estimate and s.e. derived from the final Cox and FG models for testing HRs and SHRs, respectively. To assess the robustness of our conclusion to our prediction of the population distribution given our hypotheses and because prior theoretical support for any particular BF specification is scant, we assumed three different likelihood functions for the hypotheses’ predicted effect as recommended by Dienes [47]: (i) a half-normal function using the legal removal endpoint’s point estimates to model the expected standard deviation as s.d. = point estimate, (ii) a uniform function using the legal removal endpoint for Mexican wolves as the upper bound and 0 as the lower bound, and (iii) a half-normal using endpoint-specific estimates from [19] to calculate the s.d. in the same manner as (i) [47,48]. In doing so, we follow Dienes’ [47] recommendations to use likely values while keeping our
predictions blind to the data as required by a registered report. In the absence of a base of prior literature to guide us, our use of these default variances maintains the required ‘blind’ to our data with a reasonable estimate of variability in the distribution around the point estimate. We use the legal removal endpoint estimates (rather than other imperfectly reported endpoints) in two specifications of our hypotheses because we know there is an effect (i.e. more wolves are killed legally during legalized killing periods).

We report BFs for all HRs and SHR of interest (i.e. reported poached and L TF). BFs strength of evidence for each hypothesis (or null) was interpreted as follows: 1/3 < BF < 3 would be inconclusive evidence; BF > 3 would be substantial evidence for the alternative hypothesis; BF < 1/3 would be substantial evidence for the null hypothesis (i.e. no effect) [47,48]. Given our three BF specifications for each endpoint parameter, we would conclude in favour of a particular hypothesis if most BF specifications (two out of three BFs) support that conclusion. Accordingly, we might generate contradictory evidence (strong support for each hypothesis and the null) or inconclusive evidence (failure of any hypothesis to survive a majority of the BF specifications). For purposes of comparison, and to provide estimates of policy effects on ‘total potential’ (cryptic + reported) poached, we also aggregate and run all analysis on the new endpoint LTF + POA (including the procedure for pre-specified BFs as above).

### 2.3. Diagnostic step

Because we used information from two data sources (MWRP and OLE datasets), we analysed the data in two steps to provide more nuance about the effect of the policy intervention on mortality and disappearance. Both steps employed all survival and competing risk analyses previously described. We analysed four endpoints: ‘human’, ‘natural’, ‘LTF’ and ‘agency removal’ (table 3). The drawback from this endpoint breakdown is the inability to conclude anything directly regarding any policy effects on subsets of anthropogenic mortality (e.g. poaching or non-criminal human-caused deaths).

### 2.4. Analyses

We added OLE data on human-caused endpoints and further specified which were poaching and which were deemed non-criminal (table 4). However, this comes at the expense of lower number of observations in each human-caused endpoint and reduced statistical power (fewer events per variable, see the
previous section and tables 3 and 4). Thus, results from the diagnostic step above will prove more statistically robust, but the exploration of the various anthropogenic endpoints is imperative, given evidence of different policy effects on each [19].

By evaluating the effect(s) of both liberalized killing periods (SOP 13 and revised 10(j) rule), we will strengthen the inference about the policy intervention with a better case-control design (reverse-treatment or before–during–after–during). Therefore, both policy periods will be sampled twice.

Two divisions of the USFWS did the preliminary quality check on data. First, the Mexican Wolf Recovery team collected mortality and disappearance data with a simple endpoint classification as ‘died of natural cause, died of human cause, legal removal by agency, disappeared (LTF)’. Next, for the subset of human-caused deaths above, the independent USFWS OLE classified deaths by cause (vehicle, poaching, accidental) and occasionally reclassified a human-caused death as natural after detailed investigations, some or all of which included necropsy, radiography or field investigation. Within our team, the two co-lead authors performed interobserver reliability tests by independently taking the data provided by the USFWS and summarizing it (tables 3 and 4), then comparing and resolving discrepancies (arbitrated by the senior author in the case of disagreements).

In Phase 2, the two co-lead authors separately prepared the data for analysis by aligning individual wolf survival histories with covariates and the intervention (policy period). The senior author A.T. is F.J.S.-Á.’s post-doc supervisor and N.X.L.’s PhD advisor. He and D.R.P. served as a sceptical trouble-shooter for analyses, interpretation and writing—blind to results until the Phase 2 analysis was considered complete by the two co-lead authors. This team organization and separation of powers was intended to reduce bias and improve the strength of inference.

3. Results

The two policy periods we examined which liberalized killing of Mexican wolves resulted in various changes in the hazard and incidence of endpoints of collared wolves relative to the two periods of stricter protection. The diagnostic step (electronic supplementary material, S1) and results that follow confirmed the importance of disaggregating human-caused endpoints to assess the evidence for our alternative hypotheses.

Covariates of winter and sex did not significantly affect the results of any models, and, therefore, the most parsimonious model included the policy intervention without either covariate. The proportional hazard assumption of Cox models was met for all endpoints (see electronic supplementary material, figures S7 and S8). For information about each model and their parameters, see electronic supplementary material, table S1. The best models revealed the following changes for collared Mexican wolves.

3.1. Lost to follow-up

Periods of liberalized killing were associated with a 121% increase in the hazard for the endpoint of LTF, relative to periods of stricter protection, compatible with a positive range (does not include zero) of +36% to +260% (HR = 2.21, \( p < 0.001 \); table 5 and figure 1b). The proportion of collared wolves (CIF) with the endpoint of LTF increased by 128% (SHR = 2.28, compatible interval = 38–276%, \( p < 0.001 \)) during periods of liberalized killing relative to periods of stricter protection (table 6 and figure 1a).

3.2. Reported poached

Periods of liberalized killing were associated with a 22% decrease in hazard for the endpoint of reported poached, relative to periods of stricter protection, compatible with a range that overlaps zero of −56% to +39% (\( p = 0.407 \); table 5 and figure 1d). The proportion of collared wolves (CIF) with the endpoint of reported poached decreased by 31% (SHR = 0.69, compatible interval = −62% to +25%, \( p = 0.226 \)) during periods of liberalized killing relative to periods of stricter protection (table 6 and figure 1a).

3.3. Agency removal

Periods of liberalized killing were associated with a 5% increase in hazard for the endpoint of agency removal, relative to periods of stricter protection (HR = 1.05, compatible interval includes zero, −41% to +88%, \( p = 0.863 \); table 5 and figure 1c). The proportion of collared wolves (CIF) with endpoint of agency removal decreased by 4% (SHR = 0.959, compatible interval includes zero, −48%
Table 5. Cox model of cause-specific hazards for each endpoint for 279 collared Mexican wolves. HR < 1 represents a reduction in hazard during periods of liberalized killing (lib_kil = 1) and HR > 1 denotes an increase in hazard, HR < 1 a decrease and HR = 1 no change in hazard. Only the most parsimonious model is presented (see electronic supplementary material for all models). In all cases, the proportional hazard assumption of the Cox models was met. Comp. Int., compatible interval around point estimates.

<table>
<thead>
<tr>
<th>variable</th>
<th>endpoint</th>
<th>lost to follow-up (LTF)</th>
<th>agency removal</th>
<th>reported poached</th>
<th>non-criminal</th>
<th>natural</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>HR</td>
<td>Comp. Int.</td>
<td>HR</td>
<td>Comp. Int.</td>
<td>HR</td>
</tr>
<tr>
<td>liberalized killing periods (lib_kil)</td>
<td></td>
<td>2.21*</td>
<td>1.36–3.60</td>
<td>1.05</td>
<td>0.59–1.88</td>
<td>0.78</td>
</tr>
</tbody>
</table>

*p < 0.001, all other results had p > 0.05.

Table 6. FG competing risk models of cause-specific subhazard (SHR) for each endpoint for 279 collared Mexican wolves. SHR < 1 represents a reduction in the incidence of the endpoint during periods of liberalized killing (lib_kil = 1) and SHR > 1 an increase in incidence. SHR = 1 would represent no change in relative incidence. Only the most parsimonious model is presented (see electronic supplementary material). Comp. Int., compatible intervals around point estimates.

<table>
<thead>
<tr>
<th>variable</th>
<th>endpoint</th>
<th>lost to follow-up (LTF)</th>
<th>agency removal</th>
<th>reported poached</th>
<th>non-criminal</th>
<th>natural</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SHR</td>
<td>Comp. Int.</td>
<td>SHR</td>
<td>Comp. Int.</td>
<td>SHR</td>
</tr>
<tr>
<td>liberalized killing periods (lib_kil)</td>
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<td>2.28*</td>
<td>1.38–3.76</td>
<td>0.96</td>
<td>0.53–1.75</td>
<td>0.69</td>
</tr>
</tbody>
</table>

*p-value < 0.001.
3.4. Non-criminal

Periods of liberalized killing were associated with a 42% increase in hazard for the endpoint of non-criminal causes, relative to periods of stricter protection (HR = 1.42, compatible interval includes zero, −25% to +171%, p = 0.278, table 5). The proportion of collared wolves (CIF) with the endpoint of non-criminal increased by 27% (SHR = 1.27, compatible interval includes zero, −33.7% to +146%, p = 0.463) during periods of liberalized killing relative to periods of stricter protection (table 6).

3.5. Natural

Periods of liberalized killing were associated with a 28% increase in hazard for the endpoint of natural causes relative to periods of stricter wolf protections (HR = 1.28, compatible interval includes zero, −47% to +121%, p = 0.600, table 5).
to +208%, $p = 0.582$, table 5). The proportion of collared wolves (CIF) with the endpoint of natural increased by 32%, compatible interval = −44% to +211% (SHR = 1.32, $p = 0.526$; table 6).

### 3.6. Total potential poached

Periods of liberalized killing were associated with a 42% increase in hazard for the endpoint of total potential poached (aggregated endpoint of LTF and reported poached), relative to periods of stricter protections (HR = 1.42, compatible interval = −0.7% to +103%, $p = 0.05$). The proportion of collared wolves (CIF) with endpoint of total potential poached increased by 38% (SHR = 1.38, compatible interval = −5% to +101%, $p = 0.095$).

### 3.7. Bayes factors

We calculated BF with three specifications to model the expected predicted and maximum effect (electronic supplementary material, table S2). BFs were inconclusive (1 < BF < 3) for most endpoints, suggesting the data are inconclusive for distinguishing the hypotheses from the null, following recommended criteria for BF interpretation (table 1). Indeed, all three BF specifications proved inconclusive for the reported poached and total potential poached endpoints, which does not support the killing for tolerance hypothesis. However, our presumption that agency removal increased during periods of liberalized wolf-killing was not supported (HR = 1.05 and SHR = 0.96); therefore, specifications 1 and 2 seem meaningless (table 7). By contrast, the third specification of BF based on endpoint-specific estimates of predicted effect as recommended by Dienes [47,48] were meaningful (table 7). These are conclusive evidence of an increase in LTF during liberalized wolf-killing periods (BF = 8.08); that specification was inconclusive on changes for reported and total potential poached endpoints. See electronic supplementary materials for information about the inputs used to calculate BFs (electronic supplementary material, table S2).

### 4. Discussion

Here, we report a replication of the findings of Santiago-Ávila et al. [19] that grey wolves that disappeared from monitoring did so at higher rates during periods of reduced protections (i.e. liberalized killing) than during periods of stricter protections under the US Endangered Species Act (ESA). We find stronger evidence for this pattern among collared Mexican wolves (C. l. baileyi) than was found among collared grey wolves in Wisconsin, USA [19]. Because the disappearance of collared wolves that are being monitored by VHF or GPS is most often caused by illegal activities [5,7,49], the present study further undermines the common assumption that animals lost to monitoring suffer from the same hazards and endpoints as those animals that are perfectly monitored [4].

In the paragraphs below, we first justify the assertion that the observed pattern in disappearances results from increases in cryptic poaching. Second, we conclude that our results support the ‘facilitated illegal killing’ hypothesis and do not support the ‘killing for tolerance’ hypothesis. Third, we discuss strength of inference in this subfield of wildlife science including protections against bias used in this study for the first time in this subfield to strengthen inference. Fourth, we propose that legal killing, non-lethal removal from the wild, and facilitation of cryptic poaching are all impediments to endangered wolf recovery under the ESA. Finally, we discuss the general lessons we draw from this study for the US federal agency implementing the ESA (USFWS) for wolves generally, for other countries and for anti-poaching research and intervention.

The relative stability in hazard and incidence of all known fates (not including the subset of radio-collared Mexican wolves that were designated LTF, lost to follow-up) between policy periods would suggest that if LTF wolves were in fact lost due to the same endpoints as monitored individuals with known fates, then we should observe relative stability in hazard and incidence of LTF between policy periods. This is not the case in either this study or [19]. Past work provides numerous independent lines of evidence that the majority of LTF could not be emigrants nor transmitter failures. First and most importantly, in both this study and that of Santiago-Ávila et al. [19], hazard and incidence rates of LTF changed in correlation with policies on legal killing, which could not plausibly have caused transmitter failures; see also [49] on different rates of LTF between hunting and non-hunting seasons. Also, battery life might be confounding LTF that occurred long after collaring. Contrary to this expectation, LTF was much shorter (average 788 days) than the average length of time to the natural mortality endpoint (1175...
days). If battery life were the confounding factor, we would expect the average time to LTF to be more similar to the average time to the natural mortality endpoint. Second, if LTF were largely made up of emigrants from the Mexican wolf recovery area, some of these individuals would probably have been found dead in surrounding areas by citizens with nothing to hide who presumably would have reported their observations to authorities. The USFWS databases we used contained no such cases. Therefore, LTF wolves were most likely killed and the evidence of the illegal action was concealed, e.g. by destruction of transmitters. Such cryptic poaching was first estimated by Liberg et al. [7], and subsequently explored in Treves et al. [4,5] and Santiago-Ávila et al. [19], and could have been exacerbated in the Mexican wolf recovery area by the policy of sharing radiofrequencies of collared wolves with members of the public [50]. We conclude that our results on the disappearances of collared Mexican wolves reinforce those first reported by Treves et al. [5] which demonstrated the bias introduced by excluding disappearances of marked wolves in mortality analyses for four endangered wolf populations.

We tested opposed hypotheses about the effect of legalizing killing or removal of individuals of an endangered species on the survival of collared individuals remaining in the wild. The USFWS, responsible for implementing the ESA for terrestrial species, has been a particular supporter of the ‘killing for tolerance’ hypothesis. It has repeatedly invoked this hypothesis in its endangered grey wolf management under the assumption that government-permitted killing of grey wolves would mitigate or prevent illegal killing and raise public tolerance for wolves, so ongoing recoveries would not be stopped or slowed by illicit resistance [9,51]. A federal court rejected that argument as a speculative approach to abridging the ESA prohibitions that are explicitly aimed at preventing killing [9] but in 2017, another court seemed to defer to the agency on this point when it wrote ‘… it is clear that in drafting the present Section 10(j) rule, the take provisions are critical to conciliating those opposed to the reintroduction effort,…’ [52, p. 43]. Despite this deference, the court remanded the rule to the USFWS to repair its deficiencies. We recommend the USFWS abandon the expectation and repudiate the oft-repeated and unsupported notion that liberalizing killing would reconcile opponents of wolf protection. The results of this study support the alternative and mutually exclusive hypothesis that liberalized killing policies facilitate illegal killing and join a growing body of evidence that suggests liberalized killing policies lower tolerance for wolves and slow wolf population growth substantially more than expected from legal killing rates.

This study, therefore, adds to the literature regarding policy effects on anthropogenic causes of wolf mortality. Human dimensions research using focus groups and mail-back surveys measuring attitudes of Wisconsin residents in and out of wolf range found that respondents’ tolerance for wolves decreased and reported respondents’ willingness to poach wolves increased after wolf-killing was liberalized seven times between 2003 and 2013 [12,14]. Moreover, calls for more killing of wolves followed relaxing ESA protections [13]. Further, a study of population dynamics showed with 92% certainty that there had been an unexplained decrease in the growth of wolf populations in both Wisconsin and Michigan after wolf-killing was liberalized, independent of the number of wolves killed legally [15,16]. The latter authors could only explain the repeated, parallel slow-downs by the existence of undetected mortality

<table>
<thead>
<tr>
<th>BF specifications</th>
<th>endpoint</th>
<th>LTF</th>
<th>POA</th>
<th>LTF + POA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HR</td>
<td>SHR</td>
<td>HR</td>
<td>SHR</td>
</tr>
<tr>
<td>(i) half-normal w/MX-agency removal</td>
<td>1.8</td>
<td>0.69</td>
<td>0.89</td>
<td>1.14</td>
</tr>
<tr>
<td>(ii) uniform w/upbound-MX-agency removal</td>
<td>1.41</td>
<td>1.30</td>
<td>0.93</td>
<td>0.92</td>
</tr>
<tr>
<td>(iii) half-normal w/WI POA</td>
<td>8.08</td>
<td>8.08</td>
<td>1.25</td>
<td>1.63</td>
</tr>
</tbody>
</table>

Table 7. BF calculations for reported poached. LTF and aggregated ‘total potential poached’ (LTF + POA) endpoints for collared Mexican wolves using three specifications: (i) a half-normal distribution using the Mexican wolf agency removal endpoint point estimate of HR and SHR; (ii) a uniform function using the agency removal endpoint for Mexican wolves as the upper bound and 0 as the lower bound, and (iii) a half-normal distribution and the analogous estimates of HR and SHR from Santiago-Ávila et al. [19]; see electronic supplementary material for all parameters. BFs strength of evidence for each hypothesis (or null) was interpreted as follows: 1/3 < BF < 3 (ref) would be inconclusive evidence; BF > 3 would represent substantial evidence for the alternative hypothesis; BF < 1/3 would represent substantial evidence for the null hypothesis of no association.


[15,16], a result which withstood a series of attempts at rebuttal that did not include new data [17] and in one case muddied the waters with errors and omissions [23]. The conclusion from Chapron & Treves [15,16] that the length of the policy period was predictive of the population growth slow-down independent of the reported number of wolves killed is consistent with our finding that exposing Mexican wolves to liberalized killing was associated with higher hazard and incidence of LTF, not predicted by the hazard or incidence of wolves legally killed. Therefore, three independent lines of evidence point in the same direction and opposite to the USFWS hypothesis about liberalizing killing.

Moreover, here we provide more direct, stronger inferences than ever before, against the government’s ‘killing for tolerance’ hypothesis in a new population of wolves. Given that periods of reduced protections allowed for greater flexibility in legal lethal actions towards Mexican wolves, we expected to observe a higher increase in the hazard of agency removals during periods of reduced protections (HR = 1.05). Therefore, we reject the possible explanation that increased hazard or incidence of agency removal (SHR = 0.95) during liberalized killing periods is somehow leading to an increase in disappearances (such as emigration or super-additive mortality). Rather, it was the policy period announcement or its duration per se that had the effect of increasing collared wolf disappearances. Chapron & Treves [15] proposed that reducing protections for wolves sends a policy signal lowering the value of wolves to the public including would-be poachers or reducing the likelihood of enforcement against poaching. The hypothesized ‘policy signal’ seems to convey that either the lives of individual wolves are perceived as less valuable, the benefit of wolves has declined, or prosecution of poachers will relax. We find little evidence to support the latter, because the LTF endpoint represents destruction of evidence of poaching. Instead, would-be poachers appeared to have opted to act cryptically or increase their concealment of evidence during periods of reduced protection, an inference that is supported by a recent news report [53]. The inference that would-be poachers became more concerned with law enforcement while increasing their poaching rates is consistent with the current study in Mexican wolf range and that of Santiago-Ávila et al. [19] for Wisconsin wolves.

Until sophisticated, replicable studies of confirmed poachers and their attitudes are conducted, we cannot know if would-be poachers responded to policy signals by repeating past poaching behaviour with the addition of more concealment of evidence, or if new actors began poaching with concealment. We predict a mix of both patterns, but a preponderance of the poaching during periods of liberalized killing was by individuals who now chose to conceal evidence. That pattern would be supported if the USFWS began to give out radiofrequencies of collared wolves or otherwise changed agency conduct in the field in such a way as to expose collared wolves to higher risk.

In past studies, including those from the US Midwest, as well as one performed in Scandinavia [8], periods of reduced wolf protection were associated with significant increases in hunting or government lethal removal of wolves. Rates of wolf disappearances or poached wolves also increased, but not as drastically as we observe here. These less drastic changes for other endpoints may be a result of ‘cleaning up the numbers’ [8,19]; more wolves reach the endpoint of legal killing before they can succumb to some other endpoint, such as reported or cryptic poaching, thereby muddying our understanding of the effect of legal killing policies on other fates of collared wolves. Our study is not confounded by any effect of ‘cleaning up the numbers’ because Mexican wolves were not subject to higher hazard of legal removal and the incidence of wolves lost by agency removal decreased, yet radio-collared wolves disappeared at higher rates. Rather, we detected significantly more hazardous conditions for the critically endangered Mexican wolf when the USFWS reduced ESA protections independent of agency removal.

Regarding the unexpected finding that the rate of agency removal changed little as policy periods changed from stricter protection to reduced protection, we re-examined our starting assumption. We based our starting assumption of a higher increase in agency removals during two periods of reduced protection (SOP 13 and revised 10(j) rule) on two pieces of likely misleading information. First, by examining the raw numbers of agency removals in tables 3 and 4, it appears that the prevalence of wolves being removed during periods of liberalized killing is about 150% of that being removed during periods of stricter protections. However, hazard and incidence, as we calculate here with survival analysis methods, are based off the sum of all the days each wolf was exposed to each endpoint (i.e. their aggregate time-at-risk). Therefore, time-at-risk is much greater than the number of days over particular policy periods (as reported in tables 3 and 4). We further based our expectations of the change in agency removals over policy periods on a source which claimed that agency removals more than doubled during the SOP 13 policy relative to prior years (see Methods) [31]. However, Fitzgerald [31] lacks any accompanying data.
An often-overlooked aspect of wolf mortality reporting is how the agency classifies cause of death when human-caused. Treves et al. [4] mentioned consolidating causes of death such as non-permitted trapping, shooting, poisoning into one category of poaching, especially when the agency might otherwise misidentify the primary cause of death. We observed a pattern in the data for Mexican wolves that was not detected in Santiago-Ávila et al. [19]. In particular, the incidence of the non-criminal endpoint increased by 27% during periods of reduced wolf protections (table 6). Our results (HR = 1.42 and SHR = 1.27) for the non-criminal endpoint suggest the possibility that USFWS staff classified a greater number of anthropogenic causes of death as non-criminal during periods of reduced protections. This may be a logical result of liberalizing killing, as less killing is legally classified as ‘poaching’. Indeed, some poaching could merely have been reclassified as non-criminal by USFWS staff using subjective definitions and thereby confirming the (erroneous) perception that poaching had diminished because of ‘increased tolerance’. However, the non-criminal endpoint includes vehicle collisions, and other human-caused mortalities that were classified as non-criminal after an investigation by the USFWS Office of Law Enforcement (OLE). Therefore, it is impossible to know the real cause of the increase in hazard and incidence of the non-criminal endpoint during periods of reduced protections without knowing more about the OLE investigations. We received two datasets for Mexican wolves from the USFWS. One set pooled all anthropogenic mortality in one category, which is clearly less useful for analyses such as ours that can tease apart the effect of policy interventions on specific endpoints. Hence, the second dataset from OLE which assigned criminal and non-criminal causes of death and also distinguished further subcategories was much more useful to us. We surmise it would have been more useful to managers and the public also. Therefore, we recommend the USFWS share data on mortality of endangered species that are disaggregated into no fewer than four categories (legal, illegal, vehicle collision and natural), report disappearances (LTF) systematically in the same tables along with start and end dates for time on the air. By the same token, too many categories of poaching as a cause of death can obscure the priority of illegal killing.

Some readers might wonder if frustration among would-be poachers rose in the Mexican wolf range because agency removals did not change between periods, despite the policy signal that protections were loosened. However, we argue that if this were a valid explanation, we would expect frustration with the lack of change in the rate of lethal actions to be prevalent during both policy periods, and we would anticipate the rate of disappearance of wolves to be comparable during the two periods, which we do not see. We would, therefore, expect a different pattern than in the US Midwest where the agency did use liberalized killing periods to lethally remove wolves at higher and increasing rates [19]. Proponents of the frustration hypothesis claimed Wisconsin’s would-be poachers were frustrated when protections were tightened [11]. No plausible cognitive mechanism that would differ between would-be poachers of Wisconsin and those of New Mexico/Arizona has been presented. The frustration hypothesis requires that two different cognitive behavioural mechanisms exist in the two populations, which does not seem parsimonious and is not consistent with the attitudinal data from Wisconsin (see above). This Mexican wolf study cannot support the USFWS idea that without legal recourse, actors would take matters into their own hands, because would-be poachers observing agency removals would be expected to be as frustrated in and out of the policy periods examined here.

Because this study and Santiago-Ávila et al. [19] used time-series analysis for before-and-after comparison of interventions (BACI) without randomization to control or treatment, it provided stronger inference than prior work that relied on correlation and single point estimates [11,15,16], by accepted standards from other fields [54,55]. The standards have been explained at length in [56–58] in relation to their application to evaluation of methods to prevent carnivore attacks on livestock. The current study also integrated several novel protections against bias that further strengthen the inference. An additional reduction in confounding variables in this study is that just over half of the wild Mexican wolves were marked and monitored, compared to the average of 13% marked in the Wisconsin population. That increases the strength of generalizations about Mexican wolves as a whole and increases our confidence in parameter estimates for known and unknown fates in the present study. Therefore, only evidence using experimental controls could achieve stronger inference than does the current study.

Furthermore, this study directly attempted to reduce bias in the following ways. First, we used official data as classified by the management agencies in charge (both USFWS MWRP and its OLE), not by us. Therefore, if any bias exists in the classification scheme, it reflects classification decisions by the agencies and probably random error given the agencies were apparently unaware of the hypotheses. Second, by publishing methods before completing an analysis, we ensured that the analyses could not be amended to support one or another hypothesis. Further, peer-review of the methods helped our team develop stronger analysis methods that would allow us to better interpret the strength of the evidence. Fourth,
we used BF rather than arbitrary traditional significance thresholds to assess the relative strength of evidence for our hypotheses. Our team also developed internal safeguards by having separate members of the team independently interpret the results without taking part in analysis. The ESA requires the use of best available scientific and commercial data, hence policymakers wishing to implement the ESA as intended by Congress can take comfort that the science has advanced to the highest level, rather than continuing to debate with imperfect evidence as the scientific community did from 2013 to 2019 (reviewed in the section on hypothesis tests).

We conducted a BF analysis to quantitatively assess the strength of evidence for our two competing hypotheses and the null hypothesis. Calculating BFs for each endpoint allows us to go beyond significant or non-significant results to examine whether non-statistically significant results truly represented evidence against either hypothesis [47]. To determine whether our results represent evidence for or against either opposing hypothesis or the null hypothesis, Dienes [47] recommends using prior published research to determine what our theory predicts. The theories we test here have not been widely tested; therefore, our best source for endpoint-specific parameter estimates came from Santiago-Ávila et al. [19].

Those prior results from an unrelated dataset provided a comparison for the Mexican wolf results in a registered report but prior to analysing the data. We calculated the BFs of our results using three specifications (defined in Methods) and, following our stated interpretation criteria for BFs detailed in the Methods and table 1, none of our endpoints of interest (LTF, poached, total poached) provided conclusive evidence for either of our alternative hypotheses (electronic supplementary material, table S2). However, we have greater confidence in the results calculated using the third specification; the half-normal distribution calculated using prior data; Santiago-Ávila et al.’s [19] HR and SHR values for the LTF and ‘reported poached’ endpoint. Our rationale for our confidence in the third specification is as follows: (i) the effects observed in both studies are endpoint-specific; therefore, the estimates used (19’s HR and SHR) are a result of similar mechanisms, rather than using estimates from different endpoints that probably result from different mechanisms, as in our other two specifications, both based on using the Mexican wolf agency removal endpoint for comparison; (ii) when submitting our methods as a registered report, we had to make a ‘blind’ (prior to analyses) assumption regarding the change in agency removal endpoint for Mexican wolves (i.e. that agency removals would increase with liberalized protections), which proved counterintuitively unchanged between policy periods, thereby eliminating its potential predictive power; and (iii) the agency removal and reported poached HRs are opposite in direction and the same occurs with the agency removal and LTF SHRs, so those estimates do not provide plausible parameters for the reported poached and LTF endpoints.

The only BF that was conclusive was the support for the ‘facilitated illegal killing’ hypothesis shown by the increase in disappearances of collared Mexican wolves (LTF, table 7). By contrast, the corresponding BF for the total potential poached endpoint fell below the criterion level, because the aggregated LTF and reported poached endpoints ran in opposite directions, but the increase in the proportion of wolves with fate LTF was nearly three times greater than the decrease in the proportion of wolves reported poached. None of the BF analyses supported the killing for tolerance hypothesis (table 7). We conclude the USFWS claim in federal court that lessening ESA protections with the 10(j) rule would reconcile opponents of reintroduction and in turn be harmless for the Mexican wolves in the wild [59] now seems untenable.

4.1. Implications for endangered species

Policy interventions should be effective, i.e. achieve their goals, without serious, unwanted side effects. This study finds that for Mexican wolves, there were serious side effects of the liberalized killing policies. The increase in disappearances of Mexican wolves we detected was substantial during those periods of reduced protections, despite a lack of change in the rate of government removal of wolves. Unplanned, unregulated disappearances are wasteful: a waste of taxpayer money spent on telemetry and relocation to the wild; a loss of individual animals that are unique and irretrievable by known technology; a waste of private resources used in their captive breeding; and undermines the role of the federal government as trustee of US wildlife since 1842 [3]. The effect we found also demonstrates widespread unlawful disregard for the most popular environmental law ever passed in the USA [60].

Further, the policy of liberalizing killing cannot be justified by the vague and indirect claim that it speeds population growth at the expense of individual survival because USFWS data show that the Mexican wolf population declined from 55 to 42 during a 6-year period of liberalized killing from 2004 to 2009 [50]. Similarly, after the implementation of the 10(j) revised rule in 2015, the Mexican wolf population in the wild declined 12%, partially rebounded the next year, and did not change by
2017 when the court order remanded the revised 10(j) rule to the USFWS. Thereafter, growth continued at the prior rate averaging 22% per year (fig. 5 in [50]). The latter finding replicates that of Chapron & Treves [15–17,23] for Wisconsin’s and Michigan’s grey wolves. Currently, the Mexican wolf population numbers 163 [61]. In view of these results, we hypothesize that population growth will slow, halt and maybe even reverse, given currently authorized liberalized killing, with the effect on growth mediated by the magnitude of the policy signal on disappearances; that is, on cryptic poaching rather than agency removals. However, protections for Mexican grey wolves could be strengthened in a revised 10(j) rule being considered by USFWS.

In this context, the balance tilts towards the Mexican wolves by law (quoting the court in Center for Biological Diversity v. Jewell (2018) ‘Harm to endangered or threatened species is considered irreparable, and the balance of hardships will generally tip in favor of the species. See Marbled Murrelet v. Babbitt, 83 F.3d 1068, 1073 (9th Cir. 1996) (“Congress has determined that under the ESA the balance of hardships always tips sharply in favour of endangered or threatened species.”); Amoco Prod. Co. v. Vill. of Gambell, AK, 480 U.S. 531, 545 (1987) (“Environmental injury, by its nature, can seldom be adequately remedied by money damages and is often permanent or at least of long duration, i.e. irreparable. If such injury is sufficiently likely, therefore, the balance of harms will usually favor the issuance of an injunction to protect the environment.”’) p. 23, Docket CV-15-00019-TUC-JGZ, U.S. District Court Arizona, 2018).

The issue goes beyond Mexican wolves. As recently as 14 December 2020, the USFWS continued to espouse the unsupported view that reducing or removing ESA protections will help individual wolves to survive and help wolf populations to recover [51]. In the latter letter to the State of California Fish & Game Commission, the USFWS cited outdated studies that have been superseded since 2016, with frequent communications [62–64].

There are lessons in the current work that have implications beyond the USA and beyond wolves. We suggest other national policies for killing large predators (or other non-humans) to raise tolerance or lower poaching should be scrutinized for strength of inference and the quality of evidence (e.g. [21,22]). The notion that protection for large carnivores generates poaching as a form of rural resistance has merit, but the suggestion that relaxing protections is the solution is no longer credible (contra Kalternborn & Brainerd [65]). Similarly, the long-held notion that without compensation for losses, affected people will kill wildlife illegally, needs re-examination in the light of our current results. The alternative is that compensation might encourage hostage-taking, i.e. an escalation by affected parties to threatening endangered species if they are not better compensated for property damages. Our findings join an active debate about leniency versus enforcement as more functionally effective conservation interventions.

In cases of wildlife trade, such as ivory or rhino horn, arguments for leniency are focused around creating a legal trade to inhibit the lucrative illegal trade [66,67]. However, sources of wildlife crime stemming from conflict, such as in the case of grey wolves, may not be effectively understood, nor managed in the same ways. Leniency has been tried for grey wolves, and evidence suggests leniency fails to achieve greater tolerance and reduced wildlife crime. On the contrary, leniency is associated with increased poaching of wolves in the USA. We encourage the scientific evaluation of all candidate interventions as experiments, preferably with suitable comparisons or even experimental controls, with safeguards against bias.

We suspect wolves are not exceptional among large carnivores regarding the effect of relaxing or fortifying legal protections, because the same justifications for liberalizing killing of brown bears and lions have been used whenever prohibitions on hunting or other lethal management are proposed [10,68–70]. We urge that similar studies be completed to examine whether there is in fact a difference in how liberalized killing policies affect other large carnivores. Further, we hypothesize that it is the attitudes and values of the human actors that are the unifying variable, not the nature of the environmental component or species of wildlife. Our interpretation of these findings, given their consistency with past studies, is that when policies are implemented which reduce the value of non-human beings, such as policies which enable their killing for the sole benefit of human actors, there will be increased harm to those beings and damage to the environment, including crimes.

Data accessibility. The pre-registered Stage 1 report can be found on the Open Science Framework at the following link: https://osf.io/f2kmb/. The raw datasets sources from the US Fish and Wildlife Service and the Office of Law Enforcement have been submitted to the Dryad Digital Repository and can be found at https://doi.org/10.5061/dryad.0vt4bbgck [71]. We have also included the prepared data in our Dryad Digital Repository submission which is ready to be run through the STATA code included starting on p. 11 of electronic supplementary material.
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Widespread mesopredator effects after wolf extirpation

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ABSTRACT

Herein, we posit a link between the ecological extinction of wolves in the American West and the expansion in distribution, increased abundance, and inflated ecological influence of coyotes. We investigate the hypothesis that the release of this mesopredator from wolf suppression across much of the American West is affecting, via predation and competition, a wide range of faunal elements including mammals, birds, and reptiles. We document various cases of coyote predation on or killing of threatened and endangered species or species of conservation concern with the potential to alter community structure. The apparent long-term decline of leporids in the American West, for instance, might be linked to increased coyote predation. The coyote effects we discuss could be context dependent and may also be influenced by varying bottom-up factors in systems without wolves. We make recommendations for ecological research in light of ongoing wolf recovery in parts of the West. Strong ecological effects of wolf repatriation may not occur outside of large reserves where wolves are prevented from achieving ecologically effective densities because of wolf hunting or wolf control programs. Finally, we advocate for more studies relating to the management of coyotes that compare exploited and unexploited populations and evaluate the influence of anthropogenic food subsidies on coyote densities.

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1. Introduction

Humans have a long history of altering populations of native animal species, substituting domestic forms for wild taxa, influencing food webs, and modifying interactions among species. On a worldwide basis, humans have persecuted large predators for centuries, reducing their distributions and abundances. The removal of these apex predators from much of the natural world has had diverse direct and indirect effects, oftentimes manifested through long and complex interaction chains (e.g. Estes et al., 2011). Typically, our understanding of the details of these indirect effects is still limited. Loss of large predators has been linked to irruptions of herbivore prey (Beschta and Ripple, 2009) and of smaller predators (Ritchie and Johnson, 2009). The irruption of smaller predators after extirpation of larger ones is known as mesopredator release (Crooks and Soule, 1999). Mesopredators typically are efficient hunters that are buffered against population collapse by their capacity to switch among prey species (Prugh et al., 2009). Thus, released mesopredators often achieve densities that are sufficiently high and persistent to drive the decline or extinction of prey populations, and affect community structure and stability (Holt and Lawton, 1994; Prugh et al., 2009; Loehle and Eschenbach, 2012).

In North America and Eurasia, researchers have found that through additive effects wolves (Canis lupus) with sympatric bears (Ursus arctos and/or Ursus americanus) generally limit densities of cervids (Crete, 1999; Peterson et al., 2003; Ripple and Beschta, 2012). Across a variety of environments, wolf and bear extirpation can therefore lead to cervid irruptions and a variety of ecological cascades (Berger et al., 2001; Beschta and Ripple, 2009). These cervid irruptions have been documented to have cascading impacts on plant biomass, vertebrate and invertebrate species abundance, and stream hydromorphology (Berger et al., 2001; Hebblewhite et al., 2005; Ripple and Beschta, 2006; but see Mech, 2012). Whereas much is known about irrupting herbivore prey in the American West, there is little work identifying the ecological effects of released mesopredators after wolf extirpation, specifically those of irrupting coyote (Canis latrans) populations (Berger et al., 2008; Miller et al., 2012). However, studies from other regions and continents demonstrate that the maintenance of interactions between top predators and mesopredators can play a pivotal role in structuring ecosystems and sustaining biodiversity (Ritchie and Johnson, 2009). For example, this cascading process has been shown for dingo (Canis lupus dingo) and red foxes (Vulpes vulpes) in Australia (Letnic and Dworjanyn, 2011) and Eurasian lynx (Lynx lynx) and red foxes in Scandinavia (Elmhagen et al., 2010).
Moreover, in Minnesota, increases in the gray wolf population have led to a cascade among carnivores whereby wolves suppress coyotes and indirectly release red fox populations (Levi and Wilmer, 2012).

The main objectives of this paper are to (1) develop and investigate hypotheses regarding the community-level effects of wolf extirpation in the American West, with particular focus on effects mediated by changes in the distribution and abundance of smaller coyotes, and (2) propose a research agenda to test these hypotheses. Our study area consists of the eleven most westerly states in the conterminous United States (>3 million square km). We selected this region because it is mostly comprised of federal public lands (Fig. A1) and large expanses of habitat dominated by forest, shrub, grass, and desert land covers. Livestock grazing allotments are ubiquitous on these public lands; logging and mining are also common, but urban areas and cropland are negligible except on private lands within these states.

Below, we first review the historical relationship between coyotes and wolves. Next, we describe potential ecological effects of coyotes with special focus on leporids, which are often an important component of this carnivore’s diet. We end by discussing possible interacting bottom-up factors and making recommendations for more research.

2. Historical relationship between wolves and coyotes

Interspecific competition between wolves and coyotes has been well documented, and is to be expected, based on the morphological similarity of the two species, dietary overlap, and a difference in body sizes of a factor between 2 and 5 (Donadio and Buskirk, 2006). This ratio of body sizes predisposes wolves and coyotes to a high likelihood of interference competition, including interspecific killing (Donadio and Buskirk, 2006), with the coyote being the consistent loser in these interactions. Although coyotes may benefit from carrion subsidies provided by wolves (Wilmers et al., 2003), multiple lines of evidence described below show that where wolves are abundant and ecologically effective, coyotes are absent, occur at low density, or alter their activity patterns to avoid wolves.

Prior to European settlement, coyotes were reportedly uncommon throughout much of the West (Parker, 1995) such as the Yellowstone area (Schullery and Whittlesey, 1992), but common in the prairies and grasslands of the Midwest (Parker, 1995). The American West was settled and livestock were added to the landscape mostly during the second half of the 19th and early 20th century. During that time, large predators were the targets of widespread eradication efforts over much of the American West (Dunlap, 1988). In 1915, the U.S. Congress authorized eliminating any remaining large predators. As part of this program, the United States Biological Survey systematically killed wolves, coyotes, and other predators. Wolves were effectively extirpated from nearly all the western contiguous United States by the 1930s (Fig. 1a). This period also coincided with extensive management efforts to reintroduce ungulates to historical ranges. At least partially due to wolf extirpation, wild ungulate irruptions soon followed, with most population increases taking place in the West between 1935 and 1945 (Fig. 1b). Coyote harvest numbers increased dramatically after wolf extirpation in much of the western United States. He wrote:

“There are no coyotes in the [Sierra Madre] mountains, whereas with us there is universal complaint from Alaska to New Mexico that the coyote has invaded the high country to wreak havoc on both game and livestock. I submit for conservationists to ponder the question of whether the wolves have not kept the coyotes out? And whether the presence of a normal complement of predators is not, at least in part, accountable for the absence of [coyote] irruption?”

Scientific research – some of it experimental – supports the view that coyotes are typically suppressed by wolves, with coyotes being absent or at low densities in wolf-dominated systems (Stenlund, 1955; Pimlott and Joslin, 1968; Berg and Chesness, 1978; Fuller and Keith, 1981; Thurber et al., 1992; O’Donoghue et al., 1997; Ballard et al., 2001; Berger and Gese, 2007; Levi and Wilmer, 2012). For example, the range of the coyote expanded after gray wolf reductions/extirpations in parts of the American West, Midwest, and Northeast, and after the near elimination of the red wolf (Canis rufus) in the southeast (Cier, 1975; Parker, 1995).

On the Kenai Peninsula of Alaska, wolves were extirpated by 1915, coyotes colonized the area by 1926, and the latter species
soon after achieved “unique abundance” prompting federal control (Thurber et al., 1992). Furthermore, coyotes were reduced in distribution and abundance after wolves recolonized the Kenai in the 1960s (Thurber et al., 1992). Likewise, Ballard et al. (2001) state, “In these systems [Alaska and British Columbia], wolves have effectively eliminated coyotes as serious predators of deer”.

In northern Minnesota, fewer coyotes were bountied in the major wolf range counties compared to an adjacent region to the south with lower wolf densities (Stenlund, 1955). In central Minnesota, Berg and Chesness (1978) found few coyotes where wolves were well established and that coyotes “generally avoided the wolf-occupied range”.

During 16 years of field work that started in 1979 in Wood Buffalo National Park, Alberta, numerous wolves were observed, but only 1 coyote was detected (Carbyn, 2003). Moreover, coyotes were reported to be common in this park during an earlier period of wolf control (Carbyn, 2003). Similarly, in Algonquin Park, Ontario, an area with high wolf densities, no coyotes were detected, but they were common in adjacent areas outside the park where there were no wolves (Pimlott and Joslin, 1968). With no opportunities for immigration, coyotes were driven to extinction on Isle Royale National Park in Lake Superior soon after the colonization of the island by wolves over the ice in 1948–1949 (Peterson, 1995).

In Yellowstone National Park coyotes declined by 39% after wolf restoration, and mean densities of coyotes were 33% lower at abundant wolf sites in Grand Teton National Park (Berger and Gese, 2007). Berger and Gese (2007) suggested that interference competition with wolves has resulted in localized population reductions, but not drastic overall suppression of coyote populations, in the Greater Yellowstone Ecosystem. Their findings may in fact be conservative, however, given that most of the coyotes reported on by Berger and Gese (2007) were <4 km of well-traveled roads, which are used by coyotes as refuges from wolves. Indeed, on the Kenai Peninsula, Thurber et al. (1992) found that wolves caused 67% of coyote deaths, and based on an index (coyote/wolf capture ratio), coyotes were 14 times more abundant near roads than away from them. It appears that coyotes use roaded areas as an antipredator defense (human shielding) against wolves because wolves avoid roads due to higher levels of human disturbance (Thurber et al., 1992).

Despite an extensive and decades-long control effort killing millions of coyotes, the coyote has thrived in the West (Bekoff and Gese, 2003). Indeed, after wolf extirpation, densities of coyotes varied temporally and spatially with control measures and other environmental factors (Knowlton and Gese, 1995). One of the most effective control measures involved the use of sodium monofluoroacetate (compound 1080) baiting; this approach was used in the late 1970s, 1980s, and early 1990s in the western states between 1948 and 1972 (Cain et al., 1972). By the 1970s, Knowlton (1972) estimated that coyote densities generally ranged from 0.2 to 0.4 km² over a large portion of the western United States. Using 0.3 coyotes per km² for the 11 western states comprising over 3 million square km results in roughly 1 million coyotes present now in the West. This density estimate is consistent with what field studies have found including 0.4–0.5 km² in Oregon (Dunbar and Giordano, 2002), 0.30 km² in Colorado (Gese et al., 1989), and 0.27 km² in Montana (Pyrah, 1984).

When coyotes are food subsidized near urban areas (Gehrt and Riley, 2010), significantly higher densities have been recorded, such as 2.4–3.0 km² in California (Fredriani et al., 2000). Along the Baja California coast, Coyote populations were 2.4–13.7 times denser than in adjacent inland areas that did not receive marine input as food subsidies (Rose and Polis, 1998). Conversely, with coyotes co-existing with wolves in the Yukon, coyote densities were much lower and ranged from 0.014 to 0.090 km², averaging approximately 0.038 km² (O’Donoghue et al., 1997), nearly an order of magnitude lower in density than estimated for the American West above. Lower productivity in the Yukon might account for part of these differences in coyote densities.

An alternative explanation for coyote expansion in the American West is forest harvesting. During the same period when wolves were being exterminated, humans were also logging forests and clearing land. Coyotes attain high densities in open areas, and much of their original distribution in North America was prairie and other open habitat (Parker, 1995). Accordingly, these landscape changes were conducive to coyote populations. Yet, wolves have been reported suppressing coyotes in areas both with forest harvesting (Stenlund, 1955; Berg and Chesness, 1978; Fuller and Keith, 1981; Thurber et al., 1992; Ballard et al., 2001; Levi and Wilmers, 2012) and in parks without forest harvesting (Peterson, 1995; Berger and Gese, 2007). Thus, habitat changes associated with deforestation are unlikely to have been the sole reason for the observed coyote expansion.

3. Ecological effects of coyotes

The influence of coyotes in suppressing red foxes and other smaller mesopredators has been shown to increase waterfowl, rodent and songbird abundance and diversity (Sovada et al., 1995; Crooks and Soule, 1999; Henke and Bryant, 1999). In suburban and urban areas, research has indicated that coyotes perform a vital ecosystem service by suppressing feral cat populations and possibly those of other small carnivores whose densities might otherwise be higher than normal because of human food subsidies (Crooks and Soule, 1999; Ritchie and Johnson, 2009; Gehrt and Riley, 2010). Yet, in the absence of wolves and while subsisting on alternative foods of wild and domestic ungulates, plants, or human food sources, coyotes can exert intense predation pressure on their typical prey (Fig. 2, Table 1). Indeed, the coyote has been described as a major predator of a number of vertebrate taxa that are on the U.S. Fish and Wildlife Service (USFW) threatened and endangered species list and state lists for species of concern including rodents, ungulates, carnivores, leopards, and birds (Table 1). These taxa include some preyed upon by coyotes for food (e.g. ground-nesting birds), and others that are not consumed – victims of interspecific killing (e.g. foxes, black-footed ferrets [Mustela nigripes]), the most extreme form of interference competition.

Table 1 provides evidence of proximate effects and not ultimate cause of threat for the listed species. We define proximate effect as a current cause of mortality for a species and ultimate cause as that which caused the species to originally decline. Of the two, ultimate causation is difficult to determine because species typically become rare before scientific investigation into their decline occurs. We note that the documentation of predation does not necessarily equate to predation impacts on the demography of prey. Therefore, the information in Table 1 does not imply that coyotes are the cause for endangerment of these declining species, and it is beyond the scope of this paper for us to speculate as to what degree coyotes contributed as a cause of their decline.

4. Where have all the rabbits gone?

Leporids (rabbits and hares), traditionally the primary prey of coyotes, have apparently declined precipitously in the West. For example, numbers of jackrabbits (Lepus spp.) and snowshoe hares (Lepus americanus) harvested in Colorado have dramatically declined in recent decades (Fig. 3). We hypothesize that, in some places, this decline is at least partially linked to (1) mesopredator release of coyotes after wolf extirpation and (2) additional coyote release after the coyote poison, compound 1080, was banned in 1972 (Cain et al., 1972). Interestingly, both the decline of leporids in Colorado and the coyote effects on all the other species
Consistent with this scenario are data from Minnesota and evidence that a coyote population increase in the absence of wolves may have caused a decline in white-tailed jackrabbits (*Lepus townsendii*) there (Levi and Wilmers, 2012). The white-tailed jackrabbit has also become rare since wolf extirpation in the Greater Yellowstone Area (Berger, 2008), is on species of concern lists in New Mexico, Oregon and Washington, and has recently been extirpated from western Kansas and parts of Nebraska (Armstrong et al., 2011). Meanwhile, the black-tailed jackrabbit (*Lepus californicus*) is currently on species of concern lists in Oregon, Washington, and Montana. Interestingly, black-tailed jackrabbit numbers increased following experimental coyote removal (Henke and Bryant, 1999).

In Arizona, cottontail (*Sylvilagus* spp.) harvests have fallen steeply over the past several decades from means of 360,000 between 1961 and 1989 to ~80,000 for the 1990–2009 period (t-test, p < 0.001) (Arizona Game and Fish Department, 2001, 2009). In addition, the number of cottontails harvested per hunter day in Arizona decreased from an average of 1.4 for the period of 1961–1989 to 0.8 for the period of 1990–2009 (t-test, p < 0.001). This decline in both cottontail harvest and hunter success was apparently due to a combination of a long-term decline in the cottontail population and a decline in the total number of hunter days, the latter of which dropped by 60% between the two time periods (Arizona Game and Fish Department, 2001, 2009).

The range of the pygmy rabbit (*Brachylagus idahoensis*) is believed to have shrunk substantially relative to its historical extent in the American West (Verts and Carraway, 1998, pp. 127–131). Recent research has linked continuing decline of the pygmy rabbit to heavy predation by coyotes, resulting in low survival in parts of Oregon where wolves are absent (Crawford et al., 2010). Finally, snowshoe hares also have likely decreased in the American West compared to historical times, and chronically low densities of snowshoe hares in this region may be at least partially the result of increased coyote predation after extirpation of the wolf (Buskirk et al., 2000). We note, however, that habitat fragmentation, fire suppression, and climate change are potential contributing factors. Coyotes are highly effective predators of hares (Wirsing et al., 2002). Consequently, an increased density of coyotes in the absence of wolves may be causing exploitative competition with Canada lynx (*Lynx canadensis*) via higher predation pressure on hares and potentially contributing to the threatened status of this felid in some situations (Buskirk et al., 2000). Notably, in support of this idea on the Kenai Peninsula of Alaska, Stapes (1995) found exploitation competition for hares between coyotes and lynx. Furthermore, snowshoe hare harvests decreased in wolf-free southern Quebec soon after coyote colonization there in the 1970s (see Fig. 4 in Etcheverry et al., 2005). Likewise, in the wolf-free Elk Island National Park in central Alberta, ungulates and coyotes attained high densities (0.87–1.05 coyotes/km²), while snowshoe hares apparently have remained at a relatively constant, low level without the population cycles that typify the region (Cairns, 1976; Keith and Windberg, 1978; Pruss, 2002).

We hypothesize that coyote predation, in combination with the effects of widespread livestock grazing causing reduced vegetative cover, may have contributed to reported leporid declines in the American West. This hypothesized cascade may not have played out in all areas and, instead, could have been context dependent due to interactions with other factors. Additional empirical evidence that directly links heavy coyote predation to leporid declines documented in Table 1 occurred after the 1972 ban of compound 1080, when coyote numbers likely increased in the West (Cain et al., 1972).
The importance of food subsidies to coyote population dynamics is currently limited, however, and should be a focus of future research. The purported effects of top predator removal on the abundance of leporids that we hypothesize for the American West are mirrored in the Strzelecki Desert, Australia. Here, the removal of dingoines (15–22 kg) has resulted in the irruption of red foxes (4–7 kg) and suppression of rabbits (Oryctolagus cuniculus). Where dingoines were common, foxes were rare and rabbits were abundant (Letnic et al., 2012). An analogous situation was discovered in Scandinavia involving a Eurasian lynx-red fox-hare (Lepus timidus) cascade (Elmhagen et al., 2010).

### 5. Interactions with other factors

Coyotes are known to be opportunistic scavengers and can exploit a wide variety of food sources. However, the extent to which they rely on these subsidies can vary depending on the availability and quality of alternative prey. For example, the removal of top predators such as wolves (Canis lupus) can lead to an increase in coyote abundance and a shift in their diet towards alternative prey (Ritchie et al., 2005). Researchers have documented that coyotes can compensate for the loss of traditional prey species by increasing their consumption of carrion, domestic livestock, and urban trash (Kamler et al., 2004).

#### Table 1: Coyote predation effect size on threatened and endangered species in the American West

<table>
<thead>
<tr>
<th>Killer species/status</th>
<th>Effect size</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-footed ferret (Mustela nigripes)</td>
<td>Of 137 released ferrets, coyotes caused the most losses; at least 63% of 59 deaths</td>
<td>Biggins et al. (2006)</td>
</tr>
<tr>
<td>Pygmy rabbit (Brachylagus idahoensis)</td>
<td>Annual survival of pygmy rabbits was notably low with coyotes the most common cause of mortality</td>
<td>Crawford et al. (2010)</td>
</tr>
<tr>
<td>San Joaquin kit fox (Vulpes macrotis mutica)</td>
<td>Coyote predation was the main cause of kit fox mortality</td>
<td>Cypher and Spencer (1998)</td>
</tr>
<tr>
<td>Columbian white-tailed deer (Odocoileus virginianus leucurus)</td>
<td>Coyotes took 23 of 40 radio-collared fawns during the summers of 1978, 1979, and 1980</td>
<td>USFW Service (1983)</td>
</tr>
<tr>
<td>Least tern (Sterna antillarum)</td>
<td>Nearly 100% of nesting attempts failed due to predation by coyotes</td>
<td>Atwood and Masey (1988)</td>
</tr>
<tr>
<td>Whooping crane (Grus americana)</td>
<td>Between 1975 and 1984, 14 eggs and 23–58 flightless young whoopers were lost to predators, primarily coyotes</td>
<td>Drewien et al. (1985)</td>
</tr>
<tr>
<td>Olympic marmot (Marmota olympus)</td>
<td>All mortality appeared to be due to predation by coyotes and it is likely that coyotes are the primary driver of Olympic marmot declines</td>
<td>Griffin (2007)</td>
</tr>
<tr>
<td>Swift fox (Vulpes velox)</td>
<td>Foxes had low survival and predation by coyotes was the major cause of death</td>
<td>Kamler et al. (2003)</td>
</tr>
<tr>
<td>Sandhill crane (Grus canadensis tabida)</td>
<td>Coyote predation was primarily responsible for low fledging success</td>
<td>Littlefield (1995)</td>
</tr>
<tr>
<td>Snowshoe hare (Lepus americanus)</td>
<td>The coyote was the number one predator of snowshoe hares</td>
<td>Wirsing et al. (2002)</td>
</tr>
<tr>
<td>Long-billed curlew (Numenius americanus)</td>
<td>Predation, predominantly by large mammalian predators such as coyotes, was the greatest cause of nest failure in long-billed curlews</td>
<td>Hartman and Orling (2009)</td>
</tr>
<tr>
<td>Yellow-bellied marmot (Marmota flaviventris)</td>
<td>Coyotes were the most important predators on yellow-bellied marmots. Of the 97 marmots that died during the study, 47% were confirmed as caused by coyotes</td>
<td>Van Vuren (2001)</td>
</tr>
</tbody>
</table>

The purported effects of top predator removal on the abundance of leporids that we hypothesize for the American West are mirrored in the Strzelecki Desert, Australia. Here, the removal of dingoines (15–22 kg) has resulted in the irruption of red foxes (4–7 kg) and suppression of rabbits (Oryctolagus cuniculus). Where dingoines were common, foxes were rare and rabbits were abundant (Letnic et al., 2012). An analogous situation was discovered in Scandinavia involving a Eurasian lynx-red fox-hare (Lepus timidus) cascade (Elmhagen et al., 2010).
been greatly increasing in western states in recent decades. Between 1984 and 2009, the elk population in the 11 western states grew from an estimated 710,000 to 1,010,000, a 42% increase (Rocky Mountain Elk Foundation, www.rmef.org). Thus, the ecological implications of a large carrion subsidy for coyotes are not trivial, and with more carrion from either domestic or wild ungulates, coyote pressure on native species in areas lacking wolves may be high.

![Fig. 3. Scatter diagrams showing a history of declining snowshoe hare (Lepus americanus) harvest (upper left) and jackrabbit (Lepus townsendii, Lepus californicus) harvest (upper right) for the state of Colorado. Hunter success (bottom set of graphs) for both snowshoe hare and jackrabbit hunters has also decreased over time. Note how hare harvest consistently declined after the highly effective coyote poison, compound 1080, was banned in 1972. Used together, the data on harvest trend and hunter success serve as an index of population trend, suggesting a long-term decline in snowshoe hares and jackrabbits. We hypothesize that the apparent decrease in snowshoe hare and jackrabbits is at least partially due to coyote predation in the absence of top-down forcing by wolves. Because other factors can contribute to harvest trend and hunter success, we suggest that the data presented here should be used with caution. For example, the number of hunters per year has significantly declined over time. Source: Colorado Division of Wildlife, unpublished data.]

![Fig. 4. Dot maps showing cattle (left) and sheep (right) live densities and estimated amounts of livestock carrion in the American West as of 2007. For cattle, one dot represents approximately 10,000 live individuals and 308 carcasses per year. For sheep, each dot represents approximately 1000 live individuals and 31 carcasses per year. Based on the density and spatial arrangement of the dots, both livestock and livestock carrion are ubiquitous throughout most of the American West. Both of these sources provide a large and spatially distributed food subsidy to coyotes throughout the West. Carrion carcasses were estimated assuming a 4% rate of annual livestock mortality with 77% of carcasses not being rendered. Source: US Department of Agriculture, National Agricultural Statistics Service and Informa Economics Inc. (2011).]
Domestic and wild ungulates could also affect herbivorous coyote prey (e.g., leporids, rodents, ungulates) by decreasing cover and forage available to them. For example, high domestic and/or wild ungulate densities may have contributed to the apparent decrease in leporids shown in Fig. 3. The loss of cover has been linked to increases in avian and mammalian predation on small mammals and ground nesting birds, triggering population declines (Flowerdew and Ellwood, 2001). In Africa, likely because of reduced forage and/or cover availability, the density of small mammals was significantly higher where ungulates were absent compared to where these large herbivores were present (Keessing, 2000). In livestock-affected systems where coyotes are present, researchers have observed significantly greater success ($p < 0.001$) of coyotes capturing prey in short grass ($<10$ cm high) cropped by cattle than in tall grass ($10–100$ cm high) (Bekoff and Wells, 1986).

6. Suggested research agenda

The evidence we have presented thus far suggests a link between wolf decline and an expansion in the ecological influence of coyotes. Here, we propose several lines of ecological research that should help to more rigorously test this mesopredator release hypothesis. In general, the ecological consequences of species’ loss and repatriation are difficult to determine without some form of perturbation. Accordingly, manipulative experiments represent potentially powerful tools with which to explore the influence of wolf extirpation or recovery on coyote effects. Such experiments could compare, for example, the consequences of coyote removals in areas where wolves are present vs. where wolves have been extirpated.

Natural experiments that take advantage of spatial and temporal variation in wolf abundance are also likely to yield important insights into the degree to which the presence of this top predator depresses coyote effects. For example, with the reintroduction of wolves in the northern Rocky Mountains and the recolonization of wolves in Washington and Oregon (and potentially Utah and Colorado), we see opportunities for research to take advantage of these ongoing natural experiments.

Research could examine the extent to which wolf re-establishment (1) modifies interference and exploitative competition between coyotes and smaller mesopredators [e.g., foxes, lynx, bobcats (Lynx rufus)], and (2) triggers indirect effects on the abundance, survival and behavior of species preyed on by coyotes. In some situations, the return of wolves could coincide with increases in populations of smaller mesopredators formerly suppressed by coyotes, and increases in the abundance of coyote prey. We caution, however, that the strength of mesopredator cascades triggered by wolf recolonization may be context dependent. For example, cascade strength may hinge upon whether or not wolves can achieve “ecologically effective” densities and specifically on amounts of unfragmented wolf habitat, levels of wolf harvest and removals, as well as refugia (roads and built-up areas) and food subsidies available to coyotes. This research could be conducted temporally (before vs. after wolves) or spatially (areas with and without wolves). Some of this research has already been completed for pronghorn (Antilocapra americana) (Berger et al., 2008) and small mammals (Miller et al., 2012) with results consistent with our hypothesis.

We offer four additional types of ecological studies that should provide context for and strengthen the inferences drawn from the more direct assessments of the wolf-coyote relationship listed above. First, historical records such as time series that index predation in avian and mammalian species would provide context for and strengthen the inferences drawn from the more direct assessments of the wolf-coyote relationship (e.g., Levi and Wilmers, 2012). Second, in anticipation of continued changes to wolf abundance across the American West, there is need for systematic monitoring of the abundance of coyotes and their prey, both to establish reliable baselines and identify areas where the ecological impacts of this mesopredator are likely to be acute. Third, analyses of survival and cause-specific mortality should be applied to prey species and competitors that are allegedly suffering as a result of hyper-abundant coyotes to provide a better understanding of whether coyotes are the ultimate and/or proximate cause of declining prey over space and time. Fourth, it would be beneficial to establish studies to enumerate the abundance of mammalian mesopredators, leporids, etc. similar to or in conjunction with systematic annual bird surveys across the country using the citizen science approach. Systematic and long-term data on these mammalian taxa would provide much needed insights on predator/prey dynamics at a large scale.

Mountain lions (Puma concolor) are also a predator of coyotes. Several dietary studies of mountain lions throughout the West have found that they will regularly kill and eat coyotes (Logan and Sweanor, 2001). However, no study has evaluated whether mountain lions can suppress coyote populations. If so, then maintaining or increasing mountain lion densities could also reduce coyote populations or at least limit their ecological impacts to habitats not occupied by mountain lions. Additional research is also needed on the effects of multiple predators on coyotes and coyote prey. Are the effects of wolves and mountain lions on coyotes additive, or is there sufficient interference competition between these top carnivores that their respective impacts on coyotes are merely compensatory or dispensatory? Answering these questions will be crucial to providing a more complete understanding of how carnivore competition could be used as a management tool to limit mesopredators, if such limitation is the goal.

Applied research is also needed to help advance coyote management in rural areas without wolves. While humans expend extraordinary resources to control coyote populations, these canids have proved incredibly adaptable (Bekoff and Wells, 1986). In spite of more than a century of persecution, coyotes have significantly increased in numbers and expanded their range. Although short-term endeavors can be effective, long-term efforts to suppress coyote populations in the American West have generally failed because they have not effectively controlled the breeding potential of coyote populations or stopped the emigration of coyotes from other areas (Knovolton et al., 1999; but see Nunley, 2004 for Edwards plateau in Texas and Cain et al., 1972 for compound 1080).

Indeed, control of coyote populations can actually release surviving individuals from density dependent processes such as intra-specific competition and lead to a compensatory increase in the number of breeding pairs, and an increase in litter sizes (Goodrich and Buskirk, 1995; Crabtree and Sheldon, 1999). For example, near the Idaho/Nevada border, Davidson (1980) compared coyote densities in a heavily exploited area to a lightly exploited area nearby and found no significant differences in their densities. Annual kill rates of coyotes in the heavily exploited area were 0.39 and 0.54, as compared to 0.25 and 0.12 for the lightly exploited area, for adults and juveniles respectively (Davidson, 1980). Additional empirical evidence, namely that killing coyotes may not result in significantly lower coyote densities, comes from a coyote population study in south-central Washington. Coyotes in this Washington system were unexploited (not harvested), without food subsidies, and at relatively moderate densities based on scent-post-survey indices ($\text{index} = 63$) when compared to other areas of Washington ($\text{index} = 109.5$; $n = 11$ survey lines) and the 11 western states ($\text{index} = 108.3$; $n = 22$ survey lines) where coyotes were typically both food subsidized and exploited (Roughton, 1976; Springer, 1982). In a 5-year demographic study in this same area, Crabtree (1989) estimated an average coyote density of $0.38–0.41$ km$^{-2}$, which is similar to exploited coyote population densities in the American West (as we describe in Section 2).
We suggest research on the combined effects of (1) not killing coyotes and (2) removing livestock carrion subsidies. Carrion could be sent to processors for rendering, thereby removing a critical food resource for coyotes (Sperry, 1934). These two treatments could be studied together for cumulative effects as long as they are also studied separately in order to avoid confounding results due to changing two variables at once. We hypothesize that where coyote populations are density dependent and livestock carrion is a limiting resource, coyote densities in areas without livestock carrion subsidies and without coyote killing will not be significantly higher than in areas with coyote killing and with these food subsidies. In systems without wolves, coyote social behavior (Crabtree and Sheldon, 1999) and food abundance (Knowlton and Gese, 1995) appear to set the upper limit on coyote densities. Also, unexploited coyote populations are functionally and structurally distinct from exploited ones, having very low reproductive rates and relatively low recruitment into the adult population (Knowlton and Gese, 1995).

The loss of large-bodied predators from ecological communities, or trophic downgrading, has been associated with marked changes to myriad ecosystems (Estes et al., 2011). Accordingly, we also advocate for studies on the ecological effects of potential red fox irruptions due to coyote control in areas without wolves (i.e. areas where the red fox is the largest canid predator) because in the absence of larger predators, red foxes have been shown to have increased and substantial effects on their prey (Elmhagen et al., 2010; Letnic et al., 2012). We hypothesize that removal of all or most coyotes from wolf-free areas may shift predatory impacts to waterfowl and smaller prey [i.e. prey of foxes, (see Sovada et al., 1995; Levi and Wilmer, 2012)].

7. Conclusions

Could the loss of an apex predator, the wolf, be contributing to the decline and the potential extinction of other vertebrate species in parts of the American West? If so, is more research warranted? Our answer to both questions is “yes” based on the evidence presented above. Although generally convincing, some of the evidence we supply is hypothetical or preliminary in nature and we caution that our ideas need more testing. Indeed, we envisage our hypotheses as a catalyst for further examination of wolf-coyote-community dynamics. Notably, two such examinations in Grand Teton National Park have already shown that wolves appear to have positively affected populations of pronghorn and small mammals as mediated by coyotes (Berger et al., 2008; Miller et al., 2012). However, such wolf-coyote cascades may not occur outside of large reserves where wolves do not achieve ecologically effective densities because of a lack of habitat or they are removed due to conflicts with livestock or are hunted (Berger and Gese, 2007). These factors may also interact with any food subsidies and refugia available to coyotes to additionally dampen trophic cascades.

Our mesopredator release hypothesis is consistent with theory and observations on other continents suggesting that because apex predators often exert strong influences on smaller predators, the loss of an apex predator can trigger a cascade of secondary population changes and extinctions with far-reaching consequences for ecosystem structure and function (Holt and Lawton, 1994; Borrvall and Ebenman, 2006; Ritchie and Johnson, 2009; Letnic et al., 2012). Even if the degradation of habitat or other factors were the original primary (ultimately) causes for declines of some prey species, predation by hyper-abundant mesopredators (e.g. coyotes) could contribute to continued declines to extinction.

In terms of restoration, we suggest a research agenda focused on the ecosystem perturbations that caused the rarity or hyper-abundance of the vertebrates, thus working on the underlying causes (e.g. lost trophic interactions, food subsidies) rather than just the symptoms of the problem. Although, in cases of extreme habitat loss or fragmentation, this work will be rather challenging. Moreover, we suggest that, in areas with extensive public lands, restoring wolves to ecologically effective densities and/or reducing food subsidies to coyotes could be effective alternatives to lethal control of these mesopredators.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.12.033.

References


