SURVIVAL AND REPRODUCTION OF CALIFORNIA CONDORS RELEASED IN ARIZONA

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ABSTRACT

A drastic decline in California Condors resulted in their complete removal from the wild in the 1980s and subsequent establishment of captive populations to propagate offspring for reintroductions. In 1996 The Peregrine Fund began releasing captive-produced condors in the Grand Canyon region of northern Arizona. By July 2005, 50 juvenile and 27 subadult condors had been released, and the free-flying population presently includes 14 adults, which have laid 11 eggs, fledged 3 young, and currently have 2 nestlings. Of the 77 released birds, 26 (34%) have died. Eight condors perished in their first 90 days following release and 14 in their first year (annual survival of 80%). Survival increased to 90% in the second through fourth years, and 98% from the fifth year onward. Lead poisoning from ingested shotgun pellets and bullet fragments was the greatest cause of fatalities for birds after their first 90 days free-flying, with six birds known and two suspected to have died of lead toxicity. Many surviving condors were also treated with chelation therapy at least once to reduce high blood lead levels. Under a program of intensive management, survival rates have been in the range expected for wild condors and pairs are breeding successfully. Self-sustainability, however, will require that lead in the condors' food be greatly reduced or eliminated.

The ranges of the two largest extant cathartids, the Andean Condor (*Vultur gryphus*) and slightly smaller California Condor (*Gymnogyps californianus*), have retracted greatly in historical times, and the California Condor is critically endangered, surviving in the wild almost exclusively as released birds with limited distribution. Few California Condors remained by the time Koford (1953) undertook the first concerted effort to study them, and little is known conclusively regarding their natural mortality, whether they ever occurred at high densities, or what factors limited their numbers in the past. It is certain, however, that human-related factors, including shooting, poisoning, and encroachment into breeding and foraging areas were associated with a precipitous population decline in the last two centuries (Koford 1953, Wilbur 1973, Wilbur 1978, Kiff 2000, Snyder and Snyder 2000, Fry 2003).

In the 1980s all remaining condors were brought into captivity, and captive breeding populations were established, with the ultimate goal of restoring wild populations (see Kiff 2000, Snyder and Snyder 2000). Restoration began in 1992, when two condors were released at the Sespe Condor Sanctuary in southern California. Since then the magnitude of the release program has grown, and more than 100 condors now fly freely in southern and central California, northern Arizona and southern Utah, and Baja California, Mexico.

Condors seem to have always occurred in landscapes that included rugged or otherwise inaccessible terrain for nesting, open areas with the potential for extended soaring flight, and an adequate supply of medium and large mammalian carcasses. In prehistoric times condors ranged across North America, and bred in Arizona along the Colorado River, in what is now Grand Canyon National Park (Miller 1960, Emslie 1987, Collins et al. 2000). Habitat there appears suitable for condor recovery because it still contains extensive rugged terrain with abundant potential nesting cliffs, open areas, strong updrafts, and relatively limited human disturbance, as well as an abundance of both domestic and wild ungulates (Rea 1981). Since 1996, condors have been released along escarpments 100 to 150 km north of the Park as a "nonessential experimental population" under provisions of Section 10(j) of the Endangered Species Act. To date 77 young condors have been released there and 26 of them have died. Now, as birds from the earliest-released cohorts have attained breeding age and are breeding, and as a shift toward reliance on reproduction in the wild for continued population growth and eventual stability can be contemplated, a review of mortality factors for the released birds is timely. Meretsky et al. (2000) summarized early unpublished reports on mortality of released condors in both Arizona and California, and here we update and examine the factors that have led to condor deaths in Arizona and Utah specifically.

METHODS

California Condors were released in groups of two to eight individuals (three birds were also released singly) at two sites in northern Arizona: a primary site at Vermilion Cliffs (Coconino Co.; release years: 1996, 1997, 2000 onward) and an alternate one at Hurricane Cliffs (Mohave Co., release years: 1998, 1999; see Harting et al. [1995], Johnson and Garrison [1996] for site description and release protocol). Birds to be released were always maintained together in a holding pen at the release site, generally for 4 to 6 weeks prior to release. Free-flying condors had access to the holding pen (after the first release) and they routinely interacted with the pre-release birds during this time, whereas interactions with humans were minimized. Nearly half (49%) of all birds were released in November or December, and 65% were <1 year old when released, having hatched the previous March, April, or May (Table 1). Four captive-reared adult condors were released experimentally in December 2000, but two quickly perished and the remaining two were consequently retrapped; owing to the unique nature and short duration of those releases, data from those birds were not included in this analysis (see Results for further details). The earliest releases typically consisted of cohorts of six or more juveniles released together, although this protocol has recently been replaced by successive releases of birds in smaller cohorts. Condors released in Arizona were captive-reared at three facilities: 12 birds from the San Diego Wild Animal Park, 12 from the Los Angeles Zoo, and 46 from The Peregrine Fund's World Center for Birds of Prey in Boise, Idaho. Three wild-reared young have also fledged in Arizona (Results); data from those condors, one of which died, were not included in this analysis.

All birds were released with a redundant system of dual radio transmitters, usually consisting of paired patagial transmitters, although for a few the second transmitter was tail-mounted (Wallace et al. 1980, Meretsky and Snyder 1992). At present, all transmitters are equipped with a fatality sensor, but this was not the case for birds from the earliest releases, for which death was initially inferred from lack of variation in signal strength or direction. More recently some condors have also carried GPS satellite transmitters. All birds had large numbered patagial tags for visual identification. Using radio telemetry and visual confirmation of individual identity, condors have been monitored continually since the initial release in 1996. Whenever possible, birds have been located daily, and consequently field data confirmed to within a day or so the date of most deaths. For two birds that disappeared and were presumed to have perished, however, the last day of radio contact was used as the day of death, although those birds may have lived for some time thereafter.

Carcasses were removed and chilled as quickly as field conditions permitted, and then shipped to the San Diego Zoo, San Diego, California, where necropsies were performed. Two exceptions occurred in which law enforcement agencies were involved and took possession of the carcasses. Diagnosis of lead poisoning was based on toxicological analyses routinely performed for each fatality at the San Diego Zoo and by the presence of lead bullet fragments or shotgun pellets in some poisoned birds (determined by radiograph and/or necropsy). One condor whose carcass was unrecoverable but whose death coincided with a widespread lead-poisoning event (Results) was assumed to have succumbed to lead toxicity. Fatalities ascribed to Golden Eagles (*Aquila chrysaetos*), whether resulting from aggressive interactions or predation, were characterized by partially plucked carcasses, puncture wounds about the head consistent with large talons, and field observations of eagles in the vicinity. Deaths attributed to coyote (*Canis latrans*) predation were characterized by partially consumed carcasses, chewed feathers, fresh coyote tracks and scat in the immediate area; an indication of struggle distinguished predation from scavenging.

Because the daily fates of all members of the population were almost always known, survival of released birds could be determined precisely using days of exposure, and censoring was unnecessary. For each bird, the day of first release was considered exposure day 1, and each subsequent day during which the bird was free-flying for any part of the day was considered an exposure day. All birds were periodically captured and re-released owing to concerns about transmitters, health, behavior, or to test for lead exposure, and although days of exposure were cumulative in regard to the time spent free-flying following initial release, complete days during which an individual was in captivity were not counted as exposure. More than half of the birds (64%) were captive for less than 100 days in total following their release, but 28 individuals were held for longer than 100 days, and seven of those were held for 1 to 3 years and are thus somewhat older than their days free-flying suggest.

To evaluate survivorship, we partitioned exposure into five stages based on our observations of apparent differences in survival rates. The stages were: initial release, being the first 90 exposure days following release; remainder of the first year (91 to 365 exposure days post-release); second year (366 to 730 exposure days); third through fourth years (731 to 1460 exposure days); and the fifth year onward (1461+ exposure days). We determined daily, stage, and annual survival based on Trent and Rongstad (1974): daily survival rate (*S*) was calculated as the total number of exposure days within any stage minus the number of days on which a death occurred, divided by the total number of exposure days; survival throughout specific stages was S^n, where *n* is the number of calendar days in each particular stage.

To gain an indication of what survival in the released population might have been without intensive management and chelation treatments to reduce acute blood lead levels (see Parish et al., this symposium, for methods), we also recalculated survival under two assumptions: 1) all birds with blood levels of lead >100 µg/dl died on the date of detection, and 2) only those with lead levels >250 µg/dl died. For each situation, we used a standard growth rate calculation developed by Hunt (2002) to determine lambda (λ) values, which depict the direction and strength of population trajectories, based on our calculated "juvenile" (first year following release), "subadult" (second through fourth years free-flying), and "adult" (fifth year onward) survival and hypothetical reproductive parameters determined by Meretsky et al. (2000).

For birds that bred, the date at which egg-laying occurred was determined by obvious changes in behavior of the adult birds, including periodic incubation exchanges at nest sites. Additionally, behavioral changes that characterize hatch, including the sudden onset of daily nest exchanges by the adults, were used to determine laying date, assuming a 56 to 58 day incubation. Nest sites with young were monitored carefully as the date of fledging approached, and the date and time of fledging were determined by direct observation. Where possible, nest sites were entered for close examination after the breeding effort ended.

Unless otherwise noted, all statistics are in the form mean ± SD units (*n*; range). The levels of lead in condors are frequently expressed in µg/dl when measured in the blood and ppm when measured in the liver, and we follow those conventions here; the two measurements are easily converted since 1 ppm equals 100 µg/dl. Data for comparisons in survival between groups (e.g., survival of males vs. females) included only the individuals and cohorts released before July 2004 (65 birds in total), as the more recently-released birds had not yet spent a full year free-flying (also excluded was the single bird permanently removed from the free-flying population; that bird was removed <1 year after its release). We used multiple regression to evaluate the incidence of deaths in relation to population size and the time since the onset of the release program, and X^2 tests to examine the possible role of sex, rearing method, and age at release on mortality.

RESULTS

Overview.—As of 30 June 2005, 81 condors in total (45 males and 36 females) have been released in northern Arizona: 65 at the Vermilion Cliffs site and 16 at the Hurricane Cliffs site (Table 1). All but four were released as juveniles (50) or subadults (27); the median age at release for those condors was 293 days and the average age was 394 ± 205 days (77; 172 to 965). Of the 77 young birds, 26 died, one was removed from the free-flying population, and 50 remained in the wild. The four older birds that were released (two breeding pairs 8 to 9 years old) were an experimental effort to include breeders with other released birds. Coyotes killed two shortly after release (19 and 22 days), probably a result of unsafe roosting behavior, and the other two were recaptured and permanently removed from the free-flying population. Since the first release in 1996, the number of birds in the wild generally increased over time, to a temporary maximum of 52 in March 2005 (Fig. 1). Sixty-five percent of the released birds have been free-flying for 500 days or longer (Fig. 2), and individuals have averaged 975 ± 901 days (77 condors; 4 to 3000) in the wild.

Fatalities occurred sporadically throughout the release program, with the exception of four deaths in June 2000, and the number of fatalities per 6-month interval was independent of both average population size and time since the onset of the release program ($F_{1,15}$ = 0.1, P = 0.79; $F_{1,15}$ = 0.0, P = 0.98, respectively). Neither sex nor method of rearing (parent- vs. puppet-reared) was associated with the likelihood of death: 57% of released condors (37 of 65) were male, and 52% of birds that died (13 of 25) were male as well (X^2_1 = 0.4, P = 0.53); similarly, 66% of released condors (43 of 65) were puppet-reared, and 64% of the birds that died (16 of 25) were puppet-reared (X^2_1 = 0.1, P = 0.77). In contrast, individuals that were >1 year of age when released were much more likely to survive their first year free-flying than individuals that were released at <1 year of age: 1 of 21 older-released birds (5%) perished in their first year free-flying, compared to 12 of 44 young-released birds (27%; X^2_1 = 4.5, P = 0.034).

We documented 75,053 exposure days in total, including 22,239 (77 birds) in the first year and 16,640 (20 birds) from the fifth year onward (Table 2). Annual survival through the first year, 79.6%, was heavily influenced by relatively high mortality of recently released birds; of the 14 that perished during their first year, eight died within the first three months. The likelihood of survival increased to 89.3% in the second year and was similar (89.6%) in the third and fourth years combined (89.5% for the second through fourth years). Survival from the fifth year onward was 97.8%. Deaths were rare following four years in the wild, and by the end of

June 2005 only one bird that had been free-flying for longer than four years had perished for any reason.

Using our observed rates of survival for a hypothetical population with a stable age distribution, and a conservative reproductive rate of 0.25 for breeding age females (50% breed per year with 50% breeding success), the population would be expected to grow at the rate of 2.6% per year (i.e., $\lambda = 1.026$). If the reproductive rate increased to 0.33 per year, annual growth rate would rise to 3.7%. If, on the other hand, there were no management for lead exposure, and one assumes that all condors with acute blood levels of lead of >250 µg/dl died, subadult and adult survival would have been 81.7% and 90.9% respectively, and the population would decline at 2.8% per year. On the more stringent assumption that lead levels in blood >100 µg/dl were always lethal, subadult and adult survival would have been 72.4% and 76.9% respectively, and the population would decline at the greater rate of 18.6% per year.

Sources of mortality.—Fourteen condors perished in the first year following their release, mainly from predation or other inexperience-related factors, although several died from what were probably unique situations (Table 3). Of those 14 deaths, three condors disappeared and are presumed to have perished, coyotes killed two and possibly three birds, two were killed by Golden Eagles, two succumbed to starvation-like poor body condition resulting from an unknown cause or causes, one died as a result of a collision with a power line, one was shot, one died of lead toxicity, and one died of septicemia that developed from airsacculitis following aspiration. In each case where coyotes appeared to kill a condor, the bird had roosted in a location that was accessible to coyotes. It is unknown whether poor body condition or other factors increased the susceptibility to predation of birds whose deaths were attributed to coyotes, but one bird appeared healthy and vigorous when captured by field personnel eight days prior to its death, and another was killed after only four days in the wild. Necropsy could not determine or explain what led to the poor body condition apparent in the birds that died with starvation-like symptoms, especially considering that each had been in the wild for only a few weeks and had been seen feeding at the release site during that time (lead poisoning was not implicated in either death).

Twelve condors that had been free-flying for >1 year died, and the single greatest contributor to mortality was lead ingestion, to which seven of those birds (58%) were known (5) or suspected (2) to have succumbed. Two of the other five condors that died were shot, one by a hiker who killed the condor with a small caliber handgun in Grand Canyon National Park, and another shot with an arrow in the Kaibab National Forest. One condor was killed by a Golden Eagle, one disappeared and is presumed to have perished, and the cause of death for one bird could not be determined.

At least four lead toxicity deaths and most of the chelations were associated with episodes involving multiple poisonings, but two or three birds that died of lead poisoning did so in what appeared to be isolated events. The source of lead was identified in four deaths; three involved shotgun pellets and the fourth followed the ingestion of bullet fragments. The first poisoning death occurred in February 2000, following three years during which lead levels had remained low, and the first multiple poisoning occurred in June of that year.

Within a 4-week period beginning in June 2000, at least two and as many as four birds perished from lead toxicity, and nine others with high lead levels received chelation therapy. The first of those fatalities occurred early in June, but the carcass had deteriorated by the time of recovery and necropsy was inconclusive. The second death occurred on 12 June, and followed the ingestion of at least 17 lead shotgun pellets of two or more different sizes. Another lead-poisoned bird died 16 June, but may have been poisoned in an unrelated event (see below). The cause of the fourth fatality on 25 June was uncertain because the carcass was unrecoverable, but the timing of this bird's death suggests lead poisoning. Evidence indicates that all or nearly all of the lethal and non-lethal poisonings were associated with shotgun pellets, owing to both the temporal proximity of the poisonings and the fact that shot of three different sizes was found in five of the poisoned birds. It is unlikely that groups of condors would encounter and consume enough carcasses of the smaller animals usually hunted with shotguns to explain the number of poisoned birds, and consequently we suspect that the exposure occurred at a single large carcass or many closely spaced smaller ones, loaded with shot of varying sizes. In contrast to the other poisoned birds, the condor that died 16 June was severely emaciated when captured on the day prior to its death, and lead and copper levels in the liver after death (17 ppm and 181 ppm, respectively) strongly suggest that the bird succumbed to lead poisoning. The high copper level, the bird's emaciated condition, and a lack of lead shot visible on radiographs suggest that it may have been poisoned in an unrelated incident.

Large-scale lead exposure episodes also occurred during and just after the local November hunting seasons in 2002 and 2004 (Parish et al., this symposium). During this time many deer (*Odocoileus* sp.) are killed by hunters on the Kaibab Plateau, a dominant feature in the condor's foraging range during fall (Hunt et al., this symposium). No bullet fragments or pellets appeared on radiographs of any poisoned birds during those episodes, and no birds died, but 15 received chelation therapy in response to lead levels that ranged from ca. 50 to 900 µg/dl in the blood.

The episodic pattern of wide-scale poisonings, as well as the seemingly sudden onset of lead exposures within the population, was highlighted by the fact that no bird perished or required chelation in the first 18,000 exposure days of the release program, and only a single chelation treatment was necessary in over 15,500 exposure days between August 2000 and August 2002. In the years following the first poisoning episode, however, blood lead levels determined during semi-annual and opportunistic testing have frequently been above the expected background levels of ca. 20 µg/dl. Moreover, although only three widespread poisonings have been documented, nearly all the older birds in the current population have been exposed to high lead levels and most have received chelation therapy at least once since 1999 (Parish et al., this symposium).

Reproduction.—The first breeding attempt in the new population occurred in 2001, when a 6-year-old male courted two 6-year-old females, one of which laid an egg that was broken shortly afterward. In the years since, at least nine adults (five females, four males) attempted to breed (including courtship, nest selection, and egg laying), and five of the six 10-year-olds, the oldest cohort in the population, produced one or more fledglings (the sixth is currently attending to a nestling). The average age at which the nine birds first attempted to breed (the first time an egg was laid by a pair) was 7.6 ± 1.3 years, but two birds attempted to breed at six years of age and another did not breed until its tenth year.

The population at the end of June 2005 included 14 birds seven years of age or older, five of which had not bred, but four of those five were males and thus three lacked suitable mates (Fig. 4). Breeding pairs nested at seven different sites: four in Grand Canyon National Park, two in Vermilion Cliffs National Monument, and one in the Kaibab National Forest. One site was used three times, two sites twice, and four sites were used only once. Early pair formation was sometimes equivocal: three or more birds were associated with two nesting attempts, and one male bred with at least two females in successive years; but two established pairs did not switch mates in three and possibly four breeding attempts made by each pair.

Overall, 11 eggs were laid, at least five of which hatched, and three birds fledged successfully, with an additional two nestlings currently. Breeding success for nesting attempts through 2004 was 38%, and will be 46% if the current nestlings fledge. Success has generally improved over time, however, since pairs typically failed in their first breeding attempts; success in 2001 - 2003 was 17% (1 of 6 nests), but will be 40% to 80% (2 to 4 of 5 nests) for 2004 -2005 depending on the outcome of the 2005 breeding season. The dates at which eggs were laid varied widely, the earliest being 21-22 February and the latest 7-10 April, but at least six and as many as eight eggs were laid in March. All eggs that hatched did so between 3-5 May and 4-5 June. The earliest bird to fledge did so on 5 November (184 186 days of age); the other two fledged on 23 November (195 196 days of age) and 25 November (186 187 days of age).

DISCUSSION

Impact of natural predators.—The natural predation rate on wild condors is unknown, but as for most vultures it was probably always very low, especially for adults (see, for example, Mundy et al. 1992). Few predators have been identified that prey on free-flying condors, and although harassment and/or predation by Golden Eagles and Common Ravens (*Corvus corax*) may impact egg and nestling survival, condor mortality has been mostly attributed to human-induced causes (Koford 1953, Snyder and Snyder 2000). Our data support the notion that subadult and adult condors are rarely killed by predators other than humans, since only a single fatality was attributed to predation in >52,000 exposure days for birds that have been in the wild past their first year, and moreover that death was of a 2-year-old.

The same was not true for newly-released birds, however, as predation by coyotes or Golden Eagles accounted for the deaths of five or more birds in their first year free-flying. Coyotes specifically appeared responsible for at least five of the eight predator-caused deaths in total (including the two adults released in 2000 and the 2-year-old above), a fact that may foreshadow coyote predation as a significant contributor to mortality of young or inexperienced condors that do not roost in appropriate locations. Black-backed jackals (*Canis mesomelas*), which compete for food with vultures, are known to kill juvenile African White-backed Vultures (*Gyps africanus*), and red foxes (*Vulpes vulpes*) sometimes kill recently fledged Egyptian Vultures (*Neophron percnopterus*; Mundy et al. 1992). There is, however, no historical evidence to indicate that coyotes were a cause of condor fatalities in the past, but young condors then presumably benefited by observing the behavior of adult birds, an opportunity that has been lacking until recently in the release program.

Human causes of condor deaths.—In modern times, condors and vultures must contend with hazards for which they are perhaps ill-equipped through their evolution (Mendelssohn and Leshem 1983). Collision with power transmission lines and electrocution, for example, have emerged as global threats to vulture and condor populations (e.g., Mundy et al. 1992, Sarrazin et al. 1994, van Rooyen 2000). In California, seven or eight condors have perished as a result of power line collisions since 1992. Only one condor died in a similar collision in Arizona; the lower frequency is probably related to the scarcity of power lines in the vicinity of the release sites (Harting et al. 1995), but releases in Arizona also followed the onset of aversion training to utility poles in 1995. Shooting was also a prominent source of mortality for condors in the past (Snyder and Snyder 2000), and the fact that at least three have been shot in Arizona reflects the continuation of this unfortunate human habit (although one or two of those killings possibly resulted from misidentification by turkey hunters).

Factors influencing survival of newly-released condors.—The success of any species introduction is dependent in part on survival of the young animals that are released. In Arizona, the increased vulnerability of newly-released condors explained the lack of correlation between the overall number of fatalities in the population and population size, since comparable numbers of young condors were released annually regardless of the number of free-flying birds. In assessing the loss of young birds, and especially the deaths associated with inexperience-related factors, it is constructive to consider differences in survival between birds reared and released using different methods.

Puppet-rearing is an efficient technique in the captive breeding of many rare birds slated for future release, because excess young can be produced in the absence of adults to rear them (Cade and Fyfe 1978, Wallace 1994). The technique could be counter-productive, however, if puppet-reared birds died at a substantially higher rate than parent-reared offspring. Superficially, puppet-reared birds might be assumed to be less behaviorally adept than those reared by parents, especially for social birds that are slow to mature, but our data do not support that assumption, since there was no apparent difference in mortality between the groups. Similarly, rearing method for Common Ravens (puppet- vs. human-reared) had little if any effect on post-release survival, and survival for all reintroduced birds was comparable to that of wild offspring (Valutis 1997, Valutis and Marzluff 1999).

The advantages and disadvantages of early release are also equivocal for long-lived birds that require an extended period of maturation. Increased maturity during additional time spent in captivity prior to release could result, for example, in acclimation to captivity and a reduction in age-appropriate behavior on release. On the other hand, young birds released prematurely might lack wariness or other behavioral attributes necessary for survival, some of which may be innate and slow to develop. In Arizona, 95% first-year survival of birds released when >1 year of age, compared to 73% for birds released at <1 year old, indicates strongly that older birds benefited from increased maturity prior to release, even in the absence of free-ranging experience in the wild. This finding has important implications for managing the release of young condors and perhaps other species with life histories that include long periods of juvenile dependence and maturation.

Adult survival.—For long-lived animals with low reproductive rates and few natural predators, breeding success or juvenile survival are not as critical to the stability of populations as adult survival, since even in the best of times slow breeding rates place a higher premium on longevity than fecundity (cf. Mertz 1971). Thus, viable populations of long-lived birds are generally characterized by both low adult mortality and a relatively small proportion of juveniles (e.g., Houston 1974, Weimerskirch et al. 1987), although not necessarily in newly reestablished populations (Blanco and Martinez 1996, Blanco et al. 1997). Verner (1978) and Meretsky et al.

(2000) modeled hypothetical cases of condor mortality, and both generally concluded that annual survival for adults and subadults must exceed 90% to maintain population stability (Verner: 91% adult and 89% subadult; Meretsky et al.: 90.1% for both adult and subadult), and that adult survival should approach 95% annually to compensate for subadult survival of about 85%. In Arizona, where subadult condors currently outnumber adults, subadult survival has thus far approached or surpassed those minimal requirements. Because there are still relatively few adults in the population, the long-term adult survival rate remains speculative, but it is promising that none of the 14 condors to reach adulthood has perished and that survival approached 98% for all birds free-flying for >4 years.

Reproduction and population growth.—Given the current rates of survival and reproduction, can this population become self-maintaining or possibly grow without supplementation so long as management of the lead exposure problem is continued? A near-term increase in the number of breeding pairs is complicated by the dearth of unpaired breeding-age females (Fig. 3). Two or three additional females should become potential breeders in 2006 or 2007; however, barring unanticipated catastrophes, there could be at least 15 adult females and 20 or more adult males in the population within five years. Not all adults in the new population will necessarily breed, but so far most with the opportunity to breed have done so. Moreover, breeding success improved as pairs became established, so that the reproductive rate for established pairs presently lies in the range reported for wild condors in the 1980s (Snyder and Snyder 2000). It remains speculative whether these rates are adequate for population stability or growth, but they appear to be when compared to hypothetical models of California Condor demography (Meretsky et al. 2000), as well as data on colonial Griffon Vultures (*Gyps fulvus*) in France (Sarrazin et al. 1994), and several solitary-breeding Old World vultures (Mundy 1982).

Lead poisoning and its consequences.—Poisoning by various means is a ubiquitous contemporary threat to adult vultures and condors (e.g., Mendelssohn and Leshem 1983, Mundy et al. 1992, Mundy 2000), and lead contamination is the primary concern for long-term viability of modern California condor populations (Wiemeyer et al. 1988, Pattee et al. 1990, Kiff 2000, Meretsky et al. 2000, Snyder and Snyder 2000, Fry 2003, Cade et al. 2004). Because condors are gregarious and efficient scavengers that feed principally, although not exclusively, on medium and large mammalian carcasses, they are particularly vulnerable to lead poisoning when animals are shot and carcasses are not recovered or gut piles are left. Lack of recovery may arise from unintended hunter loss or shooting activities that place little emphasis on carcass recovery, including poaching big game for trophy mounts, shooting coyotes and other predators, and killing hares, ground squirrels and other small animals. Consequently, as long as lead ammunition is used by hunters and shooters in regions where condors and other scavenging animals live, some wildlife will doubtless be killed by lead poisoning.

Meretsky et al. (2000) suggested that lead in general, and lead bullets in particular, are a pervasive component of the contemporary environment, with patterns of contamination and rates of exposure that make the reintroduction of condors untenable at present. We agree that lead contamination has hindered and will continue to hinder condor restoration, especially considering that lead poisoning was the only verified cause of mortality for adult or subadult birds past their second year in the wild. Moreover, although annual survival was nearly 98% for condors that had been free-flying for >4 years, that value does not likely represent expected survival of those birds in the absence of management, as all of them received chelation therapy one or more times, and some might have perished otherwise. How many? Acute levels of lead in blood >100 µg/dl indicate that the bird's physiology has been compromised, but they do not necessarily represent lethal levels; crop stasis and other complications resulting in death can, however, occur at blood levels in the range of 250 µg/dl (Fry 2003). Consequently, without intervention adult survival may have been 90% or less, and perhaps one third or more of the current adult population would be absent. Thus, while our data suggest that lead poisoning should not necessarily preclude the establishment of a condor population in Arizona that is stable or able to grow in numbers, the population will require continued monitoring of lead levels in blood and chelation therapy when necessary.

Conclusions.—For long-term survival and self-sufficiency of condors in Arizona, the lead that they encounter must be reduced or eliminated, since as the population grows in number and expands in range intensive management of individual birds will become increasingly difficult and costly. To that end, several factors critical in understanding the risks of lead require further study. The pattern of lead encounters that has so far emerged in Arizona includes occasional widespread episodes that have resulted in the poisoning of many birds, superimposed on a persistent background of individual poisonings. Thus, identifying the sources of lead that have caused those poisonings is essential to safeguarding Arizona's condors. The shotgun pellet-related poisonings in June 2000 were enigmatic, and it is possible that an inadvertent or unique shooting event led to the exposure. Lead shot is, however, an environmental hazard that killed many North American water birds until its use for waterfowl hunting was banned, and two additional condor deaths attributed to shotgun pellets in 2005 suggest that ingestion of lead shot may be more onerous to condors than had been presumed. Poisoning of birds during the autumns of 2002 and 2004 is more troubling still, since high exposures were likely associated with the annual hunting season on the Kaibab Plateau, where condors fed on the carcasses of deer that had been killed by hunters or poachers (Hunt et al., this symposium). The magnitude of future poisonings associated with lead-based bullets is uncertain, but lead fragments extensively contaminate the wound channel and offal of hunter-killed deer (Hunt et al., in press) and lead bullet-induced poisonings may threaten populations of Steller's and white-tailed sea eagles (*Haliaeetus pelagicus* and *H. albicilla*, respectively) in Japan (Iwata et al. 2000, Kurosawa 2000, Ueta and Masterov 2000). Finally, subclinical lead levels throughout the year often exceed anticipated background levels, and although the cumulative effects of chronic sublethal exposure on reproduction and survival are unknown, there are likely dysgenic effects on condors of continued, long-term exposure to lead (Cade et al. 2004).

Successful breeding by released birds in the wild nevertheless portends the coming of a new period in condor reestablishment. Given the production of wild-reared condors, as well as the high survival of birds after their first year free-flying, we are optimistic about the long-term prospects of establishing a self-sustaining condor population in Arizona, even considering problems associated with lead exposure. The fact that an experimental population of this, or any, endangered species is not yet adequately protected from humans and their environmental contaminants does not in itself argue for the suspension of restoration efforts, as some have maintained (e.g., Meretsky et al. 2000, Snyder and Snyder 2000). Small populations will always be vulnerable to stochastic and catastrophic events (Pimm 1991), and removal of the birds would substantially hinder our ability to identify sources of lead contamination and other biological hazards. We must instead maintain the effort to build a condor population large enough to sustain losses while working to identify the sources of lead in the environment, inform the public of the threat of lead to condors and other wildlife, and promote the adoption of environmentally safe alternatives to lead ammunition.

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Table 1. Release dates, locations, and number of juvenile and subadult California Condors released in northern Arizona between December 1996 and June 2005. All releases except those in 1998 and 1999 were at the Vermilion Cliff release site.

Release date	Condors released	Average age at release[A]	Currently free-flying
December 12, 1996	6	205 ± 9	3
May 14, 1997	4	771 ± 13	2
May 26, 1997	5	760 ± 19	4
November 20, 1997	4	211 ± 16	2
November 18, 1998	9[B]	215 ± 22	3
December 6, 1999	7[C]	246 ± 26	3
December 29, 2000	8[D]	243 ± 10[E]	6[F]
February 16, 2002	6	289 ± 14	3
September 25, 2002	3	500 ± 4	2
December 9, 2002	2	592 ± 13	2
March 3, 2003	3	315 ± 9	3
October 4, 2003	2	532 ± 2	2
November 29, 2003	2	580 ± 5	2
January 9, 2004	1	614	1
March 20, 2004	4	338 ± 5	3
October 16, 2004	3	559 ± 10	3
February 4, 2005	3	651 ± 15	3

March 1, 2005	5	298 ± 20	4
Overall	77	394 ± 205	50

[A] Days old ± SD

[B]One of these birds released singly on November 23 1998. That bird was 965 days old, and is not included in average age calculation for this release.

[C]One of these birds released singly on December 23 1999.

[D]Four adult condors were also released about this time: one pair on December 7 and the second pair on December 19.

[E]Not included in average age calculation for this release is one 586-day old condor.

[F]One bird from this cohort was removed permanently from the free-flying population.

Table 2. Survivorship for juvenile and subadult California Condors released in northern Arizona, December 1996, through June 2005.

Stage[A]	Birds	Exposure days	Deaths	Daily survival	Stage survival	Annual survival
Initial release	77	6,519	8	99.877%	89.5%	
Remain. first year	69	15,872	6	99.962%	90.1%	
Combined first year	77	22,391	14	99.937%		79.6%
2nd year	50	16,069	5	99.969%		89.3%
3rd through 4th year	38	19,953	6	99.970%		89.6%
5th year onward	20	16,640	1	99.994%		97.8%
Overall	77	75,053	26	99.965%		88.1%

[A]Initial release first 90 days following release; Remain. first year remainder of first year following release

Table 3. Causes of death for 26 juvenile and subadult and 2 adult California Condors released in northern Arizona between December 1996 and June 2005. Birds are listed by the number of days free-flying prior to death.

Source of mortality	Sex	Days free-flying	Age (days) at death	Month/year of death
Deaths during first year free-flying				
Coyote	M	4	284	02/2002
Coyote[A]	F	19	3187	12/2000
Coyote[A]	M	22	3144	12/2002
Eagle	M	23	225	01/1997
Coyote	M	37	271	12/1998
Poor Condition[C]	M	39	326	04/2005
Septicemia[B]	M	40	256	01/2000
Poor Condition[C]	F	43	287	02/2001
Eagle	F	60	317	02/2000
Unknown / lost	F	62	817	07/1997
Lead	M	105	487	08/2002
Unknown / lost	F	120	333	04/2000
Powerline	F	158	350	05/1997
Unknown / lost	F	242	509	09/2004
Gunshot	M	242	508	10/2002

Coyote suspected	M	318	501	10/1998
Deaths after first year free-flying				
Lead	F	521	768	06/2000
Lead suspected	M	524	810	06/2000
Eagle	F	537	880	09/2000
Arrow	M	540	1599	08/2002
Gunshot	F	609	1436	03/1999
Lead	M	816	1355	01/2005
Lead	M	932	1149	06/2000
Unknown	M	1021	1634	09/2003
Lead	M	1024	1785	03/2000
Lead suspected	F	1263	1491	06/2000
Lead	F	1345	1700	01/2005
Unknown / lost	F	1696	2155	02/2004

[A]These two condors were released as adults and were killed shortly after release.

[B]The septicemia that killed this condor resulted from airsacculitis owing to aspiration.

[C]Poor body condition of unknown cause lead to starvation-like deaths in these birds (see text for further details).

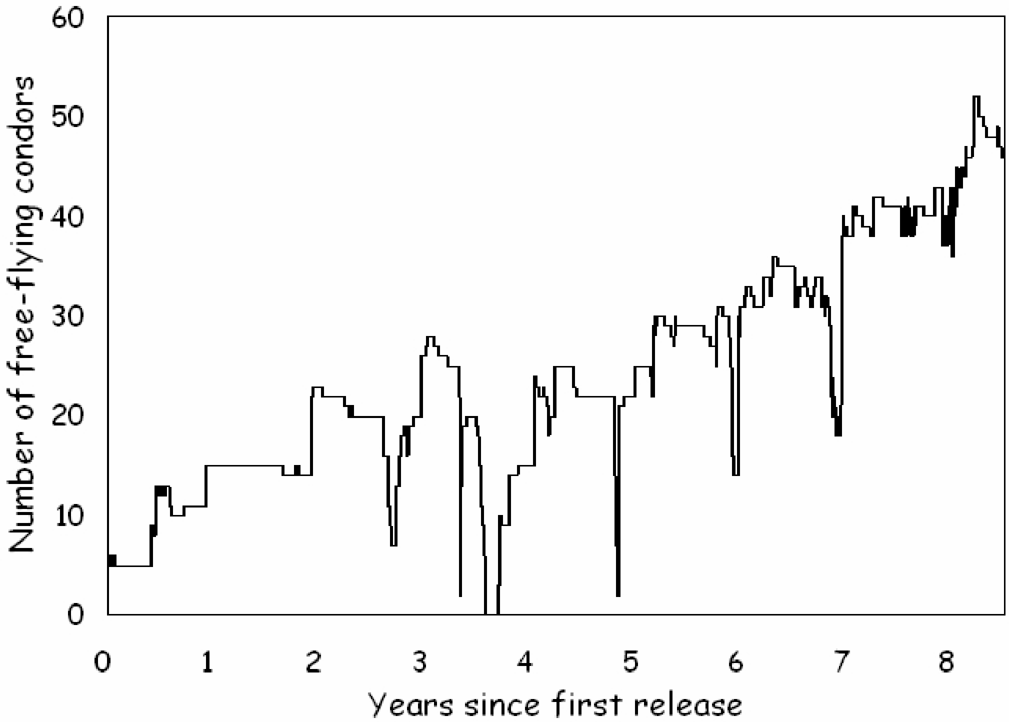

Figure 1. Number of free-flying California Condors in Arizona since the first cohort was released in December 1996. Drops in the population occurred when birds were captured and held; the population went to zero from mid-July through mid-August 2000 when all birds were held during a lead poisoning incident.

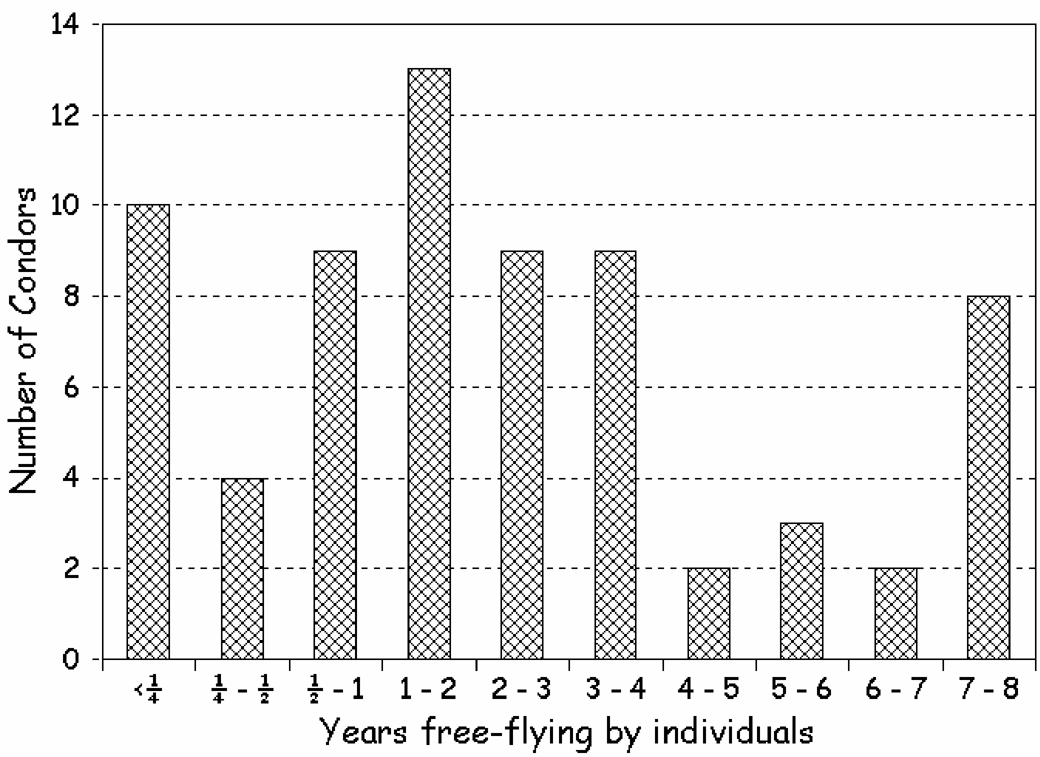

Figure 2. Time spent free-flying by 77 California Condors released in northern Arizona between December 1996 and June 2005.

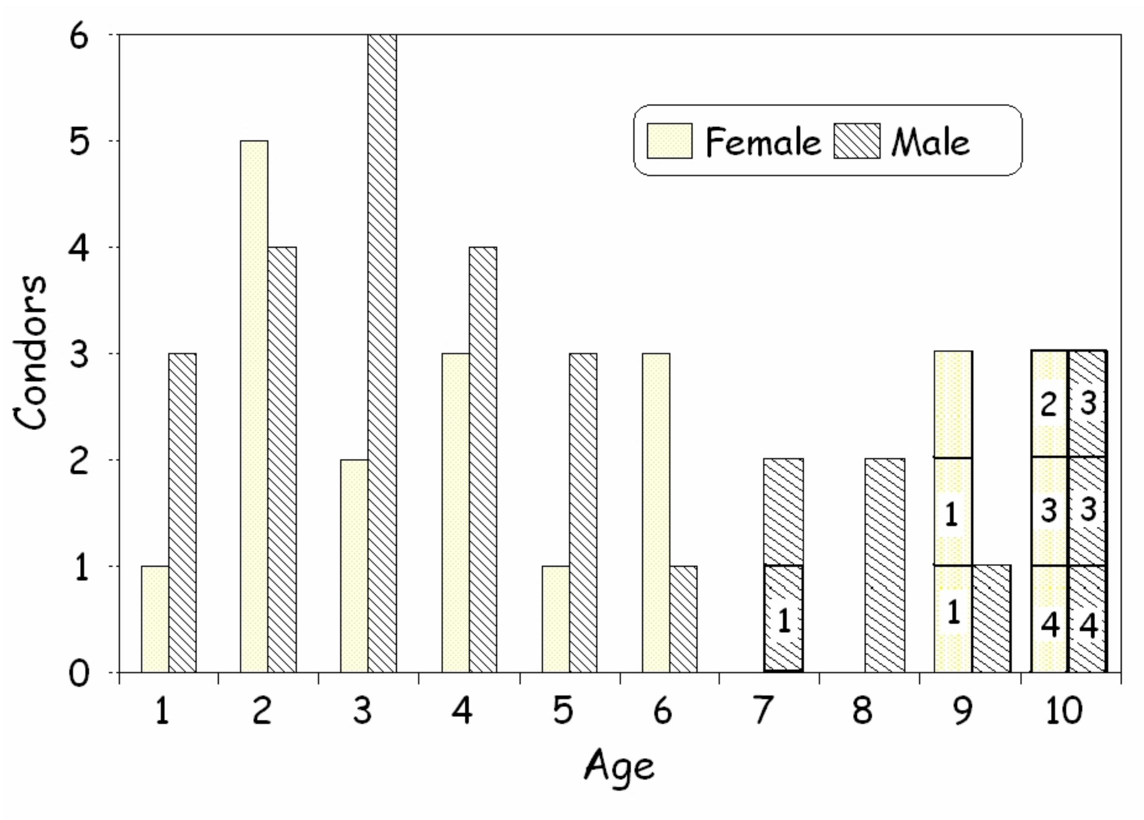

Figure 3. Age structure (June 2005) of free-flying released condors in Arizona. Numerals within bar boxes indicate the number of times that individual has bred or attempted to breed.