SREL Reprint
 # 1899

Amer. Zool., 34:397–408 (1994)

Demographics of Common Snapping Turtles (*Chelydra serpentina*): Implications for Conservation and Management of Long-lived Organisms[1]

Justin D. Congdon
Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802

Arthur E. Dunham
Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104-6018

and

R. C. van Loben Sels
Red Mountain High School, 7301 East Brown Road, Mesa, Arizona 85207

Synopsis. A study of common snapping turtles conducted from 1975 through 1992 in southeastern Michigan provided sufficient demographic data to examine how life history characteristics may constrain population responses of long-lived organisms. Females reached sexual maturity between 11 and 16 years of age. Minimum reproductive frequency was less than annual (0.85), and nest survivorship over 17 years ranged from 0 to 64% and averaged 23%. Survivorship of yearlings had to be estimated since hatchlings can pass through the mesh on traps. Actual survivorship of juveniles was over 0.65 by age 2 and averaged 0.77 between the ages of 2 and 12 years. Annual survivorship of adult females ranged from 0.88 to 0.97. A life table for the population resulted in a cohort generation time of 25 years. Population stability was most sensitive to changes in adult or juvenile survival, and less sensitive to changes in age at sexual maturity, nest survival or fecundity. An increase in annual mortality of 0.1 on adults over 15 years of age with no density-dependent compensation would halve the number of adults in less than 20 years.

The results from the present study indicate that life history traits of long-lived organisms consist of co-evolved traits that severely constrain the ability of populations to respond to chronic disturbances. Successful management and conservation programs for long-lived organisms will be those that recognize that protection of all life stages is necessary. Without protection of adults and older juveniles, programs that protect nests and headstart hatchlings have a low probability of success. Carefully managed sport harvests of turtles or other long-lived organisms may be sustainable; however, commercial harvests will certainly cause substantial population declines.

Introduction

For over a decade there have been pleas for long-term field studies that monitor populations while paying special attention to variation in both individual and population attributes (Miller, 1976; Wiens, 1977; Tinkle, 1979; Kephart and Arnold, 1982). Although there are many reasons why long-term studies are rare (Tinkle, 1979); a few notable studies of reptiles exceed 10 years in duration (Brown, 1991; Congdon and van Loben Sels, 1991; Dunham *et al.*, 1989*a*; Gibbons, 1990; Schwartz and Schwartz, 1974; Stickel, 1978; Tinkle *et al.*, 1993; Williams and Parker, 1987). Most calls for long-term studies focus on the lack of adequate

[1] From the Symposium *The Contribution of Long-Term Research to the Conservation of Biological Diversity* presented at the Annual Meeting of the American Society of Zoologists, 26–30 December 1992, at Vancouver, British Columbia, Canada.

life history data needed for tests of ecological and life history theory. However, the lack of such data can also handicap conservation efforts, particularly with regard to long-lived organisms.

Conservation programs are often formulated without adequate data on life history trait values of target species. In some cases populations of concern are so reduced in numbers that collection of data is difficult or impossible. In the absence of adequate life history data, knowledge of realistic boundaries on feasible demographic traits (those documented in nature and those that can produce a stable or increasing population in cohort population models) can be extremely important for making decisions about management and conservation of vertebrate populations (Dunham and Overall, 1994). Knowledge of feasible associations of demographic traits can be particularly important when: 1) conflicts between goals of commercial harvest conflict with plans for conservation of target organisms (*e.g.,* sea turtles, National Research Council, 1990; and sharks, NOAA Tech. Rept. NMFS 90, 1991), and 2) when the time scale for initiation of effective management is too acute to allow gathering of adequate life history data on a target species. For example, adequate study of life history traits of long-lived tortoises and freshwater turtles may take decades, and documentation of many sea turtle life history traits is not presently possible.

Recently, a combination of life history modeling (Dunham *et al.,* 1989*b*) and data from a long-term study of Blanding's turtles (*Emydoidea blandingii,* Congdon *et al.,* 1993*a*), focused attention on life history and demographic contraints of long-lived organisms. In particular, the above studies examined relationships among values of age at sexual maturity, adult survivorship, and juvenile survivorship within life histories of long-lived organisms. Results from these studies suggest that all long-lived vertebrates, such as many chelonians (Brecke and Moriarty, 1989; Congdon and van Loben Sels, 1993; Gibbons and Semlitsch, 1982), snakes (Brown, 1993); tuataras (Dawbin, 1982); crocodilians (Turner, 1977); sharks, (NOAA Tech. Rept. NMFS 90, 1991); and some fish (Roff, 1981), have coevolved life history traits that combine to limit their ability to respond to increased mortality imposed on any age group (Congdon *et al.,* 1993*a*). Understanding that long-lived vertebrates have a limited ability to respond to chronic increases in mortality is particularly important in decisions related to populations that are subject to commercial harvest of juveniles or adults (Crouse *et al.,* 1987).

Because common snapping turtles (*Chelydra serpentina*) are relatively large-bodied turtles, they are harvested for meat throughout their range by sport and commercial fishermen. Historical reports indicate harvesting levels that would probably have led to rapid and severe reductions of local turtle populations (see Brooks *et al.,* 1988). Harvesting of overwintering snapping turtles with hooked steel rods resulted in a catch of over five tons per season near Muscatine, Iowa (Clark and Southall, 1920). In addition, Clark and Southall (1920) reported that between December, 1917, and May, 1918, almost 15 tons of turtles were harvested and shipped to the New York market by the boxcar load. It is only in the past two decades that concerns about commercial harvest of snapping turtles has prompted legal protection in some states (*e.g.,* Michigan).

We present data from an 18-year study of *Chelydra serpentina.* We combined data on clutch size and nest survivorship from the literature (Congdon *et al.,* 1987) with additional data on reproductive frequency and nest survivorship of snapping turtles taken in the years from 1988 to 1992 to test whether the population was stable, and to construct a life table. We examined how life history trait values of these long-lived turtles affect their ability to respond to chronic harvest of adults. In addition, we compared the results of this study to a study of sympatric Blanding's turtles, which also have extended longevity and delayed sexual maturity, but only 0.33 the fecundity of snapping turtles.

MATERIALS AND METHODS

Snapping turtles on the University of Michigan's E. S. George Reserve (ESGR) have been studied for each of the past 18 years. Some additional data on long term

adult survival were obtained from eight female snapping turtles marked by Henry Wilbur between 1971 and 1973. Each year from 1975 through 1986 and in 1991 and 1992 intensive aquatic trapping was carried out from early May through early-September, and drift fences were usually monitored from April through June and during September and October. From 1987 through 1990 the study was conducted only from early May to early July.

A total of 1,576 hatchlings, juveniles, and adults was marked and an additional 2,474 recaptures of these individuals were made (see Congdon *et al.*, 1983, 1987, and Congdon and van Loben Sels, 1991 for descriptions of capture methods). All juvenile and adult turtles were individually marked by notching or drilling the margins of the carapace. Prior to 1983 hatchlings were also individually marked, and from 1983 to 1992 all hatchlings from a single nest were given an identical nest cohort mark. If an individual with a nest cohort mark was recaptured, its identification was changed into a unique individual mark. The straight line lengths of both the plastron and carapace were measured at each capture. All turtles except gravid females were then released at the point of capture.

The presence of eggs inside females was determined by palpation, and from 1977 through 1992 X-radiographs were taken of all gravid females (Gibbons and Greene, 1978; Congdon *et al.*, 1987). Following X-radiography, numbers were painted on, or plastic reflective numbers were glued to the female's carapace to allow identification from a distance. Females were then returned to the body of water closest to where they were captured. The time and location were recorded and the nest site marked for each nesting female. Reproductive frequency was determined from 1,398 total captures and recaptures of 106 adult females over 18 years (1975–1992).

Nesting seasons on the ESGR usually occur from mid-May through late June and have an average duration of 18 days (Congdon *et al.*, 1987). The beginning and end of the nesting season each year was defined as the first and last day, respectively, that gravid females were observed on land. From 4 to 8 people searched all potential nesting areas daily from 0600 hr until the last female was seen nesting or until we could find no turtles active on land. Each nest was observed daily and a record was kept of whether or not the nest was destroyed by predators. Nests not destroyed by predators were fenced during late August and monitored daily for hatchling emergence. Some additional details of the study of reproduction and nesting are described in Congdon *et al.* (1987).

Age class zero was assigned to the period from egg laying to emergence from the nest which occurred from late August to early October. Age class one began at emergence from the nest and covered the hatchlings' first fall, winter, and first full activity season. Turtles that were first captured with fewer than 12 growth rings were assigned an age based on the assumption that growth rings were laid down annually in juveniles and young adults (Galbraith and Brooks, 1987*a*). Recaptures of juveniles during the past 18 years support the assumption.

Annual fecundity (m_x) was defined as the number of female eggs produced annually (average clutch size/2 [to adjust for production of males by making an assumption of an equal primary sex ratio] and then multiplied by clutch frequency).

We performed two qualitatively distinct types of analyses to examine the consequences of, and potential responses to, population reduction. In both types of analyses, we set the following population parameters to long-term mean values from this study. 1) A single exception was that all females matured at minimum alpha (12 yr) in the model rather than over a range of ages from 11 to 16 years allowed in the life table. 2) The proportion of females that reproduced annually was 0.85. 3) Annual fecundity was set at 12 eggs (mean clutch size of 28 eggs which produces 14 female embryos and is reduced by annual reproductive frequency of 0.85). 4) Nest survivorship was set at the long-term average of 0.23 for the population. 5) Adult survivorship was 0.93, which includes compensation for an emigration rate of 0.5%. 6) Juvenile survivorship averaged 0.77 between 2 and 12 years of age, and 7) yearling survivorship was set at 0.47.

In the first set of analyses, we explored

the impact of changes in life history parameters on population stability. We examined which combinations of the demographic variables (1 through 4 listed above) would permit population persistence (*i.e.*, where $r \geq 0$) where r is the solution to Euler's Equation:

$$1 = \sum_{x=0}^{\infty} e^{-rx} l_x m_x$$

where l_x is the survival from both to age x, m_x is the expected fecundity of a female of age x, and e is the base of natural logarithms. Three subsets of analyses were run. 1) With fecundity fixed at 12 and nest survival at 0.23, combinations of average annual juvenile and adult survival for which $r = 0$ were calculated for values of alpha varying from 5 to 30 years. 2) With alpha fixed at 12 years and nest survival at 0.23, combinations of average annual juvenile and adult survival for which $r = 0$ were calculated for annual fecundity values from 10 to 40. 3) With alpha fixed at 12 years and annual fecundity at 12, combinations of average annual juvenile and adult survival for which $r = 0$ were calculated for nest survival values from 0.05 to 0.95. Adult and juvenile survival rates both varied from 0.005 to 0.99 in steps of 0.005.

In the second set of analyses, a single demographic variable was allowed to vary over a wide range of values while all others were held constant at the long-term average for the population. Life table variables were calculated for each unique combination of demographic variables, and the intrinsic rate of increase (r) was calculated for each result. Four subsets of these analyses were carried out allowing: 1) age-specific annual fecundity, 2) nest survivorship, 3) juvenile and 4) adult survivorship to vary in turn. Age-specific fecundity varied from 1 to 60 in steps of one, and nest survivorship varied from 0.05 to 0.95 in steps of 0.05. Juvenile and adult survivorships varied from 0.05 to 0.99 in steps of 0.005.

We also estimated the number of years it would take a population to be reduced by half under conditions of zero compensation from reduced densities of adults. We simulated harvest rates of females by increasing annual mortality rates from 0.1 to 0.9 over the mortality schedules used in the life table. For each level of harvest induced mortality, we ran a set of simulations in which the minimum age at which turtles were harvested varied from 10 to 40 years (*i.e.*, for simulations starting at age 20 all adult age classes were subjected to increased mortality rates beginning at age 20).

RESULTS

Reproduction and nest survivorship

Minimum frequency of reproduction was determined by examining the number of females that were captured while reproductive in East Marsh and associated nesting areas and comparing that to the number of females captured during the entire year in East Marsh during each of five years. The estimated minimum proportion of females that reproduced in a single year averaged 85% (min–max = 77%–88%).

Of the 378 observed nests produced over 17 nesting seasons, an average of 23% (min = 0%; max = 64%; 1 SE = 3.9%) survived predation.

Movements and immigration

Seven (5%) of the 136 snapping turtles marked in marshes surrounding the ESGR over all years of study immigrated into the ESGR population.

Survivorship of juveniles and adult females

The measured survival of age class one (min = 0.0, max = 0.17, mean = 0.09) was almost certainly an underestimate since hatchling turtles can pass through the mesh of the traps (see section on values used in construction of life tables). Survivorship of juveniles between the ages of 2 and 12 ranged from 0.65 to 0.82 (mean = 0.77; Table 1). In an analysis of all adults over all years of study, survivorship averaged 0.88 (Table 1). In addition, we calculated annual survival rates over a 20-year interval for eight females that were marked as adults by Henry Wilbur between 1970 and 1973. Four of the females were still alive in 1992, one died in 1988, one was last seen in 1975, and one each in 1988 and 1989. Overall, long-term mean

TABLE 1. *Survivorships of juveniles and adult female snapping turtles on the E. S. George Reserve.**

Age	Captures		Probability of surviving
	Total	Recaptured	
0	378	84	0.23
1	1,048	84	0.09*
2	106	86	0.81
3	134	85	0.65
4	121	79	0.65
5	107	80	0.75
6	109	81	0.74
7	90	73	0.81
8	93	72	0.77
9	76	56	0.80
10	64	53	0.82
11	55	45	0.82
12	52	42	0.81
Mean (ages 2–12)			0.77
SE			0.05
Captures of adult females of all ages	1,121	90	0.88

* Survivorships are not adjusted for emigration. Age 0 = oviposition to hatchling emergence from the nest.
** Yearling survival was adjusted to 0.47 prior to calculation of the life table (see text).

survival to 1992 for this group of turtles was 0.97.

Life tables

Values used in construction of the life table are presented in Table 2. Measured values include survival of nests (age 0), juvenile survival rates from age 2 to age 12, and the mean value of the two survivorships of adults rounded upward by 0.005 to adjust for emigration. Recapture rates of one year old turtles from seven cohorts of hatchlings marked at nests averaged 9% and ranged from 0%–17%. Since captures of yearlings were reduced due to trap mesh size, we estimated survivorship for age 1 to be 0.47 (*i.e.*, the value that resulted in $r = 0$ when used in conjunction with other measured life table values). For the life table only, age specific fecundities were adjusted from 4 to 12 over the period that females reach sexual maturity, and fecundity was set at 12 for all ages of adults (Table 3).

The resulting life table for a stable population of snapping turtles on the E. S. George Reserve resulted in a cohort generation time of approximately 25 years and

TABLE 2. *A summary of values used in construction of a life table for* Chelydra serpentina *on the E. S. George Reserve.*

Reproduction	
Mean clutch size	28.0
Clutch frequency	0.85
Annual fecundity	12 eggs
Emigration rate	0.005 per year
Survivorships (l_x)	
Nest (age 0)	0.23
Age 1	0.47
Mean (ages 2–12)	0.77
Adult females	0.93*

* Survival of adult females adjusted upward by 0.5% to account for emigration. Clutch size from Congdon *et al.*, 1987.

a doubling time of the population of approximately 2,000 years (Table 3).

The first simulations examined the relationships between juvenile and adult survival rates while allowing alpha (Fig. 1), fecundity (Fig. 2) and nest survivorship (Fig. 3) to vary. If alpha is reduced to 5 years and all other life history characteristics are held constant, then average juvenile survival (age 1 to age 12) necessary to maintain the population would be reduced to about 42%. If average alpha in snapping turtles increased from 10 to 30 years, the average juvenile survivorship required to maintain a stable population would increase from about 70% to over 85% (*i.e.*, juvenile survival rate only 8% less than that of adults).

To maintain a stable population, increases in fecundity from 10 to 40 eggs (equal to increasing clutch size from 23 to 92 eggs) per adult female would allow a reduction in average required juvenile survivorship of about 11% (Fig. 2). Annual nest survivorship in snapping turtles ranged from zero to 64%. When nest survival is reduced from 64% (the highest value recorded in all years) to 10%, juvenile survivorship must increase by approximately 11% (Fig. 3) to maintain a stable population. The relationships between annual juvenile and adult survival for all simulations (Figs. 1–3) have the characteristic of being much steeper as adult survivorship exceeds 80%.

The rate of change in population increase or decrease (deviation from $r = 0$) was least

TABLE 3. *A life table for* Chelydra serpentina *on the E. S. George Reserve.**

Age	s_x	l_x	m_x	l_xm_x	F_x	g_x	E_x
0	0.230	1.00000	0.0	0.0000	0.0000	0.0000	1.203
1	0.470	0.23000	0.0	0.0000	1.0090	0.0000	2.558
2	0.810	0.10810	0.0	0.0000	1.0090	0.0000	3.879
3	0.650	0.08756	0.0	0.0000	1.0090	0.0000	3.672
4	0.650	0.05691	0.0	0.0000	1.0090	0.0000	4.380
5	0.750	0.03699	0.0	0.0000	1.0090	0.0000	5.470
8	0.740	0.02775	0.0	0.0000	1.0090	0.0000	6.126
7	0.810	0.02053	0.0	0.0000	1.0090	0.0000	7.103
8	0.770	0.01663	0.0	0.0000	1.0090	0.0000	7.652
9	0.800	0.01281	0.0	0.0000	1.0090	0.0000	8.788
10	0.820	0.01024	0.0	0.0000	1.0090	0.0000	9.860
11	0.820	0.00840	4.0	0.0336	1.0090	0.0335	10.914
12	0.820	0.00689	6.0	0.0413	0.9754	0.0412	12.201
13	0.930	0.00565	8.0	0.0452	0.9341	0.0450	13.769
12	0.930	0.00525	10.0	0.0525	0.8889	0.0523	13.768
15	0.930	0.00489	12.0	0.0586	0.8364	0.0583	13.766
16	0.930	0.00454	12.0	0.0545	0.7777	0.0542	13.765
17	0.930	0.00423	12.0	0.0507	0.7232	0.0504	13.763
18	0.930	0.00393	12.0	0.0472	0.6725	0.0469	13.762
19	0.930	0.00365	12.0	0.0439	0.6254	0.0436	13.760
20	0.930	0.00340	12.0	0.0408	0.5815	0.0405	13.758
21	0.930	0.00316	12.0	0.0379	0.5407	0.0376	13.756
22	0.930	0.00294	12.0	0.0353	0.5028	0.0350	13.754
23	0.930	0.00273	12.0	0.0328	0.4675	0.0325	13.751
24	0.930	0.00254	12.0	0.0305	0.4347	0.0303	13.749
25	0.930	0.00236	12.0	0.0284	0.4042	0.0281	13.746
26	0.930	0.00220	12.0	0.0264	0.3758	0.0261	13.743
27	0.930	0.00205	12.0	0.0245	0.3494	0.0243	13.739
28	0.930	0.00190	12.0	0.0228	0.3249	0.0226	13.736
29	0.930	0.00177	12.0	0.0212	0.3021	0.0210	13.732
30	0.930	0.00164	12.0	0.0197	0.2809	0.0195	13.728
31	0.930	0.00153	12.0	0.0184	0.2611	0.0182	13.724
32	0.930	0.00142	12.0	0.0171	0.2428	0.0169	13.719
33	0.930	0.00132	12.0	0.0159	0.2257	0.0157	13.714
34	0.930	0.00123	12.0	0.0148	0.2098	0.0146	13.709
35	0.930	0.00114	12.0	0.0137	0.1950	0.0136	13.703
36	0.930	0.00106	12.0	0.0128	0.1813	0.0126	13.697
37	0.930	0.00099	12.0	0.0119	0.1685	0.0117	13.690
38	0.930	0.00092	12.0	0.0110	0.1567	0.0109	13.683
39	0.930	0.00086	12.0	0.0103	0.1456	0.0101	13.675
40	0.930	0.00080	12.0	0.0096	0.1353	0.0094	13.667
41	0.930	0.00074	12.0	0.0089	0.1258	0.0088	13.658
42	0.930	0.00069	12.0	0.0083	0.1169	0.0081	13.648
43	0.930	0.00064	12.0	0.0077	0.1086	0.0076	13.638
44	0.930	0.00060	12.0	0.0071	0.1010	0.0070	13.627
45	0.930	0.00055	12.0	0.0066	0.0938	0.0065	13.615
46	0.930	0.00052	12.0	0.0062	0.0872	0.0061	13.602
47	0.930	0.00048	12.0	0.0057	0.0810	0.0057	13.588
48	0.930	0.00045	12.0	0.0053	0.0752	0.0053	13.573
49	0.930	0.00041	12.0	0.0050	0.0699	0.0049	13.557
50	0.930	0.00039	12.0	0.0046	0.0649	0.0045	13.540
55	0.930	0.00027	12.0	0.0032	0.0448	0.0032	13.433
60	0.930	0.00019	12.0	0.0022	0.0308	0.0022	13.279
65	0.930	0.00013	12.0	0.0016	0.0211	0.0015	13.057
70	0.930	0.00009	12.0	0.0011	0.0143	0.0011	12.738
75	0.930	0.00006	12.0	0.0008	0.0096	0.0007	12.280
80	0.930	0.00004	12.0	0.0005	0.0064	0.0005	11.621
85	0.930	0.00003	12.0	0.0004	0.0041	0.0004	10.674
90	0.930	0.00002	12.0	0.0003	0.0025	0.0002	9.312
95	0.930	0.00001	12.0	0.0002	0.0014	0.0002	7.356
100	0.930	0.00001	12.0	0.0001	0.0006	0.0001	4.543
105	0.930	0.00001	12.0	0.0001	0.0001	0.0001	0.000

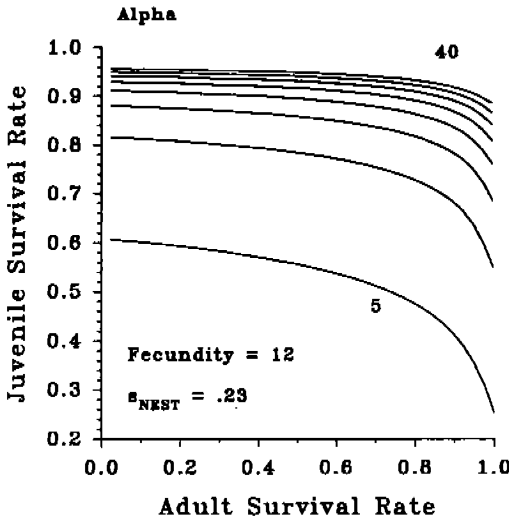

FIG. 1. The relationship between adult survival rate and juvenile survival rate while average age at sexual maturity (alpha) is allowed to vary from 5 to 40 years. Values for fecundity and nest survival are fixed.

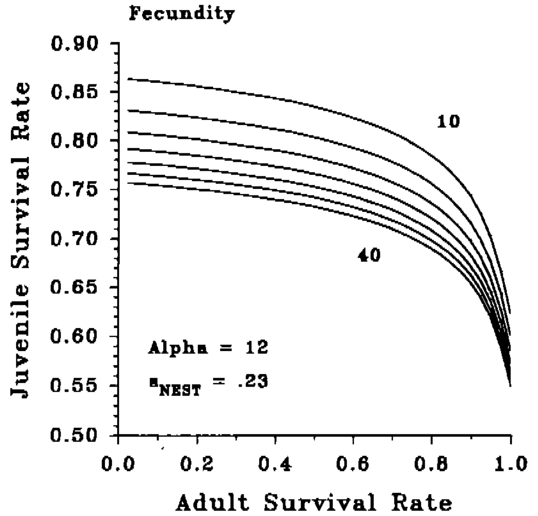

FIG. 2. The relationship between adult survival rate and juvenile survival rate while annual average fecundity is allowed to vary 10 to 40 female producing eggs per adult female. Values for alpha and nest survival are fixed.

rapid for variation in nest survivorship and fecundity (Fig. 4), and was most rapid for juvenile and adult survivorship (Fig. 4).

Results of the simulation study of effects of increased harvesting mortality on rate of population decline are shown in Figure 5. As mortality of adults of each sex above 14 years of age is increased by 0.1 annually, the population half life is approximately 10 years (Fig. 5). Postponing the onset of the same level of harvesting mortality to only individuals above age 29 years results in a population half life of approximately 30 years (Fig. 5).

DISCUSSION AND CONCLUSIONS

Minimum clutch frequency in snapping turtles on the E. S. George Reserve (0.85) is less than annual, and in over 18 years of study no individual was observed to produce more than one clutch per year. Despite the intense efforts to observe or account for all reproductive females at East Marsh, the estimate of clutch frequency must be considered minimal because there remains some chance that females were able to nest without detection. Because the cold nesting season in 1992 reduced the very early and late times of day that females had available to nest, our ability to observe them was increased. As a result we captured the highest proportion (0.88) of the females while they were reproductive. Other species of turtles reproduce less than annually (Congdon *et al.*, 1983; Tinkle *et al.*, 1981; Christens and Bider, 1986; Frazer *et al.*, 1991).

Survivorship of snapping turtle nests on

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* Data are long-term mean fecundity and survivorships for each age class of the population. Annual fecundity (12 eggs) is based on a mean clutch size of 28 eggs, reproductive frequency of 0.85, and one half of all eggs produce daughters. s_x is the age-specific probability of survival, l_x is the probability of survival from age x to age x + 1, m_x is the expected fecundity of a female age x, F_x is the probability density for the ages at which a female's daughters are produced, g_x is the probability density for the ages at which mothers give birth, E_x is the age-specific expectation of future life, R_o = net reproductive rate or the sum of $l_x m_x$, r = the intrinsic rate of population increase or the implicit solution of 1 = the sum of $l_x m_x e^{-rx}$, and T_c is the cohort generation time for the population. Population parameters are: R_o = 1.009; r = 0.000354, and T_c = 25.4 years, Doubling Time = 1959 years.

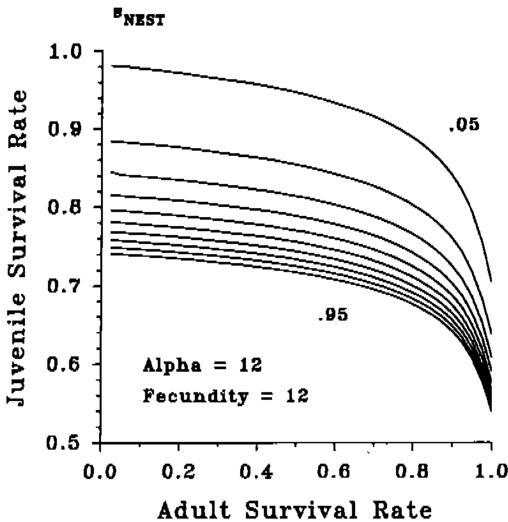

FIG. 3. The relationship between adult survival rate and juvenile survival rate while nest survivorship is allowed to vary from 0.05 to 0.95. Values for alpha and fecundity are fixed.

the ESGR was variable and averaged 23%. Survival rates of *Emydoidea blandingii* nests on the ESGR between 1976 and 1984 averaged 44%, and between 1985 and 1991 fell to less than 4% (Congdon *et al.,* 1993*a*). There was no pattern of decline in survival of snapping turtle nests during the latter years of this study. Increased densities of nest predators due to the decline in the fur bearer trapping was suggested as a possible cause of the decline in survival rates of *E. blandingii* nests (Congdon *et al.,* 1993*a*). Nesting seasons of snapping turtles and Blanding's turtles overlap and they share nesting areas and nest predators (Congdon *et al.,* 1983, 1987). Therefore, the lack of increased mortality in snapping turtles does not support the assumption of increased predator populations as a cause of reduced nest survival in *E. blandingii* (Congdon *et al.,* 1993*a*).

Survival rates of snapping turtles between hatching and the end of their first year had to be estimated because they can pass through the mesh of the turtle traps. Annual survivorship between the age of 2 and 12 years of age averaged 0.77 and were similar to the values used in the life table constructed for a population in Ontario, Canada (Brooks *et al.,* 1988). That survivorship of juveniles was already greater than 0.65 by age 2 is remarkable and is substantially higher than that measured for the earliest age juvenile *Kinosternon subrubrum* in South Carolina (Frazer *et al.,* 1991). Survivorship of adults on the ESGR is similar to the range of values (0.93–0.97) reported for snapping turtles in Ontario, Canada (Brooks, *et al.,* 1991; Galbraith and Brooks, 1987*b*), and box turtles (*Terrapene carolina*) in Indiana (William and Parker, 1987).

Snapping turtles are large bodied and have been both sport and commercially harvested for meat throughout their range, and in some wildlife areas and bird sanctuaries snapping turtles are considered pests requiring control (Hawthorne, 1980). In many states, sport harvesting of snapping turtles requires only a fishing license and the number of turtles that can be taken is essentially unregulated. An unfortunate circumstance related to the incidental take of snapping turtles is that many of the individuals taken are gravid females on land to nest. Until recently, commercial harvesting has also been unregulated and unmonitored throughout most of the species range. If the average adult snapping turtle weighed an average of 20–25 lb., then the take at Muscatine, Iowa was between 400 and 500 individuals (Clark and Southall, 1920). With continued harvest pressures as low as 0.1 of the adults above 15 years of age, halving time of a population can be as low as 15 years (Fig. 5). At the minimum age of first reproduction (12 yr) in Michigan the average mass of a snapping turtle is 2.5 kg (less than 6 lb.; Congdon *et al.,* 1993*b*); whether or not individuals of this body mass are routinely harvested is not known; however, the impact of removing females from a population prior to their producing at least one successful nest is great.

Considering the relationship between juvenile and adult survivorship in response to changes in other life history trait values, large increases in mortality caused by harvesting adults will certainly have a major impact on the population. Population size could be maintained only if there is major density dependent release that results in substantial increases in clutch size, clutch

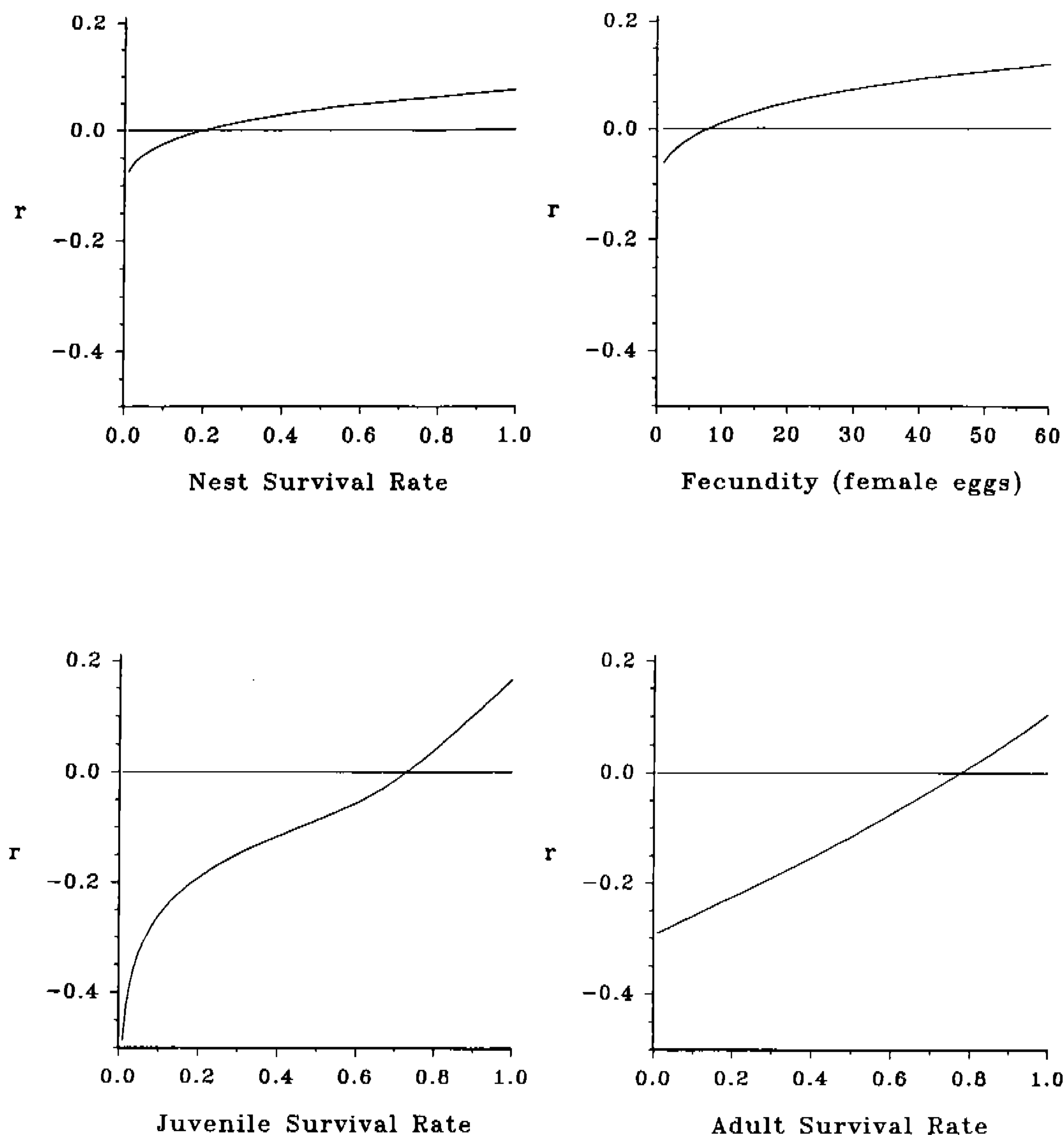

FIG. 4. The relationships between fecundity, and survivorships of nests, juveniles and adults with population stability ($r = 0$) set by life table parameters snapping turtles on the E. S. George Reserve.

frequency, or a substantial decrease in alpha. Such density-dependent compensation in response to increased mortality was not observed in common snapping turtles in Ontario, Canada (Brooks *et al.*, 1991). We hope that concern for the common snapping turtle does not have to wait until populations are so reduced that recovery will be difficult or impossible. A worthy goal for conservation programs is to keep the common snapping turtle common.

Life history similarities of snapping and Blanding's turtles (Brooks *et al.*, 1988; Congdon and van Loben Sels, 1991, 1993; Congdon *et al.*, 1993*a*) include delayed sexual maturity, extended longevity of adults, and high juvenile survivorship necessary to maintain a stable population. The major difference between snapping and Blanding's turtles is that fecundity of snapping turtles is approximately three times as high. As a result, protecting nests of snapping turtles

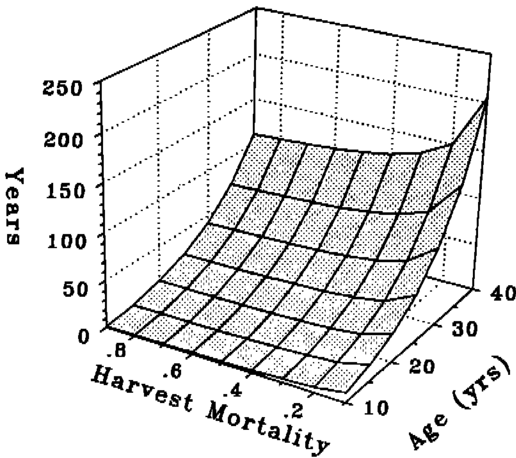

FIG. 5. The relationships among years taken to remove half a population and increased annual mortality due to harvesting adults ranging in ages from 10 to 40 years.

has a three times greater effect on hatchling recruitment in snapping turtles than it would in Blanding's turtles. However, if increased mortality of older juveniles and adults is not reduced substantially, nest protection alone will have a low probability of resulting in a stable population (Brooks *et al.*, 1988, 1991; Congdon *et al.*, 1993*a*; Frazer, 1992).

Among long-lived vertebrates, longevity (or adult survivorship) is positively correlated with delayed sexual maturity (Charlesworth, 1980; Charnov, 1990; Dunham *et al.*, 1988). Benefits to individuals that delay the onset of reproduction include increased number of young per reproductive bout, increased quality of young produced, decreased costs associated with reproduction, and decreased risk of mortality as an adult (Bell, 1977; Stearns and Koella, 1986; Tinkle *et al.*, 1970; Wiley, 1974). Costs associated with delaying sexual maturity include increased risk of death prior to first reproduction, and lengthened generation times. An inter-generational life history feature associated with delaying sexual maturity that is often overlooked is the substantial increase in annual survival of juveniles required to maintain a stable population (Dunham *et al.*, 1989*b*; Congdon *et al.*, 1993*a*).

Because of the correlation between longevity and delayed sexual maturity, some general conclusions can be made about long-lived vertebrates. The suite of life history traits that coevolve with longevity results in populations that are limited in capability to withstand chronic increases in mortality of nests and neonates, and less able to withstand increased mortality of juveniles or adults. The relatively low fecundity, low nest survival, and the high adult survival coupled with the extremely high juvenile survival required to maintain stable populations, argues strongly against justifying sustained harvests of populations of long-lived organisms with arguments based on the concept of sustained yield. Effective management and conservation programs (Frazer, 1992) will be ones that recognize the integrated nature of life histories and the extreme limitation that the evolution of longevity has placed on the ability of populations of long-lived organisms to withstand and respond to chronic increased mortality or reduced fecundity of any life history stage. In addition, managers of programs developed for recovery of depleted populations of long-lived organisms must recognize that, because of long generation times, there may be long delays before population responses are detectable.

ACKNOWLEDGMENTS

We thank the late Donald W. Tinkle for his participation in the early years of this study, J. W. Gibbons for his support and Joyce Klevering for assistance with all aspects of X-radiography. Russell W. Reister, Director of Plant Operations initiated the efforts to control Autumn Olive (an introduced plant) which was beginning to overrun turtle nesting areas on the E. S. George Reserve. We recognize the University of Michigan, Museum of Zoology and the E. S. George Reserve Committee for maintaining the E. S. George Reserve as a world class research area. The following people made notable contributions to this study: Harold and Sue Avery, Margaret Burkman, Carl and Melvin Congdon, Barbara, Nancy and Robert Dickson, Ruth Estes, Rose Fama, Robert Fischer, Matthew Hinz, Mark Hutcheson, David Kling, Shawn Meager, Roy Nagle, Tal Novak, Patricia Orleans, John Stegmier, Julie Wallin, and

Bradley, John and Dick Wiltse. Earlier drafts of this manuscript were improved by the comments of Ron Brooks, Nat Frazer, J. W. Gibbons, and Jeff Lovich. Funding was provided by NSF Grants DEB-74-070631, DEB-79-06301, BSR-84-00861 and BSR-90-19771. Editing of computer files, data analysis, and manuscript preparation were aided by contract DE-AC09-76SROO-819 between the University of Georgia and the United States Department of Energy.

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