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# Delayed Sexual Maturity and Demographics of Blanding's Turtles (*Emydoidea blandingii*): Implications for Conservation and Management of Long-Lived Organisms

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**Abstract:** *A study of Blanding's turtles conducted during 27 of the last 37 years provided demographic data sufficient to examine how life-history characteristics may constrain population responses of long-lived organisms. Eight independent estimates of annual adult survivorship exceeded 93%. Nest survival was variable and ranged from 0.0 to 63% annually, with a mean of 44% from 1976 to 1984 and 3.3% from 1985 to 1991. Recruitment of juveniles and adults was sufficient to replace individuals estimated to have died during the study. A life table for the population resulted in a cohort generation time of 37 years and required a 72% annual survivorship of juveniles between 1 and 13 years of age to maintain a stable population. 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. The results from the present study indi-*

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Maduración sexual retardada y demografía de las tortugas de Blanding (*Emyoidea blandingii*): Implicaciones para la conservación y manejo de organismos longevos

**Resumen:** *Un estudio de las tortugas de Blanding conducido durante 27 de los últimos 37 años aportó datos demográficos suficientes para examinar como las características de la historia de vida pueden limitar las respuestas poblacionales de organismos longevos. Ocho estimaciones independientes de la supervivencia anual de adultos excedió el 93%. La supervivencia en el nido fue variable y estuvo entre 0.0 y 63% anual, con una media de 44% para el período 1976–1984 y 3.3% para el período 1985–1991. El reclutamiento de juveniles y adultos fue suficiente para reemplazar individuos que se estimó murieron durante el estudio. Una tabla de vida para la población resultó en un período de regeneración de 37 años, y requirió un 72% de supervivencia anual de juveniles entre 1 y 13 años de edad para mantener una población estable. La estabilidad pobla-*

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*cate that life-history traits of long-lived organisms consist of co-evolved traits that result in severe constraints on 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. Programs such as headstarting or protection only of nesting sites, in the absence of programs to reduce mortality of older juveniles and adults, appear to be less than adequate to save long-lived organisms such as sea turtles and some tortoises. The concept of sustainable harvest of already-reduced populations of long-lived organisms appears to be an oxymoron.*

*cional fue más sensible a cambios en supervivencia de adultos o juveniles y menos sensible a cambios en edad de maduracion sexual, supervivencia en nidos o fecundidad. Los resultados del estudio presente indican que las caracteristicas de la historia de vida de organismos longevos consiste en caracteres coevolucionados que resultan en limitaciones severas sobre la habilidad de las poblaciones para responder a perturbaciones crónicas. Programas de manejo y conservación exitosos para organismos longevos serán aquellos que reconozcan que se necesita la protección de todos los estadíos de vida. Programas tales como "headstarting" o protección de los sitios de anidamiento solamente, en ausencia de programas para reducir la mortalidad de juveniles mayores y adultos, parecen ser poco adecuados para salvar organismos longevos tales como las tortugas marinas y algunas otras tortugas. El concepto de cosecha sostenible de poblaciones ya reducidas de organismos longevos parece ser una incongruencia.*

## Introduction

Development of conservation programs often must proceed without adequate data on life-history trait values of target species. Reasons for lack of data include technical and logistic problems related to obtaining life-history data on some species, and the difficulty of obtaining reliable data from populations that are already reduced or in decline. The problems that impede life-history studies in general are magnified when the species being studied are long lived (Tinkle 1979).

Studies of the variation of traits of organisms provide evidence that there are constraints on the breadth of functions that a single organism can perform. Constraints have been demonstrated at all levels of organization (genetic, historical, physiological, biomechanical, behavioral), including life histories. Examination of the limits of single traits and covariation among possible life-history trait values can suggest (1) possible selective factors that shape or constrain life histories; (2) ways that specific life-history traits may constrain the population responses of long-lived organisms; and (3) how life-history traits must be considered in the design and implementation of management and conservation programs.

A life-history feature that long-lived vertebrates have in common is delayed sexual maturity (Charlesworth 1980; Dunham et al. 1988; Charnov 1990). Benefits attributed to delaying the onset of reproduction include increased quality of young produced, increased number of young per reproductive bout, decreased costs associated with reproduction, and decreased risk of mortality as an adult (Gadgil & Bossert 1970; Tinkle et al. 1970; Wiley 1974; Bell 1977; Stearns & Koella 1986). Theoretically, such benefits combine to result in a higher lifetime reproductive success among individuals that delay sexual maturity than that attained by individuals maturing earlier. Costs of delaying sexual maturity include increased risk associated with death prior to first reproduction and lengthened generation times.

An often overlooked intergenerational life-history feature associated with delaying sexual maturity is the substantial increase in the annual survival of juveniles required to maintain a stable population (Dunham et al. 1989). Even with high annual fecundity, values of alpha approaching 20 years require annual juvenile survivorship greater than those reported for most extant vertebrates (Ricklefs 1973; Turner 1977; Dunham et al. 1988; Wilbur & Morin 1988) to maintain a stable population.

It is unknown how general conclusions drawn from the Dunham et al. (1989) model on dinosaur life histories may be, because almost all life-history attributes had to be estimated from little or no data. We first examine the generality of the results of the dinosaur model using relatively complete life-history data from Blanding's turtles (*Emydoidea blandingii*). We then examine how life-history traits may constrain potential responses to the disturbance of populations of long-lived organisms, and we discuss results from this study in relation to the conservation and management long-lived organisms in general, and of tortoises and freshwater and sea turtles in particular. Blanding's turtles are excellent models because they have life history and demographic characteristics similar to those of other freshwater turtles, sea turtles, and tortoises, and to those proposed for dinosaurs. In addition, Blanding's turtles and many other freshwater turtle species are of conservation concern in some parts of their range.

## Materials and Methods

Blanding's turtles on the University of Michigan's E. S. George Reserve have been studied for 27 of the past 37 years (1953 to 1957 by O. Sexton, 1968 to 1973 by H.

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Wilbur, 1975 to 1979 by D. Tinkle and J. Congdon, and 1980 to 1991 by J. Congdon). Estimates of long-term adult survival used in this paper are based on data from Blanding's turtles marked during all periods of study. Data on clutch size and reproductive frequency are taken from Congdon et al. (1983) and Congdon and van Loben Sels (1990), and data on age at maturity from Congdon and van Loben Sels (1993).

Each year from 1975 through 1986, and in 1991, 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 711 marked individuals were recaptured 2968 times (see Congdon et al. [1983] and Congdon and van Loben Sels [1991] for descriptions of capture methods). Each turtle was individually marked by notching the margins of the carapace, weighed, measured (straight line plastron length and carapace length), and then released at the point of capture.

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 1 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 19 growth rings and evidence of recent rapid body growth (a light-colored area near the medial line on the plastron) were assigned an age based on the assumptions that rapid growth indicated young individuals and that growth rings were laid down annually in juveniles and young adults. Recaptures of juveniles during the past 15 years support both assumptions. Unaged turtles of adult size that were first marked by Owen Sexton between 1954 and 1957 and recaptured during the present study were assigned a minimum age of 20 years at first capture. The minimum age assigned is conservative in that most turtles would be assigned an age less than their actual age.

Life tables were constructed from long-term means of all parameters except for annual survivorship ($s_x$) of juveniles between 1 and 13 years old; juvenile survivorship values were estimated to obtain values resulting in a stable population. For the life table, fecundity ($m_x$) was defined as the number of female eggs produced annually (average clutch size divided by 2 [to adjust for production of males by making an assumption of an equal primary sex ratio] and then multiplied by clutch frequency).

To examine the consequences of a reduction in survivorship of juveniles or adults, we performed two qualitatively distinct types of analyses. In both types, we set the population parameters at slightly more than long-term values to minimize the probability that the required juvenile survival necessary to maintain a stable population would be overestimated. For example, (1) all females were allowed to mature at the actual minimal alpha (14 years) for the population rather than at the average alpha of 17.5 years; (2) all females were allowed to produce a single average clutch of 10 eggs annually (annual fecundity = 5 female eggs) rather than adjusting for some females skipping reproduction each year; (3) maximum adult survival was allowed to reach 0.96 to adjust for emigration, which was not considered in adult survival values.

In the first type of analysis, we explored the impact of changes in life-history parameters on population stability. We examined which combinations of demographic variables would permit population persistence—$r \geqslant 0$, $r$ 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 birth 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 calculated with (1) fecundity fixed at five and nest survival at 0.26, combinations of average annual juvenile and adult survival for which $r = 0$ were calculated for values of alpha varying from 14 to 20 years; (2) alpha fixed at 14 years and nest survival at 0.26, combinations of average annual juvenile and adult survival for which $r = 0$ were calculated for annual fecundity values from 2 to 8; and (3) alpha fixed at 14 years and annual fecundity at five, combinations of average annual juvenile and adult survival for which $r = 0$ were calculated for nest survival values from 0.1 to 1.0.

In the second type of analysis, 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 analyses were carried out allowing (1) age-specific annual fecundity, (2) nest survivorship, (3) juvenile survivorship, and (4) adult survivorship to vary in turn. Adult and juvenile survival rates varied from 0.005 to 0.99 in steps of 0.005. Age-specific fecundity varied from 2 to 8 in steps of 1, and nest survivorship varied from 0.1 to 1.0 in steps of 0.1.

## Results

Data on reproduction used in construction of life tables were obtained from previously published literature on the E. S. George Reserve's Blanding's turtles (Table 1) and from analysis of the survival of nests and adults from the present study. Annual survivorship of observed nests

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**Table 1. Reproductive characteristics of Blanding's Turtles on the E. S. George Reserve.**

| *Variable* | *Value* | *Reference* |
|---|---|---|
| Mean Clutch Size | 10.2 | 1 |
| Clutch Frequency | 0.80 | 1 |
| Minimum Alpha | 14.0 years | 2, 3 |
| Mean Alpha | 17.5 years | 3 |
| Maximum Alpha | 20.0 years | 3 |

[1] *Congdon et al. 1983.*
[2] *Congdon & van Loben Sels 1991.*
[3] *Congdon & van Loben Sels 1993.*

over 16 years averaged 26.1% (min = 0%; max = 78%; 1SE = 6.6; $n$ = 193). Nest survival of 119 observed nests constructed from 1976 to 1984 averaged 43.8% (min = 7%; max = 78%; 1SE = 7.2) was significantly higher than that observed for 75 nests constructed from 1985 to 1991 (mean = 3.3%; min = 0; max = 17%; 1SE = 2.4).

Independent measures of minimum survival ($s_x$) of adults over eight periods ranging in duration from 31 years (1955–1986) to six years (1980–1986) averaged 93.5% (min = 91.5%; max = 94.7%; 1SE = 0.5%).

Based on an annual mortality rate ($q_x$) of 0.04 and an estimated mean (111) and maximum (150) number of adult females in the population (Congdon et al. 1986), the estimated mean and maximum number of adult females that die each year was 4.4 and 6.0, respectively. The number of new juveniles and adult females marked each year on the E. S. George Reserve (mean over 13 years = 9.4) is slightly higher than the maximum estimate of deaths in the population.

Values of annual survival ($s_x$) for age 0 for the entire study period were used to calculate a life table. Variation in alpha was accounted for by increasing fecundity ($m_x$) values used in the life table between ages 14 and 17 years. Values of $m_x$ used in the life table are the number of female offspring produced per female (using average clutch size, assuming an unbiased hatchling sex ratio, and adjusting for an 0.8 annual reproductive rate for each female). The long-term mean nest survival (0.26) requires annual juvenile survival ($S_x$) between ages 1 and 13 years to average 0.78 to maintain a stable population, and it results in a cohort generation time ($\Sigma$ $xl_xm_x/R_0$; or, in a general sense, the average age of mothers of neonates in a population with a stable age distribution) of 37 years (Table 2). A second life table calculated using average nest survival of 0.44 for the period prior to 1985, holding all other parameters constant, resulted in $r$ = 0.015, $R$ = 1.67, and a reduction in the estimated average annual juvenile survival required to maintain a stable population by less than 4%.

The first set of 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 the average alpha in Blanding's turtles

**Table 2. A life tale for *Emydoidea blandingi* on the E. S. George Reserve. Data are long-term means for the population (see text).**

| *Age* | *s(x)* | *l(x)* | *m(x)* | *l(x)m(x)* |
|---|---|---|---|---|
| 0 | 0.2610 | 1.00000 | 0 | 0.0000 |
| 1 | 0.7826 | 0.26100 | 0 | 0.0000 |
| 2 | 0.7826 | 0.20426 | 0 | 0.0000 |
| 3 | 0.7826 | 0.15985 | 0 | 0.0000 |
| 4 | 0.7826 | 0.12510 | 0 | 0.0000 |
| 5 | 0.7826 | 0.09790 | 0 | 0.0000 |
| 6 | 0.7826 | 0.07662 | 0 | 0.0000 |
| 7 | 0.7826 | 0.05996 | 0 | 0.0000 |
| 8 | 0.7826 | 0.04693 | 0 | 0.0000 |
| 9 | 0.7826 | 0.03672 | 0 | 0.0000 |
| 10 | 0.7826 | 0.02874 | 0 | 0.0000 |
| 11 | 0.7826 | 0.02249 | 0 | 0.0000 |
| 12 | 0.7826 | 0.01760 | 0 | 0.0000 |
| 13 | 0.7826 | 0.01378 | 0 | 0.0000 |
| 14 | 0.9600 | 0.01078 | 1 | 0.0108 |
| 15 | 0.9600 | 0.01035 | 2 | 0.0207 |
| 16 | 0.9600 | 0.00994 | 3 | 0.0298 |
| 17 | 0.9600 | 0.00954 | 4 | 0.0382 |
| 18 | 0.9600 | 0.00916 | 4 | 0.0366 |
| 19 | 0.9600 | 0.00879 | 4 | 0.0352 |
| 20 | 0.9600 | 0.00844 | 4 | 0.0338 |
| 21 | 0.9600 | 0.00810 | 4 | 0.0324 |
| 22 | 0.9600 | 0.00778 | 4 | 0.0311 |
| 23 | 0.9600 | 0.00747 | 4 | 0.0299 |
| 24 | 0.9600 | 0.00717 | 4 | 0.0287 |
| 25 | 0.9600 | 0.00688 | 4 | 0.0275 |
| 26 | 0.9600 | 0.00661 | 4 | 0.0264 |
| 27 | 0.9600 | 0.00634 | 4 | 0.0254 |
| 28 | 0.9600 | 0.00609 | 4 | 0.0244 |
| 29 | 0.9600 | 0.00584 | 4 | 0.0234 |
| 30 | 0.9600 | 0.00561 | 4 | 0.0224 |
| 31 | 0.9600 | 0.00539 | 4 | 0.0215 |
| 32 | 0.9600 | 0.00517 | 4 | 0.0207 |
| 33 | 0.9600 | 0.00496 | 4 | 0.0199 |
| 34 | 0.9600 | 0.00477 | 4 | 0.0191 |
| 35 | 0.9600 | 0.00457 | 4 | 0.0183 |
| 36 | 0.9600 | 0.00439 | 4 | 0.0176 |
| 37 | 0.9600 | 0.00422 | 4 | 0.0169 |
| 38 | 0.9600 | 0.00405 | 4 | 0.0162 |
| 39 | 0.9600 | 0.00389 | 4 | 0.0155 |
| 40 | 0.9600 | 0.00373 | 4 | 0.0149 |
| 45 | 0.9600 | 0.00304 | 4 | 0.0122 |
| 50 | 0.9600 | 0.00248 | 4 | 0.0099 |
| 55 | 0.9600 | 0.00202 | 4 | 0.0081 |
| 60 | 0.9600 | 0.00165 | 4 | 0.0066 |
| 65 | 0.9600 | 0.00134 | 4 | 0.0054 |
| 70 | 0.9600 | 0.00110 | 4 | 0.0044 |
| 75 | 0.9600 | 0.00089 | 4 | 0.0036 |
| 80 | 0.9600 | 0.00073 | 4 | 0.0029 |
| 85 | 0.9600 | 0.00059 | 4 | 0.0024 |
| 90 | 0.9600 | 0.00048 | 4 | 0.0019 |
| 95 | 0.9600 | 0.00040 | 4 | 0.0016 |
| 100 | 0.9600 | 0.00032 | 4 | 0.0013 |
| 105 | 0.9600 | 0.00026 | 4 | 0.0011 |
| 110 | 0.9600 | 0.00021 | 4 | 0.0009 |

*Annual fecundity (4 eggs) is based on a mean clutch size of 10 eggs, a reproductive frequency of 0.85, and the assumption that half of all eggs produce daughters.* $s_x$ *is the annual 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 aged* x, r = *the intrinsic rate of population increase or the implicit solution of* $1 = \Sigma l_x m_x e^{-rx}$, *and* $T_c$ *is the cohort generation time for the population. Population parameters are* $R_o$ = *0.995,* r = *0.0001, and* $T_c$ = *37.5 years.*

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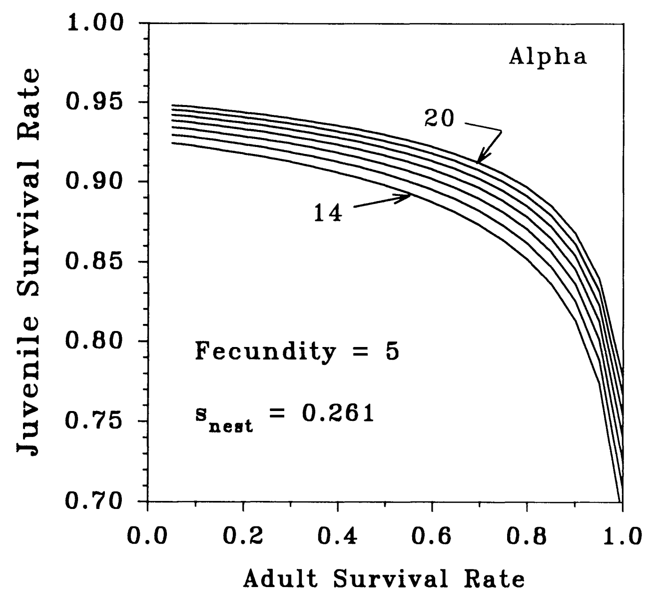

*Figure 1. The relationship between adult survival rate and juvenile survival rate while average age at sexual maturity (alpha) is allowed to vary from 14 to 20 years. Values for fecundity and nest survival are fixed.*

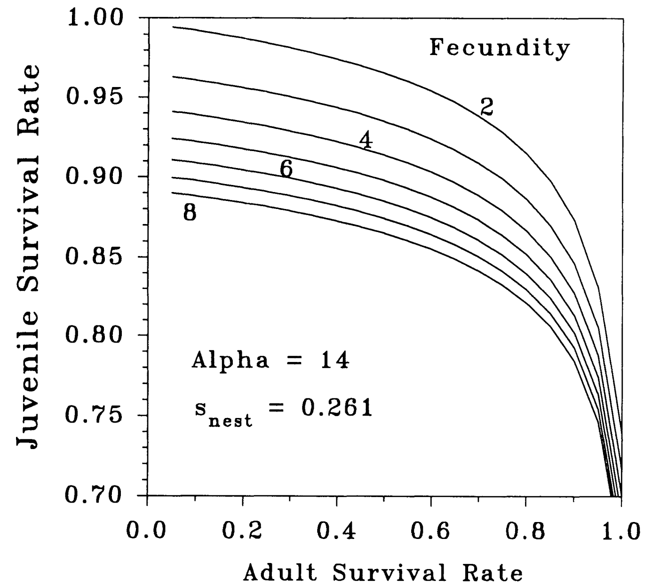

*Figure 2. The relationship between adult survival rate and juvenile survival rate while annual average fecundity is allowed to vary from 2 to 8 female-producing eggs per adult female. Values for alpha and nest survival are fixed.*

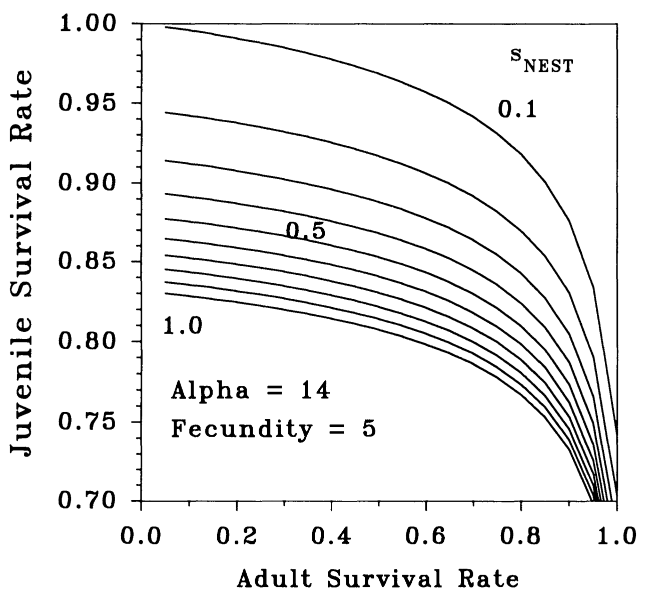

*Figure 3. The relationship between adult survival rate and juvenile survival rate while nest survivorship ($s_x$) is allowed to vary from 0.1 to 1.0. Values for alpha and fecundity are fixed.*

increased from 14 to 20 years, the average juvenile survivorship required to maintain a stable population would increase from 76% to approximately 85% (Fig. 1). To maintain a stable population, increases in fecundity from 2 to 8 female-producing eggs per adult female would allow a 10% reduction from the 84% average required juvenile survivorship (Fig. 2). When nest survival is reduced from 70% (approximately 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, 2, and 3) have the characteristic of being much steeper as adult survivorship exceeds 85%. The rate of change in population increase or decrease (deviation from $r = 0$) was least rapid for variation in nest survivorship and fecundity (Fig. 4*a,b*) and was most rapid for variation in juvenile and adult survivorship (Fig. 4*c,d*).

## Discussion

Blanding's turtles are among the longest-lived freshwater turtles for which data are available from the field (Brecke & Moriarty 1989). Some individuals marked on the E. S. George Reserve as adults in the mid-1950s remain in the population, are now approaching a minimum of 60 years of age, are still reproductive (Congdon & van Loben Sels 1991), and exhibit no signs of increased mortality or reproductive senescence (Congdon & van Loben Sels 1993). Annual survival rates of Blanding's turtles are among the highest reported for freshwater turtles (Gibbons & Semlitsch 1982; Mitchell 1988; Frazer & Gibbons 1990; Brooks et al. 1991; Frazer et al. 1991).

The decline in nest survival from 44% for the nine years prior to 1985 to 3% for the seven years after 1984

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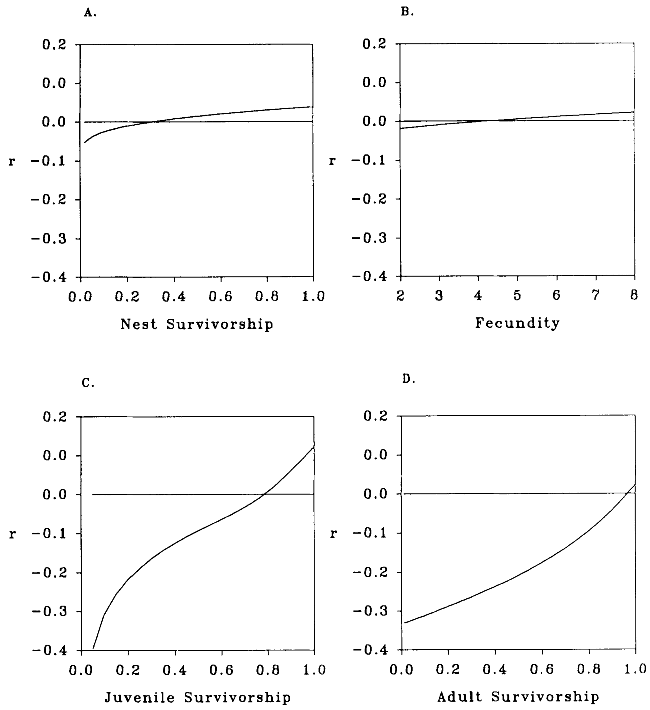

*Figure 4. The relationships between (a) fecundity, and survivorships of (b) nests, (c) juveniles, and (d) adults to population stability* (r = 0) *set by long-term mean values for Blanding's turtles on the E. S. George Reserve.*

represents a substantial problem to the population if the reduction is chronic—if nest survival remains low for more than a single generation time. Using the reduced nest survival data and keeping all other variables the same as in Table 2, the average juvenile survival from 1 to 13 years of age that was necessary to maintain a stable population increased from 75% to greater than 85%. Although the cause of the decline in nest survival is unknown, it coincided with a collapse in the fur market in general and, most important for turtles, the demand for the pelts of major nest predators such as raccoons and foxes. If (1) the decline in nest success of Blanding's turtles is caused by increasing predator populations; (2) the populations of raccoons and foxes remain high due to the absence of large predators; and (3) the growing public opinion against trapping furbearers and wearing or using wild animal furs continues, predator population control other than fur-bearer trapping may have to be implemented to maintain some turtle populations.

Female Blanding's turtles mature between the ages of 14 and 20 years, with the slowest-growing individuals maturing at the greatest ages (Congdon & van Loben Sels 1993). The average alpha of Blanding's turtles (17.5 years) approaches the limit of about 20 years predicted by demographic constraints (Dunham et al. 1989). In contrast to expectations based on (1) extended delay in alpha; (2) the marking of over 300 hatchlings prior to 1985 (Congdon and van Loben Sels 1991); and (3) the high annual survival rates of juveniles (>70%) required to maintain a stable population, few recaptures of juveniles below 9 years of age have been made. A low number of captures of juveniles has also been reported for other populations of Blanding's turtles (Gibbons 1968; Graham & Doyle 1979; Petokas 1986). Suggested reasons for the low numbers of juveniles captured include the following facts: (1) juveniles occupy habitats not trapped or typically searched by investigators (but see Pappas & Brecke 1992); (2) juveniles are very secretive, are not detected during searches, and are not susceptible to trapping; and (3) juveniles are rare and represent actual recruitment into a population of long-lived adults. The present analyses indicate that a high annual survival of juveniles is required to maintain the stable population on the E. S. George Reserve, which in turn suggests that the juveniles are present on the Reserve but are eluding capture. Being cryptic and secretive may be one way that juveniles attain high survivorships at early ages.

Two long-lived chelonians of conservation concern are sea turtles as a group and desert tortoises. Sea turtles (National Research Council 1990), desert tortoises (Turner et al. 1987), and Blanding's turtles share many life-history traits, including delayed sexual maturity, iteroparity, and high adult survival rates. Desert tortoises reach sexual maturity at between 12 and 20 years of age (Turner et al. 1987; Kristin Berry, personal communication), which is very similar to Blanding's turtles. Although the model and data from this study indicate that it is unlikely, some sea turtles may delay alpha for more than 20 years (Colin Limpus, personal communication). Demographic constraints on delaying sexual maturity makes attainment of sexual maturity at 50 years of age (Davenport 1988) virtually impossible. In years that sea turtles reproduce, they produce more and larger clutches (Lenarz et al. 1981) than do freshwater or terrestrial turtles. Since their reproductive interval may be over three years, however, their average annual fecundity is not as high as it appears from their large egg output in reproductive years (Frazer 1984). For example, a loggerhead turtle that produces four clutches of 120 eggs every four years has an average annual fecundity of 60 female-producing eggs. Desert tortoises have clutch sizes that average 4–5 eggs, and some females are capable of producing more than one clutch; however, some adult females do not reproduce every year (Turner et al. 1984; Turner & Berry 1986). As a result, fecundity in desert tortoises is approximately three to four female eggs and is similar to Blanding's turtles. Therefore, sea turtles and desert tortoises have life histories similar enough to Blanding's turtles to share the demographic constraints demonstrated in this study.

People have historically harvested both eggs and adult female sea turtles at nesting beaches for food (National Research Council 1990). More recently, nesting

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beaches have been restricted due to housing and recreational development, and mortality of adults and juveniles has increased through capture and drowning in fishing and shrimping trawls operating in near-shore waters. Desert tortoises recently have also been subjected to higher mortality associated with habitat destruction, upper respiratory tract disease, increased raven predation on hatchlings and young juveniles, harvesting for pets, and poaching (Berry 1986).

The model and data from Blanding's turtles point out that, in long-lived organisms in general and sea turtles and desert tortoises in particular, chronic reduction in the survival of adults requires an increase in the already high level of survivorship of juveniles to maintain a stable population. The probability that juvenile survival can increase substantially from the present high levels through compensatory release from density dependence, to offset even a relatively small chronic decrease in the survival of adults in long-lived organisms, seems very low (Brooks et al. 1991). Even under protected conditions on the E. S. George Reserve, the required survivorship of juveniles necessary to maintain a stable population is substantially higher than that documented for any other vertebrate (Ricklefs 1973; Turner 1977; Dunham et al. 1988; Wilbur & Morin 1988).

A general conclusion of this study is that the suite of life-history traits that coevolve with longevity results in populations that are severely limited in their ability to respond to chronic increases in mortality of neonates and even less so to increased mortality of juveniles or adults. Headstarting hatchlings in many cases will have little effect without a concomitant reduction in the causes of mortality among older juveniles and adults. In addition, the relatively low fecundity, low nest survival, and high adult survival coupled with extremely high juvenile survival required to maintain stable populations argue strongly against applying the concept of sustained harvest to populations of long-lived organisms. Effective management and conservation programs (Frazer 1992) will 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 increased mortality or reduced fecundity of any life-history stage. In addition, programs developed to aid in the recovery of depleted populations of long-lived organisms must recognize that there will be long delays before population responses can be detected.

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