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MODELS TO EVALUATE HEADSTARTING AS A MANAGEMENT TOOL FOR LONG-LIVED TURTLES¹

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Abstract. Most turtle species suffer high mortality in their first year, have a long juvenile period, and can live for decades once they reach adulthood. Conservationists have implemented a number of recovery plans for threatened turtle populations, including experimental “headstart” programs. Headstarting involves the captive rearing of hatchlings from eggs collected in the wild. The hatchlings are held for several months to help them avoid high mortality in their first year. It is hoped that these turtles survive and grow like wild turtles after release. The purpose of our study was to evaluate headstarting as a management tool for threatened turtle populations. We critically examined the population-level effects of headstarting with a series of deterministic matrix models for yellow mud turtles (*Kinosternon flavescens*), a “non-threatened,” well-studied species, and endangered Kemp’s ridley sea turtles (*Lepidochelys kempi*). We show that management efforts focused exclusively on improving survival in the first year of life are unlikely to be effective for long-lived species such as turtles. Population projections for both turtles predict that headstarting can augment increasing populations when adult survival is returned to or maintained at high levels, provided that headstarted juveniles are as vigorous as wild turtles. However, when subadult and adult survival is reduced, headstarting cannot compensate for losses in later stages. Proportional sensitivity (elasticity) analyses of stage-based matrix models indicated that annual survival rates for subadult and adult turtles are most critical; small decreases in the survival of older turtles can quickly overcome any potential benefits of headstarting. In general, the biological benefits of headstarting programs may be overestimated for turtles, and a careful examination of stage-specific mortality sources, demography, and life history can guide us toward more effective management strategies.

Key words: endangered-species management; headstart programs; *Kinosternon flavescens*; *Lepidochelys kempi*; matrix models; sea turtles; turtles.

INTRODUCTION

Headstarting is a broad term for the captive hatching and rearing of turtles through an early part of their life cycle. After reaching a prescribed age or size, headstarted turtles are released into their native habitat where they are assumed to have improved survivorship. The premise behind headstarting is to get hatchlings through their most vulnerable period, when they may be subject to intense predation. Animals with little or no parental care, relatively high fecundity, and low juvenile survival, such as threatened reptiles and amphibians, appear well suited for mass-rearing programs. But, as with any conservation method, we must carefully analyze the potential costs and benefits of headstarting before initiating such programs on a large scale.

Headstarting programs have been established on an experimental basis for several endangered sea turtle

species. A program for green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtle rearing was in operation from 1960 through 1989 in Florida (Huff 1989). In an attempt to speed the recovery of rapidly declining populations of Kemp’s ridley sea turtles (*Lepidochelys kempi*) and expand their nesting range to U.S. islands, the U.S. Fish and Wildlife Service and the National Marine Fisheries Service initiated the Kemp’s Ridley Sea Turtle Headstart program in 1978 (United States Fish and Wildlife Service and National Marine Fisheries Service 1992). Approximately 2000 eggs from Rancho Nuevo, Mexico were hatched annually and transported to holding facilities at the National Marine Fisheries Service Laboratories in Galveston, Texas. The turtles were raised in individual containers on a high-protein diet for 9–12 mo, then tagged and released offshore. The Kemp’s ridley headstart program was experimental and not considered a management tool (Wibbels et al. 1989). The expense of the program and an apparent lack of nesting by headstarted turtles led to controversy over the value of headstarting in the early 1990s (Allen 1990, Woody 1990, 1991, Taubes 1992, Eckert et al. 1992) and permits to continue egg collection at Rancho Nuevo were recently denied (By-

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les 1993). Yet many headstarting programs continue, and some conservationists have proposed headstarting as a strategy for augmenting freshwater and terrestrial turtle populations (Iverson 1991a).

In order to be a successful management tool, headstarting must increase population growth significantly. Population model analyses for loggerhead sea turtles indicated that first-year survival was much less critical than survival in later life stages, and an increase in egg and hatchling survival to 100% was unable to prevent population decline (Crouse et al. 1987, Crowder et al. 1994). Turtles are slow to mature, long-lived, and iteroparous; their life history design can compensate for high juvenile mortality so long as adult survival remains high (Congdon and Gibbons 1990). On the other hand, populations that are at very low levels may benefit from an increase in annual cohort size; this was the original justification for initiating the Kemp's ridley headstart program (Taubes 1992).

We hypothesized that headstarting is unlikely to work as a management tool for most long-lived turtles for two reasons. First, in a slow-maturing species an increase in first-year survival is unlikely to prevent population declines that are caused by reductions in the annual survival rate of larger turtles. This is particularly true in sea turtles, which may take decades to mature and are subject to incidental harvest in the sub-adult and adult stages (Crouse et al. 1987). Second, except in extremely small populations, it is infeasible to headstart enough hatchlings to have an impact on the overall survival rate of a cohort. Both of these predictions are based on demographics, and do not add the additional considerations of the effects of captive rearing on behavior, survivorship, and cohort genetic composition (Woody 1990, Taubes 1992).

To test our hypothesis, we first calculated the proportion of headstarted turtles in an annual cohort given a range of survival rates and rearing program sizes. The number of headstarted turtles in each cohort that reaches adulthood is dependent on both annual survival rates following release and the number of years to maturity. We then incorporated a series of headstart program scenarios into deterministic matrix models.

Our goal was to characterize the population-level effects of headstarting, thus evaluating it as a management tool for recovery of threatened or endangered species. Although Kemp's ridley headstarting is the most visible and controversial program, a population model for Kemp's ridley turtles is highly speculative based on the limited demographic data. Thus, we have examined the potential effects of different headstarting "programs" on a similar, well-studied species, the yellow mud turtle (*Kinosternon flavescens*). This "non-threatened" freshwater turtle has been the subject of a long-term mark-recapture study (Iverson 1991b). Iverson estimated age-specific annual survival and growth rates for yellow mud turtles, producing a complete life table. Both Kemp's ridleys and yellow mud turtles are

long lived and mature in 10–15 yr (Ross et al. 1989). This similarity in life history suggests that yellow mud turtles may be a fair model for Kemp's ridleys, although annual fecundity of the former is much lower and adult survival may be higher (see Tables 1 and 2).

Matrix models have been used to analyze population dynamics in a number of threatened species (Cohen et al. 1983, Simons 1984, Crouse et al. 1987, Lande 1988, Noon and Biles 1990, Crowder et al. 1994, Doak et al. 1994, Heppell et al. 1994). We used Leslie matrix models to examine the effects of headstarting on the population of adult female mud turtles at current survival levels and with adult survival decreased by an arbitrary 10%. We increased first-year survival according to three hypothetical headstart programs and graphed the population trajectories through time. To extend our analysis to Kemp's ridley sea turtles, we used survival estimates for similar sized loggerhead sea turtles in a series of hypothetical models with different juvenile growth rates. Finally, we compared the relative effects of changes in survival and fecundity on population growth rates in stage-based models for yellow mud turtles, Kemp's ridley sea turtles, and loggerhead sea turtles using an elasticity analysis (Caswell 1989). This analysis indicates which life history parameters are most critical to population growth, and can help focus management and research efforts (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1994, Schemske et al. 1994).

METHODS

General model

As a general model, we calculated the proportion of turtles in a cohort of age x that are from headstarting (HS) as:

$$HS = \frac{\text{headstarted turtles} \cdot l_x^h}{\text{headstarted turtles} \cdot l_x^h + \text{wild turtles} \cdot l_x^w},$$

where l_x^h and l_x^w are the proportions of headstarted turtles and wild turtles, respectively, that survive to age x . If p is the proportion of eggs moved into the hatchery and (S_x) is the ratio of headstarted-turtle survivorship to wild-turtle survivorship (l_x^h/l_x^w), the equation simplifies to:

$$HS = \frac{p \cdot S_x}{(p \cdot S_x) + (1 - p)} \quad (1)$$

Mean survivorship to adulthood may be calculated using estimates of annual survival and number of years to maturity. For a cohort that includes headstarted turtles, we calculated the proportion of hatchlings that reach maturity (AD) as:

$$AD = [(p \cdot \sigma_h) + (1 - p) \cdot \sigma_w] \cdot \sigma_{juv}^{t-1}, \quad (2)$$

where σ_h and σ_w are the first-year survival rates of headstarted turtles and wild hatchlings, respectively, σ_{juv} is the mean annual survival rate of all juvenile

turtles, and t is the number of years to maturity. This model assumes that released headstarted turtles and wild turtles have the same survival and growth rates; Eq. 2 can be easily modified to accommodate differences in age at maturity or annual survival if headstarted turtles differ in growth or time to maturity relative to their wild counterparts.

Matrix models

An age-based matrix model is a two-dimensional representation of a life table, showing the probability of transition to the next age (survival) and the number of female offspring produced annually by each age group. The similar stage-based model groups the ages into meaningful categories such as body size or life history stage (Crouse et al. 1987, Caswell 1989). For instance, our age-based model for yellow mud turtles is a 72×72 matrix with each row and column representing a single year in a turtle's life, while the comparable stage-based model has only four rows and columns, representing eggs/hatchlings, juveniles, subadults, and adults. We used age-based models to calculate population projections, as these models can predict the pattern of inherent, transient dynamics as the age distribution shifts following a change in survival rates (Crowder et al. 1994). We used stage-based models for elasticity analysis, which is a proportional sensitivity measure used to compare the relative contribution of stage-specific survival to the population growth rate, λ (see Appendix 1). Stage-based models are often more appropriate than age-based models for organisms that are difficult to age, like sea turtles, and for organisms with distinct life history stages that are subject to different management proposals (Crouse et al. 1987, Heppell et al. 1994).

There are several assumptions in deterministic, linear models. The models exclude migration, density dependence, and environmental and demographic stochasticity. Vital rates such as annual survival, growth, and fecundity are constant for each age or stage, and individuals within an age or stage are identical. While these assumptions certainly do not hold in nature, they allow for qualitative analytical results, mathematical simplicity, and interpretability. Results from these models, such as population growth rates and age distributions, are determined only after the model population has reached its stable age distribution and hence the model exhibits a constant rate of increase or decrease. We calculated the number of adult females in the population through time with a constant transition matrix; thus, our projections reflect average population trajectories and should be compared qualitatively.

Elasticity analysis

We calculated the proportional change in λ given a proportional change in stage-specific annual survival or fecundity ($E_{\text{elas}}(x)$) as:

TABLE 1. Stages used in the yellow mud turtle elasticity analysis. Data are derived from a life table (Iverson 1991b). Population growth rate: $\lambda = 1.0036$, $r = 0.0036$.

Stage	Annual survival, σ	Stage duration, T (h)
Eggs/Hatchlings	0.191	1
Juveniles	0.6375	4
Subadults	0.946	6
Adults	0.95	61

$$E_{\text{elas}}(x) = \frac{\lambda_{x+0.05x} - \lambda_{x-0.05x}}{\lambda_x \cdot 0.1}, \quad (3)$$

where $\lambda_{x \pm 0.05x}$ is the deterministic growth rate of the model with parameter x increased or decreased by 1%. The difference in the two population growth rates is then divided by the growth rate from the unperturbed matrix (λ_x) multiplied by the total perturbation (i.e., $0.05 + 0.05 = 0.1$). An elasticity analysis, unlike a non-proportional sensitivity analysis, allows us to compare the proportional effects of changes in parameters that are not on the same scale, such as survival (always < 1.0) and fecundity (often $\gg 1.0$) (Caswell 1989, Crowder et al. 1994).

Yellow mud turtle models

Our age-based Leslie matrix and stage-based matrix were derived from a life table estimated for a population of yellow mud turtles in the Nebraska Sandhills (Iverson 1991b). The age-specific survival and fecundity rates were obtained from recaptures of turtles aged by carapace growth rings. For our model simulations, we projected the model population through time using the 72-year age-based model and an initial population vector calculated from the stable age distribution of Iverson's life table (adult female population = 125 individuals). We incorporated three hypothetical headstart programs into the Leslie matrix. Our headstart scenarios assumed a captive survival rate of 90% in programs raising (1) 20 eggs per year total, all female; (2) 3% of eggs laid each year, 50:50 sex ratio, or (3) 3% of eggs laid each year, all female. We assumed that sex ratio could be manipulated by increasing the egg incubation temperature (Yntema and Mrosovsky 1980). After release at age 1 yr, we assumed that headstarted turtles survived, grew, and reproduced at the same rates as wild turtles. In our first series of projections, we used the age-specific survival rates given by the life table (Iverson 1991b). Then we reduced survival of all adult ages by 10% to evaluate the effect of each headstarting program when the population is declining.

We grouped the age classes into a four-stage matrix to compare stage-specific survival elasticities (Table 1). We calculated the harmonic mean of the age-specific survival rates in the life table to serve as our stage-specific survival rates (σ):

TABLE 2. Stage-specific annual survival rates and stage durations (*T*) used in a series of hypothetical matrix models for Kemp's ridley sea turtles. Changes in survival rates are due to management efforts: pre-1978 = no management; 1978–1990 = beach protection; post-1990 = beach protection, plus Turtle Excluder Device regulations, which decreased incidental drowning in trawls.

	<i>T</i> (yr)	Annual survival rate		
		pre-1978	1978–1990	post-1990
Model series 1 (8 yr to maturity)				
Stage				
Eggs/Hatchlings	1	0.1625	0.3250	0.3250
Juveniles	3	0.3724	0.3724	0.3724
Subadults	4	0.6758	0.6758	0.7730
Adults	...	0.7425	0.7425	0.8198
Population growth rate (λ)		0.970	1.034	1.114
Model series 2 (12 yr to maturity)				
Stage				
Eggs/Hatchlings	1	0.1625	0.3250	0.3250
Juveniles	4	0.6204	0.6204	0.6204
Subadults	7	0.6758	0.6758	0.7730
Adults	...	0.7425	0.7425	0.8198
Population growth rate (λ)		0.970	1.016	1.103
Model series 3 (16 yr to maturity)				
Stage				
Eggs/Hatchlings	1	0.1625	0.3250	0.3250
Juveniles	6	0.8120	0.8120	0.8120
Subadults	9	0.6758	0.6758	0.7730
Adults	...	0.7425	0.7425	0.8198
Population growth rate (λ)		0.970	1.006	1.089

$$\sigma_i = \left(\prod_{x=q}^r \sigma_x \right)^{\frac{1}{(r-q+1)}}, \quad (4)$$

where σ_x is the survival rate at age x , q is the first age in stage i , and r is the final age in stage i ($r - q + 1 = T$, the stage duration). Annual survival was calculated from the life table survivorships (l_x) as $\sigma_x = (l_x / l_{x-1})$. The harmonic mean accounts for the loss of individuals in each age category through time by taking the root of the product of the survival rates. All adult ages were grouped into the final stage (Iverson's annual survival rate = 0.95) and received the arithmetic mean of age-specific fecundity. We provide details on stage-based matrix parameterization in Appendix 1; for more information, see Caswell (1989).

Kemp's ridley models

Because many details of Kemp's ridley life history are unknown (Ross et al. 1989), we created three series of hypothetical four-stage models using demographic parameters pieced together from several sources. First, we assumed an age at maturity of 8, 12, or 16 yr (model series 1–3), which affected our juvenile survival estimates (Table 2). Conservation efforts have changed the survival rates of eggs and large turtles, so we produced three matrices for each age at maturity: (1) pre-1978: no conservation efforts, with an estimated population decline of 3% per year (United States Fish and Wildlife

Service and National Marine Fisheries Service 1992); (2) 1978–1990: nest protection only, which doubled egg/hatchling survival; and (3) post 1990: nest protection, plus Turtle Excluder Devices (TEDs), which have been found to reduce the number of drowned loggerhead turtles stranded on South Carolina beaches by 30–50% (Crowder et al. 1995). Thus, we produced a total of nine different matrices for our projections and elasticity analysis.

Fecundity was 105 female eggs per year per female, based on a 50:50 sex ratio and published fecundity and remigration interval estimates (Ross et al. 1989). Egg protection efforts doubled nest survival starting in 1978; thus, we halved the estimated egg/hatchling survival published in Ross et al. (1989) in each pre-1978 model. We then halved this number again to account for fish predation on hatchlings. While this mortality rate is somewhat arbitrary, it is likely to be an underestimate of total loss during the first year of life. Our final first-year survival estimate (pre-1978) was 0.1625.

Because there are no published estimates of survival for Kemp's ridleys beyond the hatchling stage, we used estimates from similar-sized loggerhead sea turtles (Frazer 1986), with survival of subadult Kemp's ridleys the same as that of large juvenile loggerheads (0.6758) and adult Kemp's ridley survival the same as subadult loggerheads (0.7425; Table 2). To simulate TED implementation, the mortality rates (=1 – survival rate) were decreased by 30%. We calculated three annual survival probabilities for juvenile survival dependent on age at maturity (8, 12, and 16 yr). For each pre-1978 model, we adjusted juvenile survival to achieve the observed population growth rate (λ) of 0.97 (Frazer 1986, Crouse et al. 1987). As we increased the duration of the juvenile stage we had to increase the estimated annual survival to maintain a $\lambda = 0.97$ (Table 2). The juvenile survival rate from each age-at-maturity series was held constant over time, as these turtles inhabit pelagic waters away from trawling activity and are not affected by TEDs.

Each of the nine stage-based models was expanded into an age-based model for our population projections. Unlike the Leslie model for the yellow mud turtle, we did not set a maximum age for Kemp's ridleys; the adults remained grouped as a stage with the annual survival rate appearing in the lower right-hand corner of the matrix. Starting with the stable age distribution generated by the pre-1978 model, we used the three matrices for each model series in succession to produce a population projection from 1978 to 2018.

RESULTS

General effects of headstarting on annual cohorts

The proportion of headstarted turtles in an annual cohort is determined by the percent of eggs going into the program and the ratio of headstart : wild survivorship in Eq. 1 (Fig. 1). Survivorship is the proportion

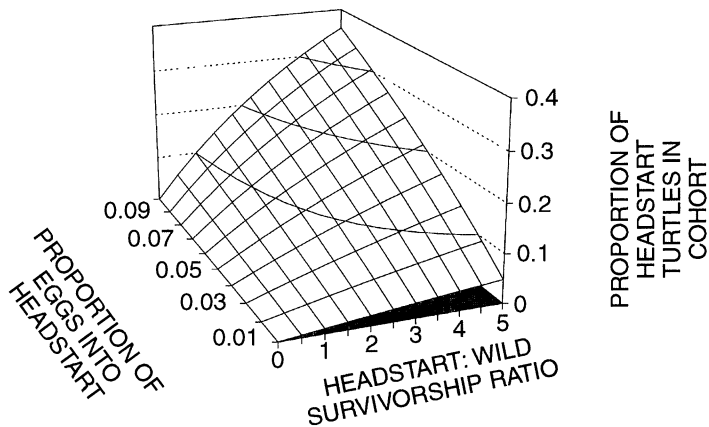


FIG. 1. Changes in the proportion of headstarted turtles in an annual cohort as the proportion of eggs going into a headstart program and the ratio of headstart: wild survivorship increases (results of Eq. 1).

of individuals that survive to a particular age, such as age 1 (when headstarted turtles are released) or age at maturity. When a large proportion of eggs laid go into headstarting and headstarted turtles have higher survivorship, the proportion of headstarted turtles surviving in the cohort increases dramatically and a headstarting program may significantly increase cohort size. In the most recent years of the Kemp's ridley headstart program, 2000 headstarted eggs comprised $\approx 2.5\%$ of the estimated total number laid at Rancho Nuevo (United States Fish and Wildlife Service and National Marine Fisheries Service 1992). At this level, only $\approx 5\%$ of a cohort would be headstarted turtles if their survivorship to a particular age was twice that of wild turtles, but nearly 13% of the cohort would be headstarted turtles if their survivorship was five times that of wild turtles (Fig. 1).

Yellow mud turtle headstarting projections

Without headstarting, the yellow mud turtle model predicted a population increase of 0.2% per year (Iverson 1991b) (Fig. 2). If a constant 20 female eggs per year are headstarted (3% of the eggs laid in 1986),

headstarting would contribute six additional adult females in the population in 30 yr, a 4.5% increase. If a constant 3% of eggs laid are put into headstarting, the increase jumps to 12 adult females in 30 yr. If the headstart eggs could all be hatched as females, the program would produce 27 additional adult females after 30 yr, a 20% increase. However, it is important to realize that 3%/yr in an increasing population results in more eggs taken each year; if yellow mud turtles were in need of enhancement, managers would have to carefully consider the feasibility of such a program. Also, due to the long time to maturity, this program would have to be long-term (i.e., decades) to fully evaluate the utility of headstarting.

But what if adult yellow mud turtles were pressured by some other mortality source, as has occurred in sea turtles? A ten percent (arbitrary) decrease in adult yellow mud turtle annual survival (from 0.95 to 0.855) causes a population decline of nearly 6%/yr (Fig. 3). None of our hypothetical headstarting programs were able to prevent this decline in the 30-yr simulation. Over 25% of all eggs laid would have to be hatched as females and headstarted to restabilize the population;

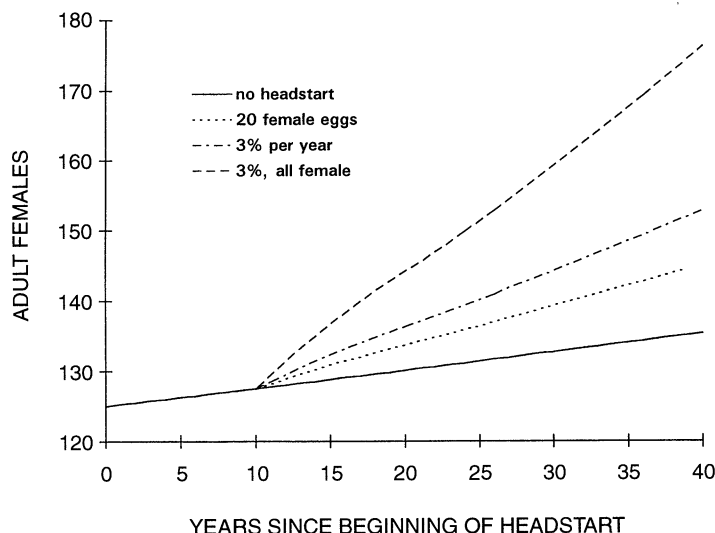
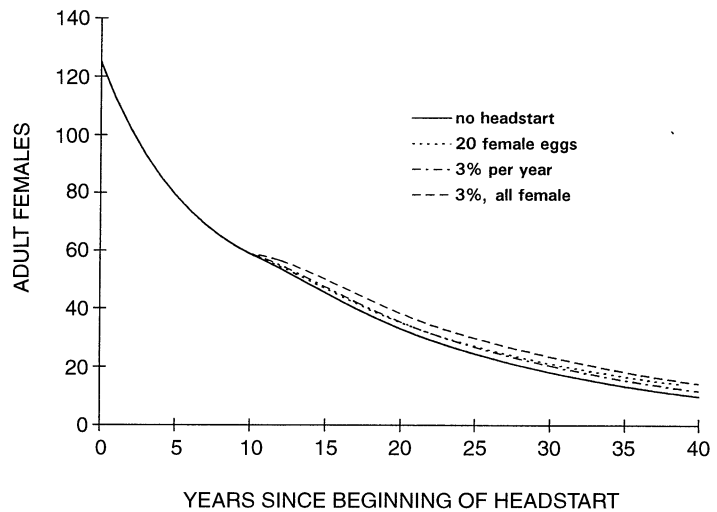


FIG. 2. Adult female population projections from a deterministic model of yellow mud turtles, showing four hypothetical headstart scenarios: no headstarting (—), headstarting 20 eggs per year incubated at a high temperature to produce all females (.....), headstarting 3% of all eggs laid each year assuming a 50:50 sex ratio (---), and headstarting 3% of all eggs laid with all headstart eggs hatched as females (-.-). Initial population size = 125 adult females, distributed according to the stable age distribution given by the Leslie matrix model. Headstarted hatchling survival = 0.9 in year 1, then equals wild turtle survival. For all simulations, we assume that headstarted turtles have the same survival, growth, and fecundity rates after release at age 1.

FIG. 3. Yellow mud turtle model projections with adult annual survival decreased by 10%. Headstart scenarios and symbols are identical to those in Fig. 2.



this is 80 eggs per year for Iverson's population. A similar increase in Kemp's ridley headstarting would be 16 000 eggs/yr.

Kemp's ridley headstarting simulations

Given the estimated number of female headstarted turtles released from 1978–1991 (Appendix 2; Cailouet and Fontaine 1992), and assuming 2000 female headstarted turtles continued to be released every year after 1991, a small increase in the number of adult females occurs in our model projections (Fig. 4). Naturally, a shorter generation time increases the potential benefits of headstarting. After 40 yr of headstarting there could be 750 additional adult females if Kemp's

ridleys mature in 8 yr, but only 450 additional females if they mature in 12 yr, and <100 additional females in the model series with 16 yr to maturity. These increases will only take place if Turtle Excluder Devices continue to reduce subadult and adult mortality by 30%, and if headstarted turtles are similar to wild turtles after release. Without TEDs, beach protection efforts that double egg survival result in a slow increase in the number of adult females when the model turtles mature in 8 yr. However, doubling egg survival in 1978 only stabilizes the population in the model with 12 yr to turtle maturity. In both of these model populations, headstarting has a negligible effect if TEDs are not implemented. If the age at maturity is increased further,

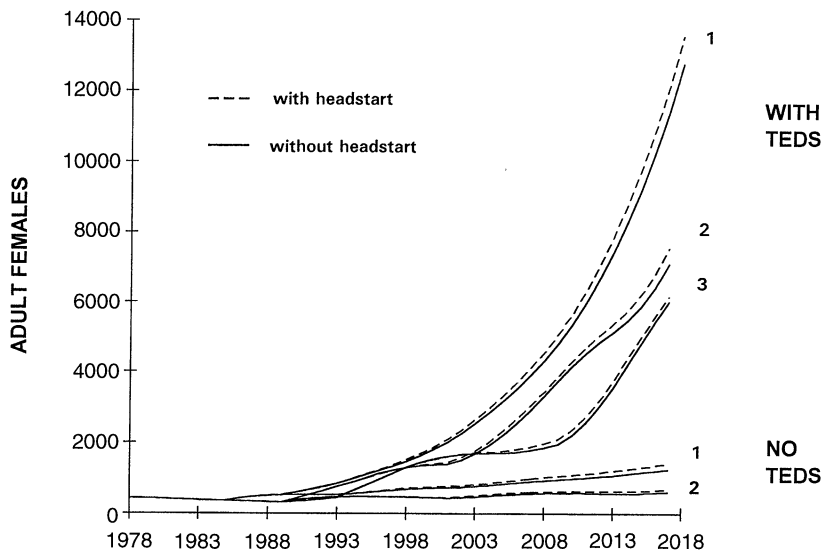


FIG. 4. Hypothetical population projections for Kemp's ridley sea turtles, produced from a Leslie model. Three matrices were used for each projection, corresponding to no management (pre-1978), nest protection (1978–1990), and nest protection with use of Turtle Excluder Devices, or TEDs (post-1990) (Table 2). The number of adult females through time is shown for 3 model series with and without headstarting, and with or without TED introduction in 1990. 1 = 8 yr to maturity; 2 = 12 yr to maturity; 3 = 16 yr to maturity. Initial population size = 447 adult females in 1978; initial population vector was determined by the stable age distribution of each model pre-1978, when the population was declining ($\lambda = 0.97$).

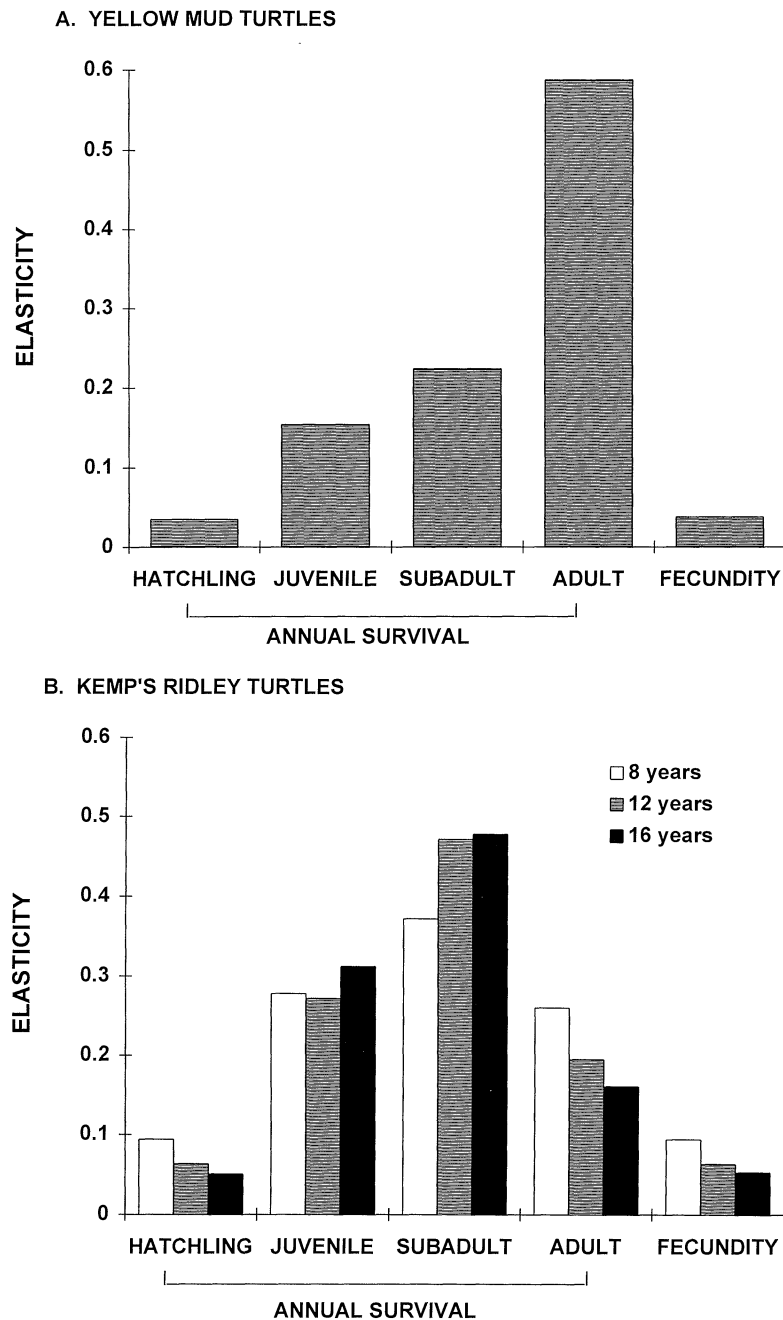


FIG. 5. Results of the elasticity (= proportional sensitivity) analyses, showing the proportional change in λ with a percent change in stage-specific annual survival and fecundity. (A) Yellow mud turtle model. (B) Three Kemp's ridley models with different ages at maturity, all post-1990 (nest protection and Turtle Excluder Devices employed).

the model population may actually decline if adult and subadult survival rates remain at pre-TED levels.

STAGE-BASED MODELS

Population growth rates

The population finite rate of increase in our yellow mud turtle stage-based model, as measured by the dominant eigenvalue of the transition matrix, was nearly identical to the growth rate obtained from the life table

(model $\lambda = 1.002$, life table $\lambda = 1.0036$). The population growth rates of the Kemp's ridley models varied from $\lambda = 0.97$ to $\lambda = 1.11$ (Table 2).

Elasticity analysis

Our elasticity analysis indicates which stage-specific vital rates are most critical to the overall population growth rate in our yellow mud turtle and Kemp's ridley sea turtle models (Fig. 5A, B). Kemp's ridley survival

elasticities are for post-1990, with beach protection (egg/hatchling survival doubled) and Turtle Excluder Devices employed (subadult and adult mortality decreased by 30%). For all models, λ is more sensitive to changes in juvenile, subadult, and adult survival than first-year survival or fecundity. In the yellow mud turtle model, elasticity peaks in the adult stage, while all three of the Kemp's ridley models show highest elasticity in the large juvenile/subadult stages. Stage-based models for loggerhead sea turtles also show peak elasticities in the juvenile stages (Crouse et al. 1987, Crowder et al. 1994). However, both yellow mud turtle and Kemp's ridley sea turtle models have very low fecundity elasticities; thus, their population dynamics are more strongly driven by the survival rates of large turtles than by fecundity or the survival rate of hatchlings. The three Kemp's ridley models demonstrate the reduction in hatchling survival elasticity as age to maturity increases (Fig. 5B).

DISCUSSION

In a demographic study of Blanding's turtles (*Emydoidea blandingii*) Congdon et al. (1993) argue that organisms with delayed sexual maturity and long lifespans are particularly susceptible to "chronic disturbance" or overexploitation. Turtle population dynamics are dependent on high juvenile and adult survival, and conservation efforts must recognize the importance of all life stages, not just eggs and hatchlings. It is likely that turtle life histories are adapted to low and variable offspring survival (Congdon and Gibbons 1990, Van Buskirk and Crowder 1994). Natural predation on eggs and hatchlings is high for most turtle species (Iverson 1991b), but adult survival is also very high. Because iteroparity gives female turtles a number of opportunities to replace themselves, it makes sense that management plans should ensure adult survival over hatchling survival (Congdon et al. 1993, Doak et al. 1994).

Eqs. 1 and 2 summarize the potential benefits of headstarting for annual cohorts. Both of these equations can help managers determine the minimum parameters necessary to make headstarting work. For instance, Eq. 1 gives the minimum headstart : wild survivorship ratio necessary if there is a target headstart contribution. If the goal is for headstarted turtles to make up 10% of the adult female population and 5% of eggs can be headstarted each year, headstart survivorship to adulthood needs to be 2.1 times greater than that of wild turtles in their cohort. Likewise, the cohort equation can be solved for the percent of eggs needed for headstarting if juvenile survival is known. The survivorship estimates can be calculated for any time period; if released headstarted turtles have the same annual growth and survival as wild turtles, the proportion of headstarted turtles in a cohort is determined at year one. On the other hand, if released headstarted turtles fare better or worse than their wild siblings the ratio of headstarted turtles to wild turtles in a cohort may not

be determined until adulthood, when females return to censused nesting beaches.

Clearly, the mortality and growth rates for both headstarted and wild individuals must be known in order to evaluate headstarting. If juvenile mortality is higher for headstarted turtles, their contribution to the adult population will, of course, diminish. But the contribution of a headstart program could increase if headstarted turtles matured earlier than others in their cohort due to their larger size. When the number of years to maturity is large, juvenile survival swamps out the effects of 1st-yr survival on population growth (Eq. 2). In other words, since the probability of surviving to adulthood is reduced exponentially by the number of years to maturity, the population dynamics of organisms such as turtles are driven more strongly by changes in annual juvenile survival than by survival in their first year of life.

Kemp's ridley turtle nests have been increasing at Rancho Nuevo since 1988 (United States Fish and Wildlife Service and National Marine Fisheries Service 1992; R. Byles, *personal communication*). While our deterministic model projections only give qualitative estimates of population size through time, it is clear that TEDs are necessary to ensure rapid population recovery. Proponents of headstarting have argued that the Kemp's ridley headstart program has been unsuccessful because prior to 1990, mortality of large juvenile and adult sea turtles related to shrimp trawling was so high that few headstarted turtles were likely to reach maturity. Our analyses support this hypothesis. Population recovery time and the contribution of the recent headstarting program are dependent on the age at maturity given similar annual survival rates in both wild and headstarted turtles. However, even with TEDs and a short time to maturity, the potential contribution of headstarting to the nesting population is incremental. Given the restricted funding afforded to endangered-species management, it would seem prudent to invest in TED development and enforcement rather than headstarting for Kemp's ridleys.

The proportional sensitivity analyses performed on the Kemp's ridley and yellow mud turtle stage-based models predict that headstarting is a relatively low-payback management option for long-lived species. The number of years in each stage and stage-specific survival determine the stable stage distribution of the model and reproductive values for each stage; elasticity values translate into a measure of importance of each stage for management and research efforts. Applying recovery methods to a single age group is likely to be less effective than management plans that enhance survival over a range of ages. TEDs, which decrease mortality for loggerheads and Kemp's ridley turtles >30 cm in length, should augment turtle populations far more than headstarting, which only affects survival in the first year of life.

Finally, these modeling exercises give us some ideas

about how different life history strategies warrant different types of species management plans. But models are purely hypothetical without good field data. It is critical for managers to have an understanding of the life history, demography, and age- or size-specific mortality sources for species in need of protection before drastic recovery measures become necessary (Congdon et al. 1993, Frazer 1992). Field biologists, land managers, and modelers can work together to determine the most effective management plan. But once a species recovery plan has been implemented, it must be monitored so that existing population projections can be updated. The impact of headstarting and other species recovery programs cannot be properly evaluated without research on the behavior and survival of both captive-reared and wild turtles.

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APPENDIX 1

STAGE-BASED MODEL PARAMETERIZATION

The annual stage transition probabilities (γ_i) were calculated assuming that all turtles spend a fixed number of years in each stage (Caswell 1989):

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1}$$

where λ is the population's finite rate of increase, or annual multiplication rate, and T_i is the duration of stage i in years. The matrix entries were P_i , the probability of surviving and remaining in stage i ; G_i , the probability of surviving and growing into the next stage; and F_i , the number of female hatchlings produced by surviving females in stage i :

$$\begin{aligned} P_i &= (1 - \gamma_i) \cdot \sigma_i, \\ G_i &= \gamma_i \cdot \sigma_i, \quad \text{and} \\ F_i &= (P_i \cdot f_i) + (G_i \cdot f_{i+1}), \end{aligned}$$

where f_i is annual fecundity. Because this model had an annual "census" just after nesting, fecundity was counted for females that survived through the year to breed ($P_4 \cdot f_4$), plus for those females that became sexually mature and were breeding for the first time ($G_3 \cdot f_4$). The final form of the matrix is identical to that used by Crouse et al. (1987) and Crowder et al. (1994) for loggerhead sea turtles, but with four rows and columns instead of five:

$$A = \begin{bmatrix} 0 & 0 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix}$$

We used the stage-based model to calculate the proportional change in λ with a small percentage in stage-specific annual survival (elasticity);

$$\text{Elasticity} = \frac{\lambda_{\sigma_i \times 1.05} - \lambda_{\sigma_i \times 0.95}}{\lambda \times 0.1},$$

where the denominator was the λ from the unperturbed matrix multiplied by the total percent change applied to σ_i . For each model perturbation, we reiterated λ to calculate γ_i . The partial differential equation given for stage-specific survival elasticity in Crowder et al. (1994: Appendix) was incorrect, as it did not account for the iteration of λ (although this correction does not change the elasticity results qualitatively, nor does it affect the authors' conclusions).

APPENDIX 2

Kemp's ridley turtles released from the Galveston Laboratory headstart program 1979–1992. Sex was determined primarily by histological examination of hatchlings that died during the program.

Year	No. headstarted turtles released	Sex of hatchlings	
		% female	No. examined
1979	2019	34.4	93
1980	1370	40.7	54
1981	1923	unknown	0
1982	1639	100.0	4
1983	1329	31.9	295
1984	190	50.0	24
1985	1040	28.6	559
1986	1534	53.7	294
1987	1727	82.8	64
1988	1280	99.6	538
1989	899	72.7	66
1990	1962	98.2	56
1991	1979	96.9	32
1992	1942	90.6	32