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Application of Life-History Theory and Population Model Analysis to Turtle Conservation

SELINA S. HEPPELL

As more reptiles find their way onto endangered species lists, it is increasingly important to identify management alternatives that can be applied across taxa. I have compared life tables from several turtle populations using elasticity analysis, a method that calculates the proportional contribution of each vital rate (age-specific survival and fecundity) to the annual population multiplication rate, λ [ln (λ) = r, the intrinsic rate of increase]. Most freshwater turtles share similar elasticity patterns across age classes, in spite of large variations in mean annual fecundity, annual survival, and age at maturity. High adult survival elasticity and low fecundity elasticity in these species suggests that conservation efforts that reduce mortality of adults are likely to stabilize declining populations. Desert tortoises and sea turtles had different elasticity patterns, with relatively higher juvenile elasticities when summed across age classes. Three different life tables for painted turtles also showed variation in elasticity patterns. Approximate elasticities can be generated for age-based matrices without a complete life table for each species, requiring only age at maturity, adult female annual survival, and population multiplication rate. This approximation may help identify sensitive life stages for poorly known species, thereby guiding research and management efforts and furthering our understanding of life-history patterns.

THIRTY-THREE species of reptiles were federally listed as threatened or endangered in the United States in 1994, and six additional species were listed as vulnerable or rare in the IUCN Red Data Book. Unfortunately, there is little demographic data available for many of these species, making it difficult to develop population models that can guide management plans. Although management alternatives that will increase habitat and/or survival rates may be easy to visualize, the potential impacts of various alternatives may not be obvious. When time and resources are limited, it may be desirable to rank management plans according to their potential benefit for species recovery and cost effectiveness (Heppell et al., 1996a). Analytical methods for calculating the proportional effects of changes in particular vital rates (fecundity, growth, survival) have been used to evaluate population models and the effectiveness of management plans for freshwater turtles (Wilbur, 1975; Congdon et al., 1993; Cunnington and Brooks, 1996), tortoises (Doak et al., 1994), and sea turtles (Crouse et al., 1987; Heppell et al., 1996a, 1996b). These analyses involve relatively simple life tables and population matrices but still require age-specific annual survival rates, fecundities, and growth probabilities. This may be particularly problematic for reptiles and amphibians, which have multiple life-history stages that occupy a variety of habitats and niches (Harless and Morlock, 1979; Wilbur and Mor-

in, 1988; Iverson, 1991a). Also, reptiles and amphibians tend to be less well studied than mammals and birds, and many reptiles have generation times that far exceed the average research funding cycle. How then can we make preliminary recovery plans with such limited biological information?

One obvious solution is to model potential management impacts on similar, well-studied species (Van Buskirk and Crowder, 1994; Heppell et al., 1996a). However, it is unclear whether phylogenetic relationship, morphological similarity, or similarity in some life-history characteristic is likely to be the most important factor in matching data from well-studied species to those of conservation concern. For example, is it best to test possible management scenarios for poorly known Berlandier's tortoises (*Gopherus berlandieri*) on a model population of congeneric gopher tortoises (*Gopherus polyphemus*) or yellow mud turtles (*Kinosternon flavescens*), which have a similar age at maturity, clutch size, and lifespan (Iverson, 1991b)? This paper will develop a method for predicting similarities in life table characteristics across species, thereby giving managers a way to predict the relative effects of a particular management plan on the population growth rate for poorly known species.

MATERIALS AND METHODS

Life tables are simple descriptions of age-specific survival and fecundity. By making the crit-

ical assumption that annual vital rates are relatively constant for each age class, we can use the life table to calculate the proportion of the population that is in each age class, the average number of mature female offspring produced by each female (R_0), mean generation time, and the asymptotic growth rate of the population (the intrinsic rate of increase, r). A life table can be converted into a two-dimensional matrix, providing analytical methods for quickly calculating population characteristics, including the effect of small changes in model parameters (Caswell, 1989).

A useful calculation for qualitative evaluation of management proposals is an elasticity analysis of a deterministic matrix model, which gives the proportional change in the annual population multiplication rate [λ, where $\log_e(\lambda) = r$] given a proportional change in age- or stage-specific survival, growth, or fecundity. This analysis allows us to compare the relative effects of proportional change in one or more life-history stages. For example, an elasticity analysis can reveal whether a 20% increase in hatchling survival will have the same population-level impact as a 5% increase in adult survival. I compared the elasticity values from life tables of a variety of turtle species in search of predictable patterns across taxa.

I examined a number of life tables from the literature and technical reports (Table 1). Life tables present the proportion of individuals remaining in a cohort after each year (survivorship, l_x) and the number of female offspring produced by females in each age class each year (fecundity, m_x). This fecundity term is an annual average that includes an interbreeding interval for those species that do not nest every year. In some cases, more than one life table was presented for a particular species or population (e.g., Frazer et al., 1990), and in others, age-specific survival and fecundity rates were given without a complete life table (e.g., Mitchell, 1988). Some of the life tables include preliminary survival estimates or those derived by assuming the population is at stationary equilibrium ($r = 0.0$). I did not attempt to judge the accuracy of each life table, but the results shown should be robust to minor changes in annual fecundity or age-specific annual survival.

I converted the life tables into age-based Leslie models (Leslie, 1945), with each row and column representing a single year in a turtle's life:

$$M1 = \begin{bmatrix} F_1 & F_2 & \cdots & F_{xmax-1} & F_{xmax} \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & G_{xmax-1} & 0 \end{bmatrix} \quad (1)$$

where F_x is the number of one-year-old female offspring produced by a female in age-class x (= annual fecundity × first-year survivorship, $m_x \times l_1$), G_x is annual survival probability (l_{x+1}/lx) and $xmax$ is the maximum age provided in the life table. This is a prebreeding census model, where individuals are "counted" just prior to the breeding season (Caswell 1989). The actual maximum lifespan is unknown for most turtles, and several of the life tables had a maximum age set at the point where less than 0.01% of adult turtles remained in the population. Although many turtles exhibit an increase in clutch size with female body size (Wilbur and Morin, 1988; Congdon and Gibbons, 1990; Van Buskirk and Crowder, 1994), most of the life tables gave an average fecundity for all adults, and all had a constant annual survival rate for adults. To simplify my matrices and eliminate the arbitrary maximum age, I lumped all the adults into a single age class, represented in the final column of the matrix:

$$M2 = \begin{bmatrix} 0 & 0 & \cdots & 0 & F \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & G_{\alpha-1} & P \end{bmatrix} \quad (2)$$

where P is the mean annual survival rate for adult females and α is age at maturity. Population growth rates and elasticity values were virtually identical between matrices with and without the lumped adult age class; the results I present here are for model type $M2$ [equation (2)].

To calculate elasticities, I used the software program Mathcad® to determine the stable age distribution (w_x) and age-specific reproductive values (v_x), which are the right and left eigenvectors associated with the dominant eigenvalue, λ. The elasticity matrix ($E_{x,y}$), which shows the proportional change in λ given a proportional change in each matrix parameter ($M2_{x,y}$), is given by:

$$E_{x,y} = \frac{\partial \log \lambda}{\partial \log M2_{x,y}} = \frac{M2_{x,y}}{\lambda} \times \frac{v_x \times w_y}{\langle v|w \rangle} \quad (3)$$

where $\langle v|w \rangle$ is the inner product of the two vectors, or $\Sigma(v_x \times w_x)$ (de Kroon et al., 1986; Caswell, 1989). Elasticities of matrix elements sum to 1.0; thus, the elasticities can be interpreted as proportional contributions of each matrix parameter to the population multiplication rate, λ (de Kroon et al., 1986). Elasticities differ from sensitivities, which are simply the change in λ given a change in a matrix parameter ($\delta\lambda/$

TABLE 1. SOURCES AND MEAN VITAL RATES USED TO COMPARE TURTLE LIFE HISTORIES.

Common name	Scientific name	Source	Age at maturity (yr)	Mean annual fecundity (female eggs/female)[a]	Population multiplication rate (λ)
Common mud turtle	*Kinosternon subrubrum*	Frazer et al., 1991	4	0.86, 0.96, 1.07[b]	0.89, 0.962, 1.074
Slider turtle	*Trachemys scripta*	Frazer et al., 1990	7	1.28, 1.28, 1.62[b]	0.777, 0.867, 1.006
Yellow mud turtle	*Kinosternon flavescens*	Iverson, 1991b	11	2.55	1.005
Blanding's turtle	*Emydoidea blandingii*	Congdon et al., 1993	14	4	1.002
Snapping turtle A	*Chelydra serpentina*	Cunnington and Brooks, 1996	19	16.18	0.976
Snapping turtle B	*Chelydra serpentina*	Congdon et al., 1994	13	12	1.0
Desert tortoise	*Gopherus agassizi*	Turner et al., 1987	14	4	1.021
Loggerhead sea turtle (U.S.)	*Caretta caretta*	Crowder et al., 1994	22	76.5	0.952
Loggerhead sea turtle (Australia)	*Caretta caretta*	Heppell et al., 1996b	35	32.54	1.000
Painted turtle	*Chrysemys picta*	Wilbur, 1975	7	6.6	1.001
		Tinkle et al., 1981	7	2.8	1.04
		Mitchell, 1988	8	2.05	1.018

[a] Assumes 50:50 sex ratio.
[b] Three values represent best, average, and worst-case scenarios (respectively) presented by the authors.

$\delta M2_{x,y}$). By calculating the proportional change in λ, we can compare the effects of proportional changes in fecundity and annual survival, which are on different scales (Caswell, 1989).

In general, management plans impact a life-history stage rather than a particular age group (e.g., reducing incidental trawling mortality in sea turtles increases survival probabilities for large juveniles, subadults and adults, spanning a number of age classes; Crowder et al., 1994). To compare the proportional effects of increasing annual survival in different life stages, I summed the elasticities for those years designated by stages denoted juveniles, subadults, and adults. Many of the life tables I analyzed did not designate the number of years spent as juveniles versus subadults, which should be based on size or habitat preference. I arbitrarily separated juveniles from subadults based on survival probabilities; subadults were those animals that experienced higher and/or more consistent annual survival probabilities (Table 2).

RESULTS

Life-table elasticities.—The elasticities for most freshwater turtles were very similar, in spite of differences in age at maturity (Fig. 1). Adult survival had the greatest influence on λ for all life tables, whereas fecundity elasticity was always very low. The summed juvenile and subadult survival elasticities varied, depending on the number of years spent in each stage. In all cases, adult survival elasticity was far greater than fecundity/first year survival elasticity.

In the desert tortoise and sea turtle models, juvenile and subadult survival elasticities were relatively much higher, and outranked adult survival elasticities in the two loggerhead populations (Fig. 2). Unlike the freshwater species, a large proportion of the sea turtle populations occurs in the juvenile stages. Thus, if management impacts were predicted to result in a 5% increase in annual survival for a particular sea turtle stage, it would be best to invest in plans that enhanced survival of subadults (U.S. loggerheads) or juveniles (Australian loggerheads) rather than adults. The results for desert tortoises are different; adult survival still has the highest elasticity, but subadult survival also has a large proportional effect on population growth.

Within-population elasticities.—The qualitative patterns generated by elasticity analysis can be robust for a given population, even when vital rates from one set of data are considerably different from those in another set (Fig. 3). Be-

TABLE 2. STAGE LENGTHS AND ANNUAL SURVIVAL RATES DERIVED FROM TURTLE POPULATION STUDIES CITED IN TABLE 1.

	Hatchlings[a]		Juveniles[b]		Subadults		Adults
	Age (yr)	Mean annual survival	Age (yr)	Mean annual survival	Age (yr)	Mean annual survival	Mean annual survival
Common mud turtle:							
Worst case	0	0.060	1	0.569	2–3	0.727	0.876
Average case	0	0.261	1	0.724	2–3	0.803	0.876
Best case	0	0.340	1	0.876	2–3	0.876	0.876
Slider:							
Worst case	0	0.010	1–3	0.248 (1) 0.774 (2–3)	4–6	0.774	0.774
Average case	0	0.105	1–3	0.539 (1) 0.829 (2–3)	4–6	0.814	0.814
Best case	0	0.275	1–3	0.829	4–6	0.854	0.854
Painted turtle:							
Wilbur (1975)	0	0.080	1–3	0.82	4–6	0.82	0.820
Tinkle et al. (1981)	0	0.670	1–3	0.76	4–6	0.76	0.760
Mitchell (1988)	0	0.193	1–2	0.457	3–7	0.944	0.960
Yellow mud turtle	0	0.191	1–4	0.663	5–10	0.946	0.950
Blanding's turtle	0	0.261	1–6	0.783	7–13	0.783	0.960
Snapping turtle A	0	0.064	1–9	0.754	10–18	0.754	0.966
Snapping turtle B	0	0.230	1–6	0.678	7–12	0.807	0.930
Desert tortoise	0	0.470	1–5	0.779	6–14	0.836	0.941
Loggerhead sea turtle (U.S.)	0	0.675	1–7	0.750	8–21	0.704	0.809
Loggerhead sea turtle (Australia)	0	—	1–20	0.827	21–34	0.861	0.910

[a] Includes egg survival and survival to age one.
[b] Stage lengths for juveniles and subadults set arbitrarily based on annual survival rates; subadults = annual survival ≥ 0.8.

cause of uncertainty in their survival and fecundity rates, Frazer et al. (1990, 1991) presented three different life tables for common mud and slider turtles, representing "best," "worst," and "average" scenarios (Tables 1–2). Both populations showed qualitatively similar elasticities across the three scenarios, in spite of large differences in annual survival probabilities. Adult survival had the highest elasticity for all three cases; and although juvenile and subadult survival elasticities increased from worst to best scenarios, the same general pattern could be inferred from all three models.

Between-population elasticities.—Two life tables for snapping turtles (Congdon et al., 1994; Cunnington and Brooks, 1996) showed qualitatively similar elasticity patterns with very high adult annual survival elasticity (Fig. 1). However, the elasticity patterns generated by three life tables for painted turtles were different due to large differences in vital rates (Fig. 4). In a population from southeastern Michigan (Wilbur, 1975), adult survival elasticity was lower than ju-

venile and subadult elasticities combined. An update of Wilbur's life table provided new fecundity and nest survival rates (Tinkle et al., 1981). The updated life table predicted a rapidly increasing population, which increased the relative contribution of survival in the preadult age classes. In contrast, painted turtles from central Virginia (Mitchell, 1988) showed elasticity patterns similar to other freshwater turtles. Thus, there is no guaranteed pattern of elasticities, and we need some way to estimate and compare them even when we have poor life-history data.

New method: elasticity approximation.—As discussed by Caswell (1989), in an age-based matrix, all prereproductive age-class survival elasticities are identical and are equal to the fecundity elasticity summed across all adult age classes in a Leslie model, type $M1$ [equation (1)]. In an age-based model with adults grouped into a single stage [$M2$, equation (2)], the fecundity elasticity and each juvenile survival elasticity are equal. This is because population growth is de-
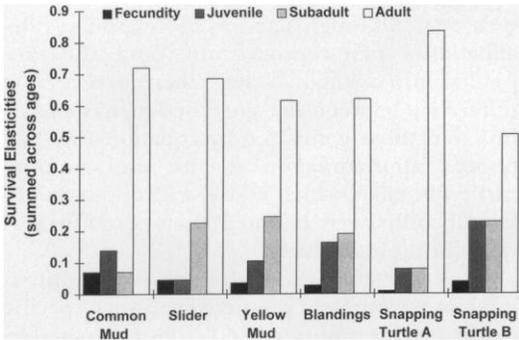
Fig. 1. Elasticities from freshwater turtle population models. Elasticity = proportional contribution of fecundity or annual survival to λ, the population multiplication rate. Age-specific elasticities were summed within life-history stages (juvenile, subadult, adult). Life table sources, stage lengths, and vital rates listed in Tables 1 and 2. Fecundity includes survival to age one (prebreeding census model). Snapping turtle A = Cunnington and Brooks, 1996; snapping turtle B = Congdon et al., 1994.

pendent on net reproductive rate (R_0) and survivorship to maturity (l_α). A proportional change in the annual survival rate of any prereproductive age class will equally affect λ, due to the commutative property of multiplication. For example, a 5% increase in age-1 survival has the same effect on survivorship to maturity as a 5% increase in age-2 survival:

$$l_\alpha = l_1 \times G_1 \times G_2 \times G_3 \times \ldots G_{\alpha-1}$$

$$l_1 \times (G_1 \times 1.05) \times G_2 \times G_3 \times \ldots G_{\alpha-1}$$

$$= l_1 \times G_1 \times (G_2 \times 1.05) \times G_3 \times \ldots G_{\alpha-1}$$

$$= l_\alpha \times 1.05 \tag{4}$$

Thus, the elasticities of an age-based matrix of form M2 [equation (2)] always look like this:

Fig. 3. Elasticities for worst, average, and best case scenarios expressed in life tables for common mud turtles and slider turtles (Frazer et al., 1990, 1991). Each life table included lowest, average, and highest survival and fecundity rates measured for each species (Table 1 and 2).

$$E = \begin{bmatrix} 0 & 0 & 0 & 0 & E_{fec} \\ E_{fec} & 0 & 0 & 0 & 0 \\ 0 & E_{fec} & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & (E_{fec})_{\alpha-1} & 1 - \sum_{x=1}^{\alpha} [(E_{fec})_x] \end{bmatrix}$$

$$\tag{5}$$

where α is age at maturity and E_{fec} is the elasticity of fecundity. Because matrix elasticities sum to 1.0, all the elasticities of an M2-type matrix can be reconstructed if E_{fec} is known. By examining the eigenvectors of matrix M2, I found that:

$$E_{fec} = \frac{P - \lambda}{(\alpha - 1)P - \alpha\lambda} \tag{6}$$

In other words, if age at maturity (α), adult survival (P), and annual population multiplication rate (λ) can be estimated from mark-recapture
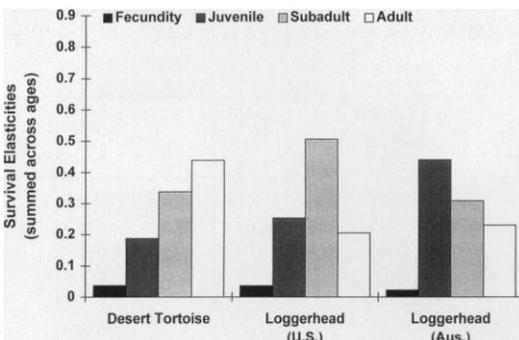
Fig. 2. Elasticities from desert tortoise and loggerhead sea turtle models. Loggerhead models generated from populations at Little Cumberland Island, Georgia (U.S.) and Heron Reef, Australia (Aus.).
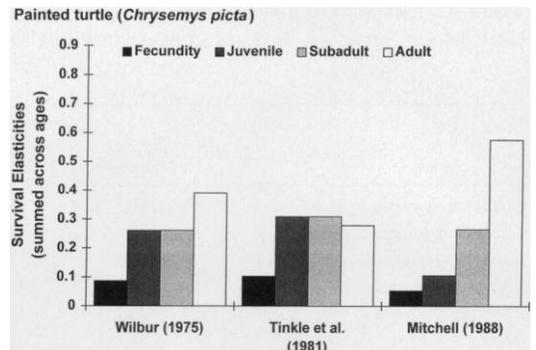
Fig. 4. Elasticities for three painted turtle life tables. Tinkle et al. (1981) is an updated life table for Wilbur's (1975) population in southeastern Michigan; Mitchell (1988) is for a population in central Virginia.

TABLE 3. ELASTICITIES FROM LESLIE MATRIX MODEL DERIVED FROM COMPLETE LIFE TABLES (SUMMED OVER RELEVANT AGES) AND APPROXIMATED FROM EQUATION (6) FOR DESERT TORTOISES (TURNER ET AL., 1987; λ = 1.01), BLANDING'S TURTLES (CONGDON ET AL., 1993; λ = 1.0), AND SNAPPING TURTLES (CONGDON ET AL., 1994; λ = 1.0).

Model	Fecundity	Juvenile survival	Subadult survival	Adult survival
Desert tortoise				
Leslie matrix	0.0351	0.1755	0.3159	0.4735
Equation (6)	0.0349	0.1746	0.3141	0.4765
Blanding's turtle				
Leslie matrix	0.0266	0.1596	0.1862	0.6276
Equation (6)	0.0264	0.1584	0.1848	0.6304
Snapping turtle B				
Leslie matrix	0.0393	0.2358	0.2315	0.4934
Equation (6)	0.0380	0.2283	0.2283	0.5055

and long-term census data, the proportional effect of changing fecundity or any age-specific survival rate can be approximated without a complete life table. Note that this approximation is only useful when the adult age classes can be treated as a single stage with mean annual survival and fecundity, as is often done for turtles in life-table analyses (e.g., Congdon et al., 1993).

I used arithmetic mean values for adult survival and annual fecundity of desert tortoises, Blanding's turtles, and Congdon et al.'s snapping turtles to compare the elasticities approximated by equation (6) with those pooled from a complete Leslie matrix (type $M1$; Table 3). The complete life tables for these three species include an increase in survival and/or fecundity

with age. Although age-specific elasticities decline after first reproduction, once they are pooled into a single "stage" there is very little difference between the age-based matrix elasticities and those generated by equation (6). The poorest approximation was for the snapping turtle life table, which had low fecundity values for subadults aged 11 and 12 to account for early-maturing individuals.

To demonstrate the usefulness of the approximation technique, I predicted the stage-specific elasticities for a number of turtles compared in a recent paper by Shine and Iverson (1995; Table 4). I assumed stable populations for the analysis (λ = 1.0) and summed E_{fec} across all preadult age classes. Species with high adult annual survival (> 0.9) also had very high adult survival elasticities. However, juvenile elasticity outranked adult elasticity for some species with late maturity, such as *Gopherus polyphemus*. This is in part due to the large proportion of a population in the preadult age classes for species that take many years to reach maturity. Thus, a change in the juvenile survival rate may affect a much larger proportion of the population than a similar change in adult annual survival, provided that the change affects all preadult age classes.

DISCUSSION

Many researchers have explored the similarities of life-history characteristics across species, phylogenetic groups, and body sizes and examined correlations between characters such as fecundity and age at maturity, age at maturity and adult lifespan, and so on (Stearns, 1992). Wilbur and Morin (1988), Iverson (1991a), and Congdon and Gibbons (1990) concluded that

TABLE 4. HATCHLING, JUVENILE, AND ADULT SURVIVAL ELASTICITIES CALCULATED FROM TURTLE LIFE HISTORIES COMPILED BY SHINE AND IVERSON (1995; TABLE 1) USING EQUATION (6) AND ASSUMING A STABLE POPULATION (λ = 1.0).

Species	Age at maturity	Adult annual survival	Hatchling (age 0) survival elasticity	Juvenile (preadult) survival elasticity	Adult survival elasticity
Podocnemis voglii	10	0.92	0.047	0.423	0.530
Chelodina longicollis	10	0.98	0.017	0.153	0.830
Kinosternon sonoriense	7	0.86	0.076	0.456	0.468
Terrapene ornata	11	0.83	0.063	0.630	0.307
Terrapene ornata	9	0.91	0.052	0.416	0.532
Mauremys leprosa	8	0.79	0.085	0.595	0.320
Gopherus polyphemus	11	0.90	0.050	0.500	0.450
Geochelone gigantea	23	0.97	0.018	0.396	0.586
Testudo graeca	12	0.88	0.052	0.572	0.376
Psammobates geometricus	6	0.61	0.132	0.660	0.208

turtles share common features of low annual fecundity, low and variable egg and hatchling survival, and long lifespan due to high adult survival rates. However, Iverson (1991a), Shine and Iverson (1995), and Cunnington and Brooks (1996) also suggested that differences may exist between freshwater, terrestrial, and marine turtle life histories because of variation in body size, growth rates, and annual fecundity. Age at maturity is highly correlated with adult annual survival across taxa (Shine and Iverson, 1995). My analysis shows that age-specific elasticities are dependent on these two life-history variables.

Van Buskirk and Crowder (1994) found some similarities in the reproductive characteristics of related sea turtle species but also found considerable variability within species. Because of strong differences in the reproductive traits of different populations, these authors cautioned against a "general" sea turtle population model. I found that elasticity patterns can be quite different for congeneric species and perhaps even populations of the same species (e.g., painted turtles) due to differences in estimates of age at maturity and adult survival rate. As initial management and research guides, models should be applied to species with similar life-history characteristics.

Calculating elasticities allows us to compare the effects of a proportional increase in a life-history stage. In practice, management options will have different levels of impact. For example, although adult survival of a particular population may only be increased by 5% (Plan A), it may be possible to increase juvenile survival by 25% (Plan B). The elasticities give a rough measure of how each management option could be ranked according to its potential impact on population growth:

$$\textit{Proportional increase in } \lambda \approx \textit{Proportional increase in survival} \times \textit{Elasticity} \qquad (7)$$

For this example, assume that the current population is declining at a rate of 5% per year (λ = 0.95). If adult survival elasticity is 0.6 and juvenile survival elasticity is 0.2, the increase in λ for Plan A would be approximately 0.05 × 0.6 = 0.03 (3% increase, λ = 0.95 × 1.03 = 0.9785), whereas Plan B would generate an increase of approximately 0.25 × 0.2 = 0.05 (5% increase, λ = 0.95 × 1.05 = 0.9975). In spite of the much greater elasticity of adult survival, management Plan B would be the better option according to the population model. However, the effects of large proportional changes in annual survival rates may not be adequately predicted by elasticity analysis in this manner, be-

cause the elasticities themselves will increase or decrease depending on the model parameters.

It is important to remember that elasticities represent the effects of proportional changes in age- or stage-specific survival or fecundity. This does not invoke a value on individuals; in fact, because adults have the highest reproductive value and are often a small proportion of a population, conservation efforts that save a few individual adults may have a very large proportional impact on stage-specific annual survival. Thus, in addition to calculating elasticities, some analysis of the potential costs and benefits of various management alternatives must be considered (Green and Hirons, 1991; Heppell et al., 1996a).

One criticism of the usefulness of elasticity analysis has been that the life-history stage with greatest elasticity may be inaccessible to management (Green and Hirons, 1991). But a high elasticity value should focus research into possible anthropogenic mortality sources that affect that stage and should indicate a high potential for population extinction should a new source of mortality affect that stage. Examples of this include proposed harvest of adult snapping turtles in Ontario (Brooks et al., 1991) and sargassum harvest affecting small juvenile sea turtles (Crowder et al., 1994). Congdon et al. (1993) suggested that turtle life histories make them particularly prone to overexploitation when adults suffer increased mortality, primarily because the low probability of reproductive success each year demands extreme iteroparity. My elasticity results for freshwater turtles support these hypotheses and predict a similar trend for all species that have very high adult survival rates.

Perhaps the best use for elasticity analysis is to determine which management proposals are unlikely to work, based on their impact on long-term population recovery. The "headstarting" program for Kemp's ridley sea turtles is just such an example (Heppell et al., 1996a). Turtles were hatched and reared in individual containers for nine months and then released. Without additional conservation efforts that reduced large juvenile and adult mortality (Turtle Excluder Devices that reduce incidental drowning in shrimp trawls), there was little chance that such a program could ever impact the population, given the low elasticity of first-year survival in long-lived species. Even if headstarting results in overall hatchling survival increases of 100–200%, such a program would probably have little effect on the growth rate of a population with age-0 survival elasticities of less than 0.05. Most important, increasing age-0 survival can-

not compensate for high adult mortality (Heppell et al., 1996a). However, successful captive rearing programs can produce large cohorts to "boost" a recovering population once its principle source of decline has been identified and reduced.

I have compared and approximated elasticities of simple age-based models with adults grouped into a single stage. The models are deterministic and assume that the populations are at a stable age distribution, where the proportion of individuals in each age class is constant over time. Naturally, this assumption is not met in most populations, and elasticities should be compared with caution. Because elasticities represent relative contributions to λ, large perturbations in annual survival may not translate directly into proportional changes in population growth [equation (7)]. Finally, variable growth rates and stage-specific habitats suggest that turtles, like other poikilotherms, should be classified by size rather than age. However, the age-specific methods described here could be applied to stage-based models that have been converted to age, as described by Cochran and Ellner (1992).

Age-specific elasticities can be approximated algebraically if adult annual survival, age at maturity, and population growth rate can be estimated. This information may still be difficult to attain for many species, but a range of possibilities could be plotted to predict which life stages are most critical to population recovery. Particularly problematic may be the population multiplication rate, which is often calculated from the life table itself. However, long-term censusing may give a general idea of whether a population is increasing or decreasing, and many life-history analyses assume that vital rates reflect stable populations. The approximation method should be regarded as a way to guide initial research and management efforts before more complete demographic data are available. Future research and monitoring of adaptive management programs will help resolve whether simple, deterministic models can adequately predict population responses to conservation efforts and perturbations.

Long-term field studies are critical to effective management and recovery of endangered or threatened species (Congdon and Dunham, 1994). Models that produce quantitative population projections, probabilities of persistence, and the impact of variability on population size and structure ultimately are needed for proper management (Soulé, 1987; Shaffer, 1990; Meffe and Carroll, 1994). Until complete data are available, the equations I present provide a way to compare life histories and determine which life stages have the greatest influence on population growth. Elasticity analysis can suggest which demographic variables need the greatest research. Once a set of management alternatives has been evaluated and initiated, additional data are necessary to produce predictive models and to monitor the impacts of human intervention.

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