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Ecology, Vol. 81, No. 3. (Mar., 2000), pp. 654-665.

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LIFE HISTORIES AND ELASTICITY PATTERNS: PERTURBATION ANALYSIS FOR SPECIES WITH MINIMAL DEMOGRAPHIC DATA

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Abstract. Elasticity analysis is a useful tool in conservation biology. The relative impacts of proportional changes in fertility, juvenile survival, and adult survival on asymptotic population growth λ (where $\ln(\lambda) = r$, the intrinsic rate of increase) are determined by vital rates (survival, growth, and fertility), which also define the life history characteristics of a species or population. Because we do not have good demographic information for most threatened populations, it is useful to categorize species according to their life history characteristics and related elasticity patterns. To do this, we compared the elasticity patterns generated by the life tables of 50 mammal populations. In age-classified models, the sum of the fertility elasticities and the survival elasticity for each juvenile age-class are equal; thus, age at maturity has a large impact on the contribution of juvenile survival to λ . Mammals that mature early and have large litters ("fast" mammals, such as rodents and smaller carnivores) also generally have short lifespans; these populations had relatively high fertility elasticities and lower adult survival elasticities. "Slow" mammals (those that mature late), having few offspring and higher adult survival rates (such as ungulates and marine mammals), had much lower fertility elasticities and high adult or juvenile survival elasticities. Although certain life history characteristics are phylogenetically constrained, we found that elasticity patterns within an order or family can be quite diverse, while similar elasticity patterns can occur in distantly related taxa.

We extended our generalizations by developing a simple age-classified model parameterized by juvenile survival, mean adult survival, age at maturity, and mean annual fertility. The elasticity patterns of this model are determined by age at maturity, mean adult survival, and λ , and they compare favorably with the summed elasticities of full Leslie matrices. Thus, elasticity patterns can be predicted, even when complete life table information is unavailable. In addition to classifying species for management purposes, the results generated by this simplified model show how elasticity patterns may change if the vital rate information is uncertain. Elasticity analysis can be a qualitative guide for research and management, particularly for poorly known species, and a useful first step in a larger modeling effort to determine population viability.

Key words: age-based model; conservation; elasticity analysis; life history; life table; mammal; management; matrix model; population model.

INTRODUCTION

Elasticity analysis can be used to categorize populations according to the response of population growth λ to perturbations that affect vital rates. An elasticity pattern is composed of the relative contributions of matrix entries to population growth that are grouped in biologically meaningful ways for comparative analysis. For example, in animal populations, we may want to compare the relative contributions of fertility, ju-

venile survival, and adult survival; while, in plants, the categories are often growth, reproduction, and stasis. Elasticity patterns are similar for populations or species that share life history characteristics. Comparisons have been made across taxa for plants (Silvertown et al. 1993, 1996), birds (Sæther et al. 1996, Sæther and Bakke 2000), and turtles (Cunnington and Brooks 1996, Hepppell 1998). These elasticity patterns may provide general rules of thumb for categorizing populations according to their relative responses to perturbations of particular life stages. Although general patterns exist for certain taxa, such as long-lived freshwater turtles, there is often considerable variation in the elasticity patterns of closely-related species, and even populations within a species, due to habitat characteristics or disturbance regimes that affect vital rates (Silvertown et al. 1996, Oostermeijer et al. 1996). Be-

Manuscript received 9 October 1998; revised 26 May 1999; accepted 29 May 1999. For reprints of this Special Feature, see footnote 1, p. 605.

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cause of variance and uncertainty in vital rates, it is important to know what combinations of vital rates and population growth rates give rise to particular elasticity patterns.

There is a practical need for a classification of populations according to their likely response to perturbation. Conservation management plans cannot be assessed for most species, because demographic data to construct detailed age- or stage-specific models are unavailable. Obtaining complete estimates of vital rates, including their temporal variances and covariances, is time consuming for any species and may be impossible for those that have long life spans or that cover wide geographic ranges, such as marine taxa (Boyce 1992, Caughley 1994, Heppell and Crowder 1998). Green and Hirons (1991) suggested that <2% of threatened bird populations have enough biological data to parameterize even simple population models. Consequently, demographic models are generally used on a case-by-case basis for particular, well-studied species, rather than as a general framework for setting management priorities (Caughley 1994, Groom and Pascual 1998). Although quantitative analysis of extinction risk is included as one criteria for risk categorization used by the International Union for the Conservation of Nature (IUCN), most species are classified by population size, as well as observed rates of decline or habitat loss (IUCN 1996). While the status of a population and its habitat is clearly an important factor, it does not provide guidance for optimizing management efforts (Mace and Hudson 1999). Because demographic information is incomplete for most threatened taxa, it is clear that a generalized approach is needed to guide research and management for poorly known species (Carroll et al. 1996).

Life history strategies are inexorably linked to vital rates. Thus, the impact of a perturbation to survival, growth, or fertility should be in part dependent on the life history strategy of the affected population. For example, a decrease in adult survival rate should be more detrimental to population growth in populations that are long lived with low annual reproductive success, than in those that are short lived and highly fecund. Recently, members of the IUCN fish conservation group suggested that life history characteristics be included as a weighting factor for risk classification, with early-maturing, highly fecund cod and tuna classified as less at risk than slow-growing species such as sharks (IUCN 1997). However, an objective method for assessing risk to threatened species according to their life history characteristics has yet to be developed.

Correlations among life history characteristics have been well studied for mammals, birds, reptiles, and other taxa (see Charnov (1993) and references therein). Many life history variables are strongly correlated with adult body size (Western 1979, Stearns 1983, Wootton 1987) and can be constrained by phylogeny (Stearns 1983, Harvey and Pagel 1991). Other relationships are

less intuitive and independent of body size (Harvey and Zammuto 1985, Gaillard et al. 1989, Read and Harvey 1989, Charnov 1993). Mammal life tables are common in the literature and have been used in comparative studies of life history tactics (Millar and Zammuto 1983, Promislow and Harvey 1990, Purvis and Harvey 1995). Several authors have used their results to categorize mammals on a "fast-slow" continuum, with species that reproduce early, have large litters, and exhibit short generation times contrasted with those with late maturity, one or fewer offspring per year, and long generation times (Read and Harvey 1989, Promislow and Harvey 1990). Links between elasticity patterns and the fast-slow continuum may provide a useful tool for classifying mammals according to their likely response to stage-specific perturbations.

However, elasticity analysis requires a population model, and the formulation of even a simple deterministic projection matrix requires a large amount of demographic information for a population, including a complete birth and death schedule. If data are scarce, we need a way to predict relative responses to perturbations based on elasticity analysis of approximate models. We can use elasticity patterns generated from models of similar, well-studied species. One problem with this approach is how to determine what constitutes a "similar" species, that is, should we rely on phylogeny, body size, or some suite of life history characteristics? Alternatively, we can develop simple models based on minimal demographic data, such as partial life cycle analysis (Caswell 1989). The characteristic equations of certain kinds of simplified models make it easy to interpret the source of elasticity patterns.

Life tables are easily converted to age-based projection matrices for elasticity calculations. We present here an analysis of 50 published life tables for mammals, many of which were used in past life history analyses. We compare elasticity patterns across and within mammalian orders to identify the source of elasticity patterns, i.e., the relative proportional contributions of reproduction, juvenile survival, and adult survival to the growth rate of a population. We then derive a new method to estimate elasticities without a complete life table, and we compare the results with those of complete age-based models. Our results reveal much about how mammals and other vertebrates can be categorized by life history types, and how elasticity patterns may shift with changes or uncertainties in age at maturity, adult survival, and population growth rate. We hope to provide a valuable tool for making predictions about the effects of perturbations for poorly known species.

METHODS

Analysis of mammalian elasticity patterns

We examined 50 published life tables for 44 mammal species representing 10 orders and 25 families (Ap-

pendix A). Order and family classifications are listed according to Wilson and Reeder (1993). In 32 cases, the life tables included age-specific reproductive rates (female newborns per female per year), which generally varied according to proportion of females who were mature in a given age class. In the remaining life tables, survivorship and age at first breeding were the only age-specific data available, so the mean fertility provided by the author(s) was prescribed to all mature age classes. Life tables that were constructed on half-year intervals were rounded to the next integer year.

We calculated several standard life history measures for each life table, including the net reproductive rate for the population R_0 , mean generation time T_c , survivorship to first maturity l_α , and life expectation at birth \hat{e}_0 , and life expectation at maturity \hat{e}_α (expectation of further life; Pianka [1978]):

$$R_0 = \sum_{i=0}^k l_i m_i \tag{1}$$

$$T_c = \frac{\sum_{i=0}^k i l_i m_i}{\sum_{i=0}^k l_i m_i} \tag{2}$$

$$\hat{e}_0 = \sum_{i=0}^k l_i \tag{3}$$

$$\hat{e}_\alpha = \frac{\sum_{i=\alpha}^k l_i}{l_\alpha} \tag{4}$$

where l_i is the survivorship of a cohort to age i , m_i is the number of female offspring produced annually by a female aged i , k is the maximum age, and α is the age at first reproduction (the first age class with $m \neq 0$).

We then converted each life table to a prebreeding, birth pulse projection matrix (Leslie matrix [Leslie 1945, Caswell 1989]) in which the survival probability P_i and fertility F_i of age class i are given by the following:

$$P_i = \frac{l_{i+1}}{l_i} \tag{5}$$

$$F_i = l_i m_i. \tag{6}$$

F_i thus includes survival to age 1. We calculated the elasticity matrices \mathbf{E} from the eigenvectors of each projection matrix \mathbf{A} (Caswell et al. 1984, de Kroon et al. 1986):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{7}$$

where \mathbf{v} and \mathbf{w} are the left and right eigenvectors of the projection matrix \mathbf{A} , and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the two vectors. We summed the elasticities of λ to

changes in P_i and F_i across age classes to obtain the following quantities of interest:

0 1. Fertility elasticity, which is the effect of a proportional change in reproductive output for all adult age classes (the sum of elements in the top row of \mathbf{E}).

1 2. Juvenile survival elasticity, which is the effect of a proportional change in all annual survival rates for age 1 to the year just prior to maturation (the sum of the subdiagonal elements of \mathbf{E} from column 1 to column $\alpha - 1$, where α represents the first age class that includes breeding females).

2 3. Adult survival elasticity, which is the effect of a proportional change in all annual survival rates for mature individuals (the sum of the subdiagonal elements of \mathbf{E} from α to k).

To examine the relationship between mean fertility, mean adult survival, and elasticity patterns, we calculated weighted means of age-specific adult survival P_i and age-specific fertility F_i . We weighted the means according to the probability of survival to age i , so that

$$\bar{P} = \frac{l_\alpha P_\alpha + \dots + l_{k-1} P_{k-1}}{l_\alpha + \dots + l_{k-1}} = \frac{\sum_{i=1}^{k-\alpha} (l_{\alpha+i})}{\sum_{i=0}^{k-\alpha-1} (l_{\alpha+i})} \tag{8}$$

and

$$\bar{F} = \frac{l_\alpha F_\alpha + \dots + l_k F_k}{l_\alpha + \dots + l_{k-1}} = l_1 \frac{\sum_{i=0}^{k-\alpha} (l_{\alpha+i} m_{\alpha+i})}{\sum_{i=0}^{k-\alpha} (l_{\alpha+i})}. \tag{9}$$

We plotted the summed elasticities from each matrix on a three-way proportional graph after Silvertown et al. (1993), where maximum elasticities for fertility, juvenile survival, and adult survival occur at the apexes of the triangle. We grouped the species broadly: "rodents" (including rabbits), "carnivores" (including bats), "marine" (whales, seals, sea lions, and manatee, all restricted to at most one offspring per year), "grazers" (ungulates, zebra, hippopotamus, and elephant), and primates. We also plotted the proportional contributions of fertility, juvenile survival, and adult survival to population growth, in order to show which species have similar elasticity patterns and how the patterns are affected by generation time. Although a correlation analysis of life table results and all of the summed elasticities was inappropriate, due to the proportional nature of elasticities (Shea et al. 1994), we calculated Spearman rank correlation coefficients for adult survival elasticity and life table results to show how these results are related. To compare relationships within vs. between mammalian orders, we also calculated the correlation coefficients for life tables of orders Artiodactyla, Rodentia, and Carnivora. Life table calculations and matrix analyses were performed using Mathcad software (MathSoft, Cambridge, Massachusetts, USA).

Spearman rank correlations were calculated according to Zar (1984).

We note the following useful property of elasticities. The first row of an age-classified projection matrix contains the fertilities F_i , which adopt the value of zero for $i < \alpha$, where α is the age at first reproduction. In the characteristic equation, the survival probabilities for age classes 1 through $\alpha - 1$ appear only as the product $P_1 P_2 \dots P_{\alpha-1}$. A proportional change in any of these probabilities has the same effect on this product. Thus, the elasticities $e_{p_1}, e_{p_2}, \dots, e_{p_{\alpha-1}}$ are identical. Because the sum of any row in an elasticity matrix \mathbf{E} equals the sum of the corresponding column (de Kroon et al. 1986), the sum of the fertility elasticities must equal e_{p_1} , and, by extension, $e_{p_2}, \dots, e_{p_{\alpha-1}}$. If $\alpha = 1$, there are no prebreeding age classes in the projection matrix (recall that we are constructing matrices with a prebreeding census), hence no juvenile survival elasticity. When $\alpha > 1$, the relationship between the summed juvenile survival elasticity and the summed fertility elasticity is

$$\sum_{i=1}^{\alpha-1} e_{p_i} = (\alpha - 1) \sum_{j=1}^k e_{F_j} \tag{10}$$

Elasticity patterns of a simplified demographic model

Because a complete age-classified life table requires a large amount of data, we consider a simplified model, in which adult survival is assumed to have the age-invariant value \bar{P} , and annual fertility is assumed to have the age-invariant value \bar{F} . Such a model is a good approximation for long-lived organisms with little senescence, but it can be applied to any species. In at least some cases where detailed comparisons have been possible, simplified models have done a good job of capturing the essentials of full age-classified models (Brault and Caswell 1993, Levin et al. 1996). The transition matrix is given by the following:

$$\mathbf{B} = \begin{bmatrix} 0 & 0 & \dots & 0 & \bar{F} \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & \vdots \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & P_{\alpha-1} & \bar{P} \end{bmatrix} \tag{11}$$

where \bar{P} is the weighted mean of adult annual survival (Eq. 8). In the prebreeding census models used in this analysis, survival to age 1 is included in the weighted mean fertility term \bar{F} (Eq. 9) (Caswell 1989). Adults that survive remain in the final stage indefinitely. The characteristic equation for this matrix is given by

$$1 = \frac{\left(\prod_{j=1}^{\alpha-1} P_j\right) \bar{F} \lambda^{-(\alpha-1)}}{\lambda - \bar{P}} \tag{12}$$

Again, the juvenile survival probabilities appear only

as their product; thus, all prereproductive survival elasticities are equal, as well as being equal to the elasticity of λ to changes in \bar{F} . Because the elements of the elasticity matrix sum to unity, the elasticity of λ to changes in mean adult survival for matrix \mathbf{B} is

$$e_{\bar{p}} = (1 - \alpha e_{\bar{f}}) \tag{13}$$

This relation also follows directly from loop analysis, as \mathbf{B} is composed of two loops (the birth-to-maturity loop and the adult stasis loop), whose elasticities must sum to unity (van Groenendael et al. 1994). Thus, the elasticity matrix of a prebreeding census model with a single adult stage looks like this:

$$\mathbf{E}_{\mathbf{B}} = \begin{bmatrix} 0 & 0 & 0 & 0 & e_{\bar{f}} \\ e_{\bar{f}} & 0 & 0 & 0 & 0 \\ 0 & e_{\bar{f}} & 0 & 0 & 0 \\ \vdots & 0 & \ddots & 0 & \vdots \\ 0 & 0 & 0 & e_{\bar{f}} & e_{\bar{p}} \end{bmatrix} \tag{14}$$

The eigenvectors of \mathbf{B} lead to a simple equation for $e_{\bar{f}}$ (see Appendix B):

$$e_{\bar{f}} = \frac{\bar{P} - \lambda}{(\alpha - 1)\bar{P} - \alpha\lambda} \tag{15}$$

Because adult survival is age independent, cohorts persist indefinitely in this model. If adult survival rate is high, it can be many years before a cohort becomes so small that it has no influence on population growth. To partially compensate for this, we discounted \bar{P} for maximum life span using an equation given by Caswell (1989) for calculating the probability of leaving a stage given that it has a fixed duration:

$$\gamma = \frac{\left(\frac{\sigma}{\lambda}\right)^T - \left(\frac{\sigma}{\lambda}\right)^{T-1}}{\left(\frac{\sigma}{\lambda}\right)^T - 1} \tag{16}$$

where σ is the annual survival, and T is the stage length in years. We used $\sigma = \bar{P}$ and $T = (k - \alpha + 1)$ to calculate γ , from which we computed an adult survival rate:

$$\hat{P} = \bar{P}(1 - \gamma) \tag{17}$$

When \bar{P} is replaced with \hat{P} , cohorts still persist indefinitely, but survival is reduced to mimic the effect of senescence.

Using Eqs. 13 and 15, it is possible to calculate the elasticities of λ to changes in fertility, juvenile survival, and adult survival knowing only \bar{P} (or \hat{P}), α , and λ . Juvenile annual survival rates, while necessary to complete matrix \mathbf{B} itself, are not needed to determine the elasticities of \mathbf{B} , if λ can be estimated by other means. In the absence of detailed demographic information, a crude estimate of the elasticities can be obtained by setting λ to a value based on observed long-term pop-

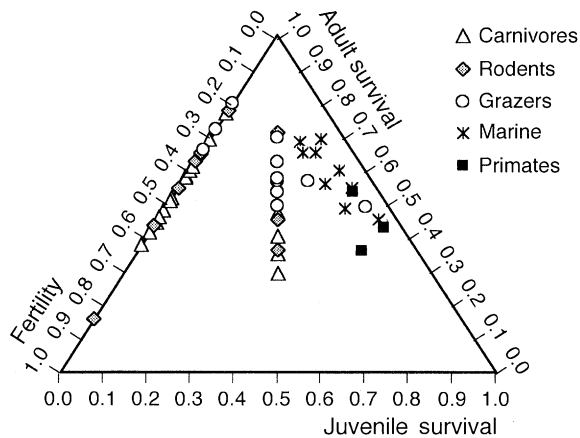


FIG. 1. Three-way proportional graph of the survival elasticities calculated for 50 mammal life tables. Species are sorted generally into five groups: "marine" (whales, pinnipeds, manatee), "primates," "carnivores" (including bats), "rodents" (including rabbits), and "ungulates" (including elephant and hippopotamus). Because the three elasticity values sum to unity, the position of each point on the plot gives the relative contribution of survival in each stage to population growth. Points close to a corner have high elasticities for that life stage. Points along the left-hand side of the triangle are species that mature in a single year and do not have a juvenile stage.

ulation trends (assuming stable age distribution, Crouse et al. 1987), or to a default value of 1.0, corresponding to a stationary population. These estimates can be used to explore how age at maturity, adult survival, and population growth rate affect elasticity patterns in poorly known species.

Comparing matrix elasticities with elasticity approximations

Because model **B** replaces age-specific survival and fertility with their mean values, we compared the elasticities from the matrices **A** and **B**, which were calculated from the same data, using linear correlation (Excel 7.0 [Microsoft, Redmond, Washington, USA]). Because 22 of the life tables did not include a juvenile stage (age at maturity = 1 yr) the correlation analysis for juvenile survival elasticity was restricted to the remaining 28 populations.

RESULTS

Mammalian elasticity patterns

Plotted together on a three-way proportional graph, elasticity patterns cluster according to age at maturation (Fig. 1). The distance from a point to a corner of the triangle represents the inverse of its value; for example, points close to the adult survival corner have high adult elasticities. The line of points along the left margin of the triangle has a juvenile survival elasticity of zero, because those points represent populations that mature at age 1 and, therefore, do not have a juvenile stage. The vertical line of points in the middle of the

triangle are populations that mature at age 2, where fertility and age-1 survival elasticities are equal (Eq. 10). The remaining points are from populations that mature in ≥ 3 yr. Marine mammals and primates cluster along the right side of the triangle; with late maturation and long life spans, these species have low fertility elasticities. Two "grazers" also fall in this group: the elephant and hippopotamus. All of the ungulates in the sample mature by age 2, but generally have higher adult survival rates and adult survival elasticities than "carnivores" or "rodents." The larger grazers, marine mammals and primates, all have adult survival elasticities near or in excess of $10\times$ the fertility elasticity.

When the elasticities for each population are plotted according to the three age-at-maturation groups (1, 2, and 3+), the patterns become more discernable (Fig. 2). There is a general decrease in fertility elasticity with increasing generation time (T_c , Eq. 2). Adult survival elasticity increases with generation time within the $\alpha = 1$ and $\alpha = 2$ groups (Fig. 2A and B, respectively). Juvenile survival elasticity is more variable, but also increases with age at maturity (Fig. 2C). This is in part due to the fact that, for a given adult survival rate, an increase in age at first reproduction results in a proportionately larger juvenile stage. Note that the differences in elasticity patterns among the mammals that were sampled are also related to body size, with later age at maturation and smaller litter sizes in larger animals. Mammals with similar elasticity patterns are often not related; reindeer and yellow-bellied marmots have different vital rates (see Appendix A), but nearly identical summed elasticities (Fig. 2b).

To explore the relationship between summed elasticities and life history properties, we calculated rank correlations between adult survival elasticity and the life table statistics given in Appendix A. These results are displayed in Table 1. Recall that juvenile survival elasticity is fertility elasticity multiplied by $(\alpha - 1)$ (Eq. 10); thus, fertility elasticity correlates strongly with age at maturity and all life table results that are dependent on age at maturity, while correlations with the summed prereproductive elasticities (fertility + juvenile survival) are simply opposite those shown for adult survival elasticity. For all mammal life tables combined, adult survival elasticity was negatively correlated with fertility, and positively correlated with survivorship to maturity, as well as with variables associated with adult survival and life span. Surprisingly, adult survival elasticity was not significantly correlated with generation time. A plot of adult survival elasticity vs. generation time reveals a hump-shaped correlation where populations with very long generation times have lower adult survival elasticities (Fig. 3). Within the rodents, which generally have short generation times, generation time is positively correlated with adult survival elasticity. Some other within-order correlations were stronger than those calculated for all life tables combined, but most were insignificant due to

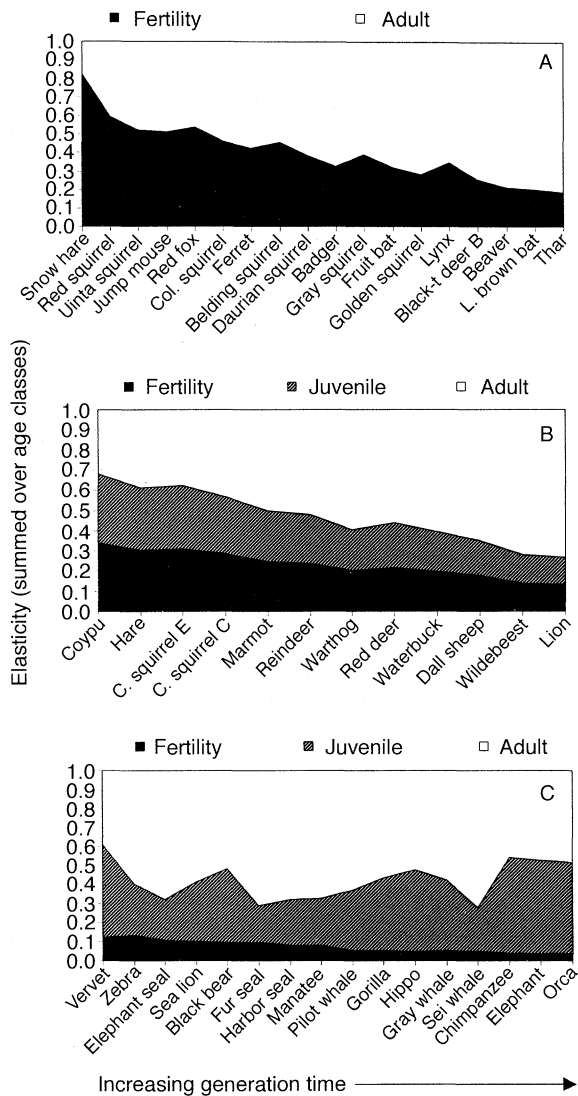


FIG. 2. Area plots showing the stage-specific elasticities for each mammal population, grouped by age at maturity and ordered by increasing generation time. (A) Age at first maturity = 1 yr; no juvenile stage. (B) Age at first maturity = 2 yr; fertility elasticity = juvenile survival elasticity (see *Methods*). (C) Age at first maturity >2 yr.

small sample size (Table 1). Within the Artiodactyla, there was a strong negative correlation between age at maturity and adult survival elasticity, which was neither a significant relationship for the other orders nor the combined data set. In addition, the signs of several of the correlations within this order are reversed, although the relationships are not significant. This is in large part due to the hippopotamus life table, which is quite different from the other Artiodactyla (see Figs. 1 and 2C). There was no correlation between adult survival elasticity and net reproductive rate R_0 or λ for any of the three orders, nor for the entire data set combined.

Elasticity patterns generated by a simplified model

The results of the mammal life table analysis suggest that elasticity patterns, when summed across age classes, depend on adult survival and other demographic characteristics that could be measured or estimated from limited field data. To explore this, we examined the elasticity patterns generated by a simplified model without adult age structure (matrix **B**, Eq. 11). The elasticities of this matrix are determined by age at maturity, adult annual survival, and λ (Eqs. 13 and 15; see also Appendix B).

Fig. 4 shows the elasticity patterns generated by Eqs. 13 and 15 for a complete range of adult survival rates, and four different ages at maturity, in populations that are declining ($\lambda = 0.8$), stable ($\lambda = 1.0$), or increasing ($\lambda = 1.2$). For the declining populations, the plots are truncated at $\bar{P} = 0.8$, as a population cannot decline faster than the survival rate of adults, even if there is no recruitment to the adult population ($\bar{P} \leq \lambda$). These results elucidate the source of the patterns from the life table analysis. For example, fertility elasticity is negatively correlated with generation time (Fig. 2). Long generation times may be due to late age at maturity, high adult survival (which increases the mean age of mothers and, hence, T_c ; Eq. 2), or both (see Appendix 1). Fig. 4 shows that populations that mature later have low fertility elasticities, and fertility elasticity decreases with increasing adult survival (moving to the right of each plot). As \bar{P} approaches λ , the elasticity of λ to changes in adult survival increases rapidly. Changes in juvenile survival or fertility have little or no effect on λ in these cases, because these populations are in “stasis,” and adult survival completely determines population growth. Thus, long-lived species at low population growth rates have high adult survival elasticities and low fertility elasticities. Summed juvenile survival elasticities are not predictable from generation time for populations with age at maturity >2 yr (Fig. 2C). For a given adult survival rate, the relative contribution of juvenile survival increases as α increases. \bar{P} cannot be greater than unity, so adult survival elasticity is reduced, relative to juvenile survival elasticity, as juvenile stage length increases. Increasing λ for a given age at maturity also increases the relative contribution of juvenile survival, which has a greater contribution over all adult survival rates when $\lambda > 1$ than when $\lambda < 1$. Over these ranges of parameters, elasticity patterns are more sensitive to adult survival and α than to λ .

We compared the elasticities estimated from the simplified model (**B**) with those from the age-classified mammal projection matrices (**A**). Parameters for **B** were estimated as follows: α , earliest age class with a fertility estimate; \bar{F} , the mean annual fertility rate (Eq. 9); \bar{P} , the mean adult survival rate (Eq. 8), and λ , obtained from the life table matrix. Fertility elasticities from the two models were highly correlated ($r =$

TABLE 1. Spearman rank coefficients (r_s) for several life table results and adult survival elasticity.

Variable	All life tables ($N = 50$)	Artiodactyla ($N = 10$)	Carnivora ($N = 10$)	Rodentia ($N = 16$) [Sciuridae ($N = 13$)]
Age at earliest maturity (α)	-0.192	-0.811**	0.138	0.085 [-0.167]
Maximum age (k)	0.317*	-0.352	0.480	0.619* [0.461]
Fertility (\bar{F} , weighted mean; includes survival to age 1)	-0.375**	-0.067	-0.709*	0.099 [-0.324]
Adult survival (\bar{P} , weighted mean)	0.300*	0.152	0.685*	0.482 [0.338]
λ	-0.091	-0.030	-0.394	0.471 [0.209]
R_0	-0.056	0.006	-0.455	0.413 [0.118]
Generation time (T_c)	0.252	-0.042	0.479	0.519* [0.338]
Survivorship to maturity	0.310*	0.012	-0.097	0.393 [0.066]
Life expectation at birth (\hat{e}_0)	0.258	-0.248	0.479	0.309 [0.157]
Life expectation at maturity (\hat{e}_a)	0.313*	0.115	0.624*	0.469* [0.439]

Note: Coefficients have been corrected for ties (Zar 1984).
* $P < 0.05$, ** $P < 0.01$.

0.958). However, juvenile and adult elasticities were not as well correlated ($r = 0.697$ and 0.722 , respectively; $P < 0.001$). One likely reason for the scatter is that the two models yield different values of λ . After discounting adult survival by maximum age (Eqs. 16 and 17), which reduced λ , the correlation coefficients increased to $r = 0.967$ for fertility elasticities, $r = 0.93$ for juvenile survival elasticities, and $r = 0.857$ for adult survival elasticities. When we calculated estimated elasticities using \hat{P} and $\lambda = 1.0$, the correlations between the two model types were again very high ($r = 0.958$, 0.792 , and 0.815 for fertility, juvenile survival, and adult survival elasticities, respectively). The residuals for each correlation showed that Eq. 15 tended

to slightly overestimate adult survival elasticity (hence underestimating prereproductive elasticity), as age at first reproduction increased. For most populations in this study, though, combining adult age classes into an adult stage did not dramatically affect the elasticity pattern; thus, Eq. 15 can be used to predict the summed elasticities of λ to changes in fertility, juvenile survival and adult survival.

DISCUSSION

How elasticity patterns relate to life history characteristics in mammals

Because survival, growth, and fertility rates determine elasticities, relationships exist between elasticities and basic life history parameters. Both fertility and juvenile survival elasticities are strongly correlated with age at maturation, mean fertility, generation time, and life expectancy. Fertility contributes more to growth rates of populations with early age at maturation and short generation times. Populations with high mean adult survival rates have low fertility elasticities and higher adult survival elasticities, with juvenile survival elasticity dependent on the proportion of life that is spent as a juvenile. Although the parameters in the life tables of this study are variable within families and even genera, the qualitative nature of fertility elasticities are predictable from age at maturation and generation time alone (Figs. 2 and 4). These are the same variables that have been shown to predict life history patterns, with age at maturation highly correlated with adult survival (Millar and Zammuto 1983, Read and Harvey 1989, Promislow and Harvey 1990).

Further connections can be drawn between demo-

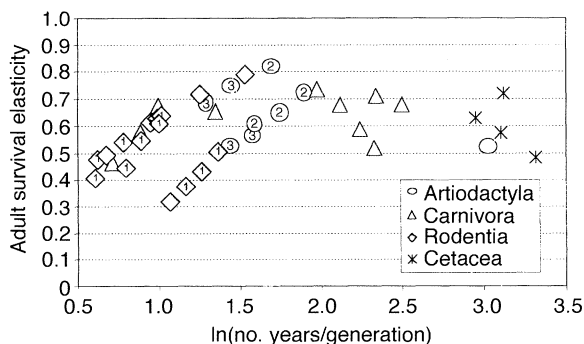


FIG. 3. Adult survival elasticity vs. generation time for three mammalian orders examined in the correlation analysis (Table 1): Artiodactyla, Carnivora, and Rodentia. Order Cetacea, whose four life tables all have very long generation times, is shown for comparison. Key to numbers inside symbols: 1 = Family Sciuridae, 2 = Family Bovidae; 3 = Family Cervidae.

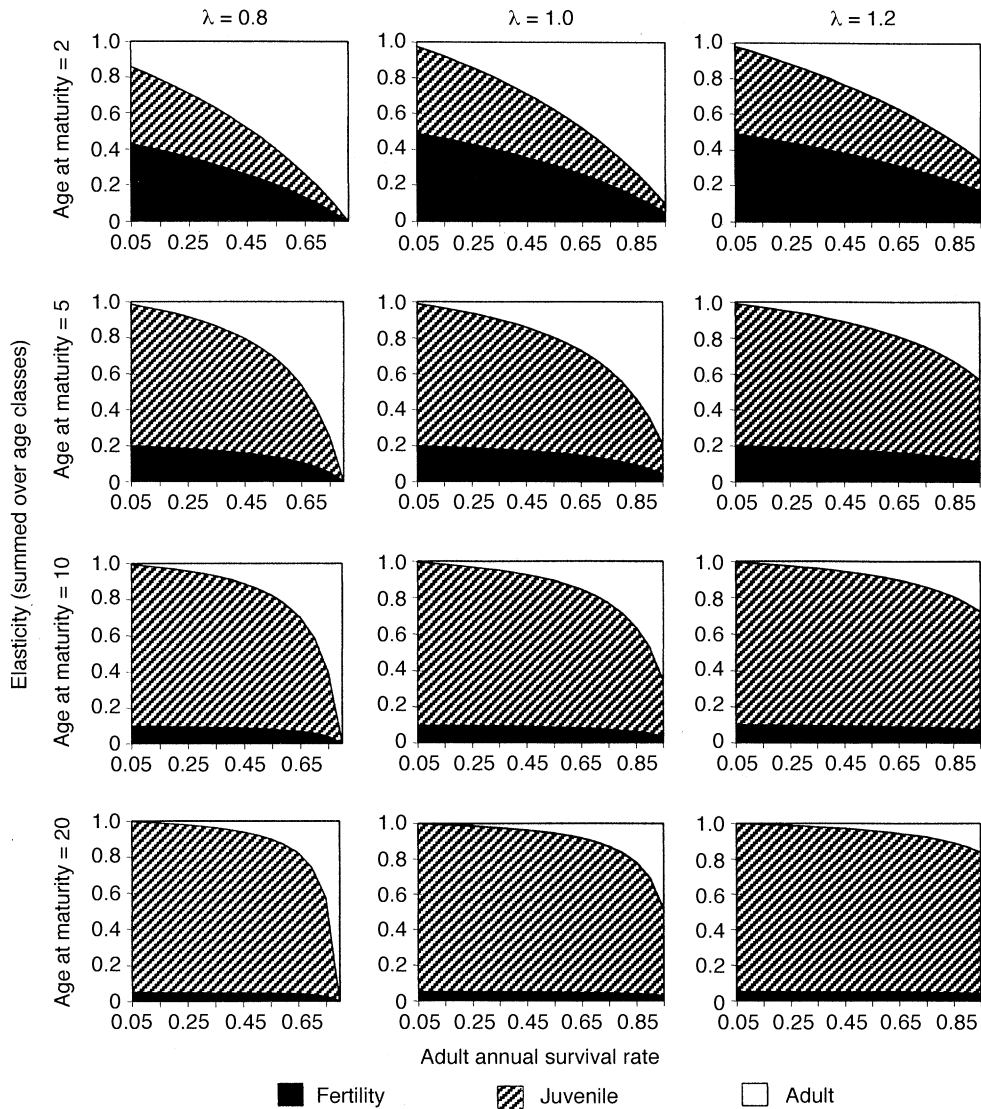


FIG. 4. Results of Eqs. 13 and 15, showing the effects of age at maturity (rows), λ (columns), and adult annual survival rate (x-axes), on summed survival elasticities (y-axes). Each area plot is for a range of elasticities with increasing adult annual survival for a given age at maturity and annual survival rate. In the first column, populations are declining, in the middle column populations are stable, and in the right column populations are increasing. The maximum adult survival rate is 0.8 for models with $\lambda = 0.8$, as λ cannot be less than adult survival in models of type **B** (Eq. 11).

graphic elasticities and the life history patterns observed in mammals. In long-lived species that mature late and have few offspring (Read and Harvey's "slow" mammals (1989)), fecundity and early offspring survival are less critical than juvenile survival to maturity. Thus, increasing juvenile survival (quality), through large offspring size at birth, small litter size, and parental care, has a greater effect on fitness than does increasing litter size. In contrast, mammals that mature early and have shorter life spans ("fast" mammals) have much higher fertility elasticities; individuals with these life history traits will benefit more from an increase in offspring number (quantity). A similar ar-

gument has been made for birds (Sæther et al. 1996, Sæther and Bakke 2000).

Phylogenetic constraints have confounded some comparative studies of mammal life history traits, and numerous techniques have been developed to remove these effects (Harvey and Pagel 1991). Results from various analyses have been conflicting, primarily due to different comparative methodologies. Sæther and Bakke (2000) found that phylogenetic corrections did not alter their correlations between elasticities and life history traits of birds. We found that elasticity patterns for mammals were dependent on generation time and its components, age at maturity and adult annual sur-

vival. Elasticity patterns must be loosely dependent on phylogeny, to the extent that these variables are correlated with body size and constrained by phylogeny. Although the elasticity patterns of the broad taxonomic groups we defined cluster somewhat in Fig. 1, the relative impacts of perturbations to fecundity, juvenile survival, and adult survival do not appear to be generalizable by these groups. This makes sense, because elasticities are determined directly by the survival and fertility rates, which may vary dramatically even among populations subjected to different environmental conditions. The general pattern of decreasing fertility elasticity with generation time that we observe for all early maturing species (Fig. 2) also occurred within the ground squirrels (*Spermophilus* spp.). However, ground squirrels with short generation times, such as *S. armatus*, have summed elasticities that are more similar to red fox and black-footed ferret than congeneric ground squirrels with delayed maturity. Thus, phylogeny is often not a reliable indicator of which vital rates will have the greatest impact on population growth. Future analyses of elasticity patterns could utilize new techniques for statistically evaluating compositional data (e.g., Aitchison 1986, Billheimer et al. 1998) with a larger data set, perhaps one with elasticities generated by Eq. 15.

Elasticity patterns of age-based models

In age-classified matrices, the proportional contributions of each of the prereproductive age classes, as well as the sum of the fertility elasticities, are equal. If the adult age classes are combined into a single stage, with mean annual survival and fertility (matrix **B**, Eq. 11), the elasticity of λ to fertility, juvenile survival, and adult survival can be estimated algebraically. This generalization only applies to age-based models where age-specific annual survival and fertility rates are the only model parameters, as in life tables. However, because most mammals and birds have age-dependent vital rates, and many other vertebrates have good age-length relationships, these predictions of summed age-class elasticities should hold qualitatively for a wide range of taxa.

An important part of understanding the limitations of a method is to know how various parameters will affect the results. While one of our main objectives is to seek patterns in elasticities across species for comparative analysis, this also serves to help us predict how the elasticities will change if our parameter estimates change or are incorrect (Caswell 1996). We did not carefully screen our sample of published life tables for reliability or consistency of methods. Unreliable life table parameters may lead to faulty interpretations of population growth rates and, potentially, elasticity values (Wisdom et al. 2000). Populations that have undergone recent changes in vital rates may not be appropriate for certain life table calculations that depend on a stable age distribution (Caughley 1966). Fur-

thermore, they may show different responses to perturbation than are predicted by the elasticities. Our analysis shows that incorrect adult survival rates or age at first reproduction may have a substantial effect on elasticity patterns, but faulty fertility or juvenile survival rates may be less critical, because the relative values of summed elasticities change less dramatically with changes in λ (Fig. 4). Shifts in elasticity patterns may be predictable for some changes in vital rates that result in changes in λ , such as density-dependent reductions in annual juvenile survival (Grant and Benton 2000).

Applications to conservation biology

For conservation purposes, our analysis of mammal elasticity patterns suggests that the population growth rates of "fast" mammals that mature early will respond to improved survival of offspring, while the growth rates of "slow" mammals that mature late and have few offspring per year will respond better to improved adult or juvenile survival rates. A similar result has been found for bird species (Sæther and Bakke, 2000). In populations with very late age at maturity, or relatively low adult survival, the elasticity of λ to changes in juvenile survival may become primary (Fig. 4; Huppell 1998). The decision to concentrate management efforts on a particular life stage should be influenced by variables such as age at maturation and mean annual adult survival, rather than taxonomic relationships, and will depend on the level of potential increase in survival rates (Green and Hirons 1991, de Kroon et al. 2000).

The elasticity approximation equation (Eq. 15) provides a shortcut for life history analysis that may be very useful for categorizing species for management. Full life table data are notoriously difficult to collect, but estimates of age at maturity and average adult survival may be more accessible. These parameters should be priorities in initial research efforts. Estimates of λ may be difficult to obtain (only ~20% of the Habitat Conservation Plans reviewed in a recent study (Savage 1998) contained information about population trends) but Fig. 4 shows that λ has less effect on predicted elasticity patterns than age at maturity or adult survival. Elasticity approximations have at least two important applications: (1) to make preliminary management proposals that account for life history characteristics of data-poor populations; and (2) to categorize species or populations according to their elasticity patterns, as a first step in various modeling efforts, such as choosing a "model" species for simulations. The elasticity patterns generated by Eq. 15 cannot substitute for detailed, long-term studies of wild populations. However, the patterns are relatively robust and permit qualitative comparisons of management alternatives.

Conservation biologists should apply elasticity analysis cautiously. Uncritical prioritization through elasticities for various life stages can result in poor pre-

scriptions for research or conservation efforts (Sæther et al. 1996, Silvertown et al. 1996, Wisdom et al. 2000). In particular, interventions targeted at one life stage may affect other vital rates in surprising ways. Unless those effects can be included in the calculations, changes in λ cannot be predicted. Perhaps most importantly, elasticities give us information about population projections, given that current conditions (vital rates or prescribed changes in vital rates) are maintained, leading to a stable age distribution. Although it may be tempting to use the quantitative differences in elasticity values to rank management options, the assumptions and restrictions of deterministic elasticity analysis make qualitative comparisons much more prudent (de Kroon et al. 2000). Elasticity of λ often does an excellent job of qualitatively predicting the elasticities of other indices appropriate for models that include density dependence, environmental or demographic stochasticity, or spatial structure (Caswell 2000, Grant and Benton 2000, Neubert and Caswell 2000). In the best of all worlds, elasticity analysis would be a first step in a larger framework of population viability analysis that included stochastic simulations, multiple models, and detailed sensitivity analysis (Ferrière et al. 1996, Beissinger and Westphal 1998).

ACKNOWLEDGMENTS

We would like to acknowledge R. Powell, Jim Gilliam, A. Read, and W. Morris, who provided insightful comments on this work. C. Pfister, H. de Kroon, N. Schumaker, and two anonymous reviewers offered many useful suggestions for the manuscript. This work was part of a dissertation (S. Heppell) at Duke University and was supported by a grant from the National Marine Fisheries Service and the University of North Carolina Sea Grant (R/MER-21 and NOAA/NMFS NA90AA-D-S6847), as well as a postdoctoral appointment from the U.S. Environmental Protection Agency, National Health and Environmental Effects Research Laboratory. H. Caswell acknowledges support from National Science Foundation Grant DEB-9582740, Woods Hole Oceanographic Institute Contribution 9931.

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APPENDIX A

Detailed life tables, including sources, parameters, and results for 50 mammal populations, may be found in ESA's Electronic Data Archive: *Ecological Archives* E081-006.

APPENDIX B

In this Appendix we derive the expressions (Eq.13) and (Eq.15) for the elasticities of λ to changes in the simplified model given by the matrix **B** in (Eq.11). The elasticity of λ to any element is given by

$$\frac{b_{ij}}{\lambda} \frac{\partial \lambda}{\partial b_{ij}} = \frac{\partial \log \lambda}{\partial \log b_{ij}} = \frac{b_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{B.1}$$

where **w** and **v** are the right and left eigenvectors and $\langle \mathbf{w}, \mathbf{v} \rangle$ is their scalar product (de Kroon et al. 1986). These can be written directly from the life cycle graph corresponding to the matrix, using the characteristic equation to simplify some of the expressions. The results are:

$$\mathbf{w} = \begin{bmatrix} 1 \\ P_1 \lambda^{-1} \\ P_1 P_2 \lambda^{-2} \\ \vdots \\ \prod_{i=1}^{\alpha-2} P_i \lambda^{-(\alpha-2)} \\ \lambda \bar{F}^{-1} \end{bmatrix} \tag{B.2}$$

$$\mathbf{v} = \begin{bmatrix} 1 \\ \lambda P_1^{-1} \\ \lambda^2 (P_1 P_2)^{-1} \\ \vdots \\ \lambda^{\alpha-2} \left(\prod_{i=1}^{\alpha-2} P_i \right)^{-1} \\ \bar{F} (\lambda - \bar{P})^{-1} \end{bmatrix} \tag{B.3}$$

With this scaling, the scalar product is

$$\langle \mathbf{w}, \mathbf{v} \rangle = \alpha - 1 + \frac{\lambda}{\lambda - \bar{P}}. \tag{B.4}$$

Using these results, we find that the elasticity of λ to changes in \bar{F} is

$$\begin{aligned} e_{\bar{F}} &= \frac{\bar{F}}{\lambda} \left[\frac{v_1 w_\alpha}{\langle \mathbf{w}, \mathbf{v} \rangle} \right] = \frac{1}{\alpha - 1 + \lambda/(\lambda - \bar{P})} \\ &= \frac{\bar{P} - \lambda}{(\alpha - 1)\bar{P} - \alpha\lambda}. \end{aligned} \tag{B.5-B.7}$$

Let $e_j = \sum_{i=1}^{\alpha-1} e_{i+1,i}$ be the summed juvenile survival elasticity. Because the elasticities of all the juvenile survival probabilities are equal,

$$e_j = (\alpha - 1)e_{21} \tag{B.8}$$

and we know that

$$e_j + e_{\bar{F}} + e_{\bar{P}} = 1. \tag{B.9}$$

Because $e_{\bar{F}} = e_{21}$, this implies that

$$e_{\bar{P}} = 1 - \alpha e_{\bar{F}} \tag{B.10}$$

as given by (Eq. 13).

Thus, the complete elasticity pattern of the matrix **B** is determined by α , λ , and \bar{P} .