

The Relative Importance of Life-History Variables to Population Growth Rate in Mammals: Cole's Prediction Revisited

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ABSTRACT: The relative importance of life-history variables to population growth rate (λ) has substantial consequences for the study of life-history evolution and for the dynamics of biological populations. Using life-history data for 142 natural populations of mammals, we estimated the elasticity of λ to changes in age at maturity (α), age at last reproduction (ω), juvenile survival (P_j), adult survival (P_a), and fertility (F). Elasticities were then used to quantify the relative importance of α , ω , P_j , P_a , and F to λ and to test theoretical predictions regarding the relative influence on λ of changes in life-history variables. Neither α nor any other single life-history variable had the largest relative influence on λ in the majority of the populations, and this pattern did not change substantially when effects of phylogeny and body size were statistically removed. Empirical support for theoretical predictions was poor at best. However, analyses of elasticities on the basis of the magnitude (F) and onset (α) of reproduction revealed that α , followed by F , had the largest relative influence on λ in populations characterized by early maturity and high reproductive rates, or when $F/\alpha > 0.60$. When maturity was delayed and reproductive rates were low, or when $F/\alpha < 0.15$, survival rates were overwhelmingly most influential, and reproductive parameters (α and F) had little relative influence on λ . Population dynamic consequences of likely responses of biological populations to perturbations in life-history variables are examined, and predictions are made regarding the numerical dynamics of age-structured populations on the basis of values of the F/α ratio.

Keywords: Cole's prediction, elasticity analysis, population consequences of life-history patterns, partial life cycle model, population regulation, relative importance of life-history variables.

Biological populations exhibit a great diversity in patterns of life history, and such patterns can have substantial population consequences. Early theoretical work by Cole (1954) and Lewontin (1965) established that the pattern of life history determines the dynamics of biological populations and that life-history variables differ with respect to their influences on population dynamics. Subsequent theoretical and empirical works have extended this idea (MacArthur and Wilson 1967; Meats 1971; Green and Painter 1975; Law et al. 1977; Snell 1978; Caswell and Hastings 1980; Stearns 1992; Leips and Travis 1999; Dobson and Oli 2001).

Theoretical studies dealing with the relative importance of life-history variables to population growth rate have focused on the sensitivity of the finite rate of population growth, λ (or $r = \ln[\lambda]$), to changes in various life-history variables. While some authors have suggested that there ought to be straightforward relationships between λ and various life-history variables or metrics derived from them (MacArthur and Wilson 1967; Meats 1971; Green and Painter 1975; Snell 1978; Caswell and Hastings 1980), others have suggested that the relationships will vary with the overall pattern of life histories (Roff 1992; Stearns 1992).

Substantial progress has been made in demographic methods since the publication of Cole's and Lewontin's influential papers (Tuljapurkar and Caswell 1997; Caswell 2001; Oli and Zinner 2001a, 2001b). In particular, elasticity analyses allow direct quantification of the relative importance of life-history variables to λ (de Kroon et al. 1986, 2000). Patterns of elasticities have been investigated in some age-structured (Heppell et al. 2000; Sæther and Bakke 2000) and stage-structured (Silvertown et al. 1993; Enright et al. 1995; Franco and Silvertown 1997; Pfister 1998) populations, but theoretical predictions regarding the relative importance of life-history variables to λ have not been tested using empirical data. Furthermore, the likely response of λ to changes in life-history variables could have substantial implications in the study of population regulation, a topic of tremendous ecological and

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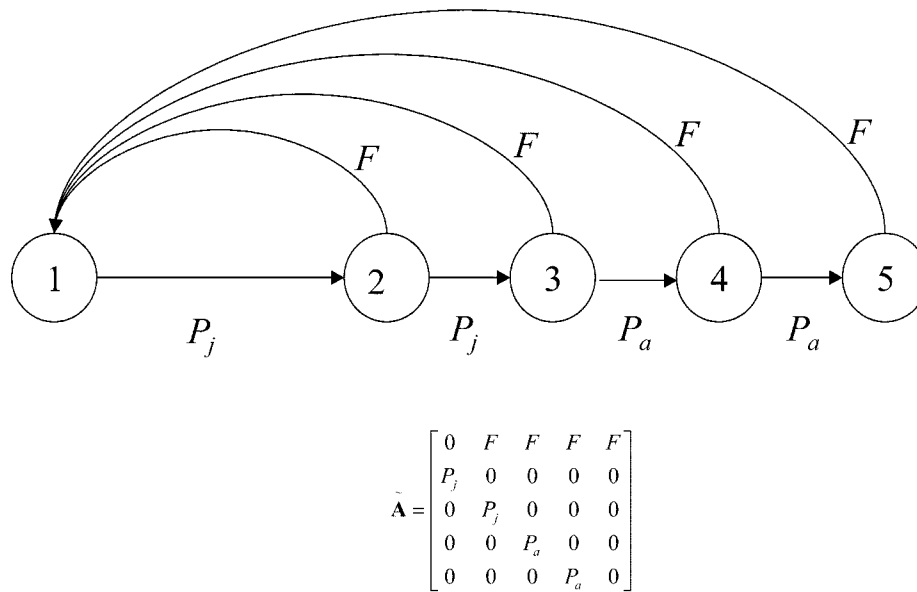


Figure 1: Postbreeding census partial life cycle graph for age at maturity ($\alpha = 2$ and age at last reproduction ($\omega = 5$). In a partial life cycle model, age-specific fertilities (F_i) are approximated by a parameter F , age-specific survival probabilities until age at first reproduction by a parameter P_j , and age-specific survival probabilities for age classes greater than α by a parameter P_a . A population projection matrix corresponding to the partial life cycle graph is also given (Oli and Zinner 2001a).

evolutionary importance (Murdoch 1994; Dobson and Oli 2001), but population dynamic consequences of the relative importance of life-history variables to λ have not been explored.

Using elasticities to quantify the relative importance of life-history variables to λ (de Kroon et al. 2000), we investigated the relative importance of five life-history variables (age at maturity [α], age at last reproduction [ω], juvenile survival [P_j], adult survival [P_a], and fertility [F]) to λ in mammals. Specifically, we tested the following theoretical predictions: first, α should have the largest relative influence on λ (Cole 1954; Lewontin 1965); second, the pattern of the relative importance of life-history variables to λ should depend on the λ/P_a ratio (Caswell and Hastings 1980); third, the pattern of relative importance should depend on the values of λ and α (Stearns 1992); fourth, the pattern of the relative importance should depend on λ and should differ between increasing and near-equilibrium/declining populations (Meats 1971; Snell 1978); and fifth, the pattern of the relative importance of life-history variables to λ should depend on the magnitude of reproduction relative to the onset of reproduction (our prediction).

Recent comparative studies suggest that evolutionary history (Stearns 1983, 1984; Dunham and Miles 1985; Read and Harvey 1989; Miles and Dunham 1992) and body size (Western 1979, 1983; Western and Ssemakula

1982; Millar and Zammuto 1983; Peters 1983) can have substantial influences on life-history patterns. Because elasticities are emergent properties of life-history patterns, they might be influenced by phylogeny and body size. Thus, we tested these possibilities by examining the pattern

Table 1: Summary statistics for body mass (kg), life-history variables, population growth rate (λ), and elasticities ($N = 142$)

Variable	Mean	SE	Minimum	Maximum
Mass (kg)	74.869	20.963	.004	2,770.000
α	2.056	.143	1.000	15.000
ω	13.176	.786	3.000	60.000
P_j	.561	.019	.111	.969
P_a	.714	.014	.232	.978
F	.542	.026	.068	1.774
λ	1.055	.020	.671	2.619
Elasticity of λ to changes in:				
α (absolute value)	.400	.030	.010	1.584
ω	.049	.005	.000	.378
P_j	.311	.010	.136	.633
P_a	.340	.013	.057	.705
F	.349	.018	.043	.807

Note: Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. For α , mean \pm 1 SE = 713.73 \pm 55.23, range = 15–5,475 d. For ω , mean \pm 1 SE = 4,296.71 \pm 273.89, range = 84–21,535 d.

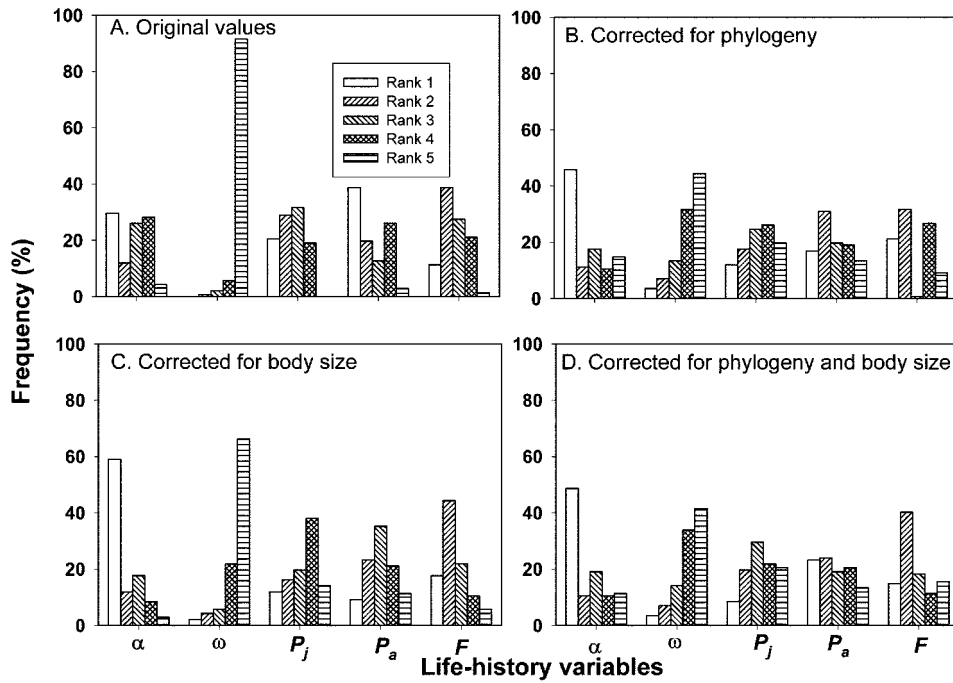


Figure 2: Frequency distribution (%) of ranks of absolute value of elasticity of λ to changes in a life-history variable p , $e(p)$. Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. For each population, we ranked absolute values of $e(p)$ in a descending order such that a life-history variable with the largest relative influence on λ would receive a rank of 1, and the variable with the smallest relative influence on λ would receive a rank of 5. Frequency distribution of ranks of elasticities are given for (A) original absolute values of $e(p)$, (B) $e(p)$ corrected for phylogeny, (C) $e(p)$ corrected for body size, and (D) $e(p)$ corrected for phylogeny and body size simultaneously ($N = 142$).

of elasticities after statistically removing the effects of phylogeny and body mass.

Methods

Data Sources

Life-history data were obtained from published sources. Age-specific life-history data are difficult to collect; consequently, such data are available only for a few species of mammals. To strike a balance between the quality of available data and sample size requirements, we used life-history data if age-specific (or otherwise detailed) survival rates and at least average fecundity rates were available; life-history data based only on the male segment of populations or those based on laboratory studies were not used. References for data used in this study are presented in the appendix in the online edition of the *American Naturalist*.

Demographic Analyses

Using survival and fecundity data, we estimated parameters for an age-classified projection (Leslie) matrix \mathbf{A} for each population. We estimated age-specific fertilities (F_i) and survival probabilities (P_i) using the birth-pulse, post-breeding census formulation of Caswell (2001):

$$P_i = \frac{l_i}{l_{i-1}}, \quad (1)$$

$$F_i = P_i m_i, \quad (2)$$

where l_i is the survivorship (probability at birth of surviving to age i) and m_i is the fecundity (the average number of daughters born to a female of age i). An age-classified Leslie matrix \mathbf{A} was then constructed for each population. Although the Leslie matrix model adequately incorporates age-specific life-history data, life-history variables such as α and ω do not appear explicitly in age-structured models. Consequently, the sensitivity or elasticity of λ to changes in these variables cannot be estimated using standard analytical techniques. Also, species of mammals show tremendous variation in life history, with very different pat-

Table 2: Results of nested ANOVA for elasticity of population growth rate (λ) to changes in α , ω , P_j , P_a , and F in mammals

Source	df	F	P	R ²
Elasticity of λ to changes in α :				
Order	10	6.69	<.0001	.625
Family (order)	23	2.47	.001	
Elasticity of λ to changes in ω :				
Order	10	2.03	.0373	.337
Family (order)	23	1.31	.178	
Elasticity of λ to changes in P_j :				
Order	10	4.33	<.0001	.501
Family (order)	23	2.24	.0030	
Elasticity of λ to changes in P_a :				
Order	10	5.86	<.0001	.614
Family (order)	23	2.41	.0013	
Elasticity of λ to changes in F :				
Order	10	6.99	<.0001	.672
Family (order)	23	3.88	<.0001	

Note: Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. Values of R^2 represent proportion of variation in elasticity of λ to changes in each life-history variable explained by the nested ANOVA model.

terms of age structure, age at maturity, and longevity. Such differences cause the size of Leslie matrices to be different and are thus incomparable among species with different patterns of life history.

Despite wide variation, mammalian life histories can be simplified into a two-stage life cycle with juvenile (pre-

Table 3: Results of linear regression of log-transformed body mass on the elasticity of population growth rate (λ) to changes in α , ω , P_j , P_a , and F in 142 populations of mammals

Source	Intercept	Slope	P	R ²
Elasticity of λ to changes in α	.472	-.048	<.0001	.174
Elasticity of λ to changes in ω	.051	-.001	.464	.004
Elasticity of λ to changes in P_j	.294	.011	.0005	.082
Elasticity of λ to changes in P_a	.307	.022	<.0001	.190
Elasticity of λ to changes in F	.398	-.033	<.0001	.232

Note: Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. P values for the test of hypothesis that the slope of the regression line is 0 and the coefficient of determination (R^2) are also given.

reproductive) and adult (reproductive) stages. Juveniles survive to reach adulthood with a survival probability P_j , and it takes them α time units to do so. Once they attain sexual maturity, they reproduce with an average fertility F and survive each time unit with a probability P_a until the age at last reproduction, ω . This simplified life cycle can be graphically represented as a partial life cycle graph (fig. 1) from which a corresponding partial life cycle model can be derived (Oli and Zinner 2001a). Although some age-specific information is lost, the partial life cycle model has several desirable properties (Oli and Zinner 2001a, 2001b). First, α and ω explicitly appear as model parameters in the partial life cycle model, and the sensitivity as well as elasticity of λ to perturbations in these life-history variables can be directly estimated using standard analytical techniques. Second, the life cycle of mammals with any age structure can be modeled using five parameters (α , ω , P_j , P_a , and F), thereby making the life history of mammals with vastly different life history or age structure compa-

Table 4: Results of nested ANCOVA (with log-transformed body mass as a covariate) for elasticity of population growth rate (λ) to changes in α , ω , P_j , P_a , and F in 142 populations of mammals

Source	df	F	P	R ²
Elasticity of λ to changes in α :				
Body mass	1	6.65	.0113	.647
Order	10	4.49	<.0001	
Family (order)	23	2.75	.0002	
Elasticity of λ to changes in ω :				
Body mass	1	1.74	.190	.345
Order	10	2.21	.022	
Family (order)	23	1.38	.139	
Elasticity of λ to changes in P_j :				
Body mass	1	4.00	.048	.519
Order	10	3.77	.0002	
Family (order)	23	2.15	.0047	
Elasticity of λ to changes in P_a :				
Body mass	1	8.00	.0056	.641
Order	10	4.42	<.0001	
Family (order)	23	2.79	.0002	
Elasticity of λ to changes in F :				
Body mass	1	14.11	.0003	.710
Order	10	4.95	<.0001	
Family (order)	23	4.48	<.0001	

Note: Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. Values of R^2 represent proportion of variation in elasticity of λ to changes in each life-history variable explained by the nested ANCOVA model.

Table 5: Correlation matrix (Spearman's) for body mass (kg), life-history variables, population growth rate (λ), and elasticity of λ to changes in five life-history variables

	Body mass	Life-history variables					λ	Elasticity of λ to changes in				
		α	ω	P_j	P_a	F		α	ω	P_j	P_a	F
Body mass												
α	.449 <.0001							-.373 <.0001	-.174 .038	-.002 .983	-.121 .150	-.258 .002
ω	.481 <.0001	.738 <.0001						-.378 <.0001	-.263 .002	-.050 .558	-.008 .920	-.273 .001
P_j	.493 <.0001	.650 <.0001	.673 <.0001					-.408 <.0001	-.071 .401	-.017 .842	-.055 .513	-.332 <.0001
P_a	.519 <.0001	.692 <.0001	.748 <.0001	.663 <.0001				-.451 <.0001	-.110 .193	.010 .904	-.002 .986	-.349 <.0001
F	-.443 <.0001	-.385 <.0001	-.549 <.0001	-.562 <.0001	-.579 <.0001			.440 <.0001	.074 .381	.130 .122	.017 .841	.292 <.0001
λ	.038 .655	-.105 .215	.078 .359	.278 .0008	.180 .032	.303 .0002		.052 .537	-.051 .543	.053 .532	-.015 .852	-.128 .129
Elasticity of:												
α	-.538 <.0001	-.663 <.0001	-.766 <.0001	-.881 <.0001	-.736 <.0001	.841 <.0001	.022 .791					
ω	-.014 .867	-.014 .864	-.416 <.0001	-.208 .013	.077 .361	-.212 .012	-.496 <.0001	.045 .598				
P_j	.326 <.0001	.836 <.0001	.484 <.0001	.647 <.0001	.442 <.0001	-.241 .004	-.155 .065	-.575 <.0001	.059 .483			
P_a	.480 <.0001	.501 <.0001	.770 <.0001	.484 <.0001	.799 <.0001	-.773 <.0001	-.142 .093	-.748 <.0001	.081 .340	.235 .005		
F	-.523 <.0001	-.896 <.0001	-.857 <.0001	-.690 <.0001	-.837 <.0001	.659 <.0001	.168 .015	.834 <.0001	-.049 .561	-.703 <.0001	-.814 <.0001	

Note: Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. Values above the main diagonal represent correlation coefficients after effects of phylogeny and body size were removed using a nested ANCOVA; P values for $H_0: r_s = 0$ are given below each correlation coefficient. Absolute values were used for elasticity of λ to changes in α and for values of elasticity of λ to changes in all life-history variables after removing the effects of body size and phylogeny.

table. Finally, the dynamical properties of the age-classified model are generally retained in the partial life cycle model (Levin et al. 1996; Oli and Zinner 2001a, 2001b). Therefore, we used the postbreeding census partial life cycle model of Oli and Zinner (2001a) for demographic analyses.

In a partial life cycle model, age-specific fertilities F_i are approximated by an average fertility parameter F , age-specific survival P_i until reproduction is accomplished (i.e., juvenile survival) by a juvenile survival parameter P_j , and age-specific survival from the first reproductive event until age at last reproduction ω by an adult survival parameter P_a (fig. 1). The characteristic equation for this type of life cycle is (Oli and Zinner 2001a)

$$1 = FP_j^{\alpha-1}\lambda^{-\alpha} - FP_j^{\alpha-1}P_a\lambda^{-\alpha-1} + FP_j^{\alpha}\lambda^{-\alpha-1} - FP_j^{\alpha}P_a^{\omega-\alpha}\lambda^{-\omega-1} + P_a\lambda^{-1}. \quad (3)$$

The population growth rate λ is the largest real root of equation (3) and was obtained numerically. For the partial

life cycle model, α and ω were the first and last age class with nonzero fertility, respectively. When age-specific or otherwise detailed demographic data were available, F , P_j , and P_a were estimated from the age-classified projection matrix as weighted averages, weighted according to the contribution of each age class to the stable age distribution (Oli and Zinner 2001a):

$$F = \frac{\sum_{i=\alpha}^{\omega} w_i F_i}{\sum_{i=\alpha}^{\omega} w_i}, \quad (4)$$

$$P_a = \frac{\sum_{i=\alpha+1}^{\omega-1} w_i P_i}{\sum_{i=\alpha+1}^{\omega-1} w_i}, \quad (5)$$

$$P_j = \frac{\sum_{i=1}^{\alpha} w_i P_i}{\sum_{i=1}^{\alpha} w_i}, \quad (6)$$

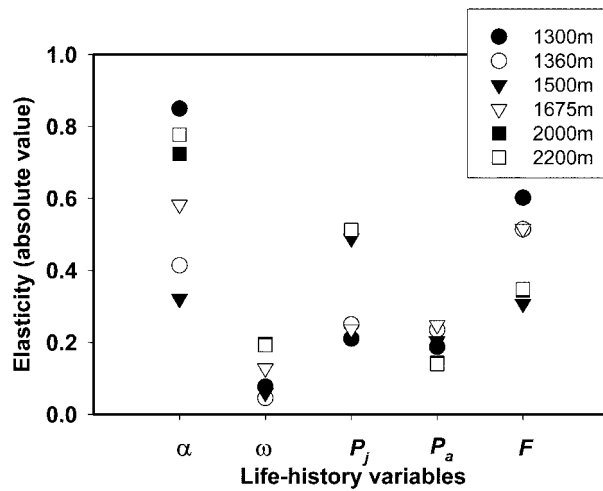


Figure 3: Pattern of elasticities in six populations of Columbian ground squirrels (*Spermophilus columbianus*) along an elevation gradient. Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. Data from Zammuto (1987).

where w_i is the i^{th} entry of the right eigenvector corresponding to the dominant eigenvalue of the age-classified projection matrix A .

Quantification of the Relative Importance:
Sensitivity and Elasticity Analysis

In a partial life cycle model, λ is a function of five life-history variables (α , ω , P_j , P_a , and F); changes in any one of these variables will cause changes in λ . How λ would change in response to small perturbations in a life-history variable p can be quantified by the sensitivity of λ to changes in that parameter (Caswell 2001; Oli and Zinner 2001a, 2001b). However, sensitivity of λ to perturbations in various life-history variables may not be comparable with each other because they are measured in different units (e.g., P_a and P_j are probabilities and may only take values between 0 and 1, whereas F is not under such a restriction). To address this problem, the concept of elasticity has been introduced (Caswell et al. 1984; de Kroon et al. 1986, 2000; Caswell 2001). Elasticities are proportional sensitivities and quantify potential changes in λ with respect to proportional changes in life-history variables (de Kroon et al. 1986, 2000; Caswell 1997, 2001; Horvitz et al. 1997). As scaled, dimensionless quantities, elasticities are directly comparable among life-history variables that appear in a partial life cycle model and across populations or species (de Kroon et al. 2000; Oli and Zinner 2001a, 2001b). Because of these desirable properties, we used elas-

ticities to quantify the relative importance of five important life-history variables (α , ω , P_j , P_a , and F) to λ .

The sensitivity of λ to changes in a model parameter p is the partial derivative of λ with respect to p (i.e., $\partial\lambda/\partial p$, where p is α , ω , P_j , P_a , or F) and can be obtained through implicit differentiation of equation (3) (see Oli and Zinner 2001a for formulas). Elasticities were calculated by multiplying sensitivity of λ to a model parameter p by p/λ (i.e., $[\partial\lambda/\partial p][p/\lambda]$, where p is α , ω , P_j , P_a , or F (de Kroon et al. 1986; Caswell 1997, 2001; Horvitz et al. 1997; Oli and Zinner 2001a). For brevity, we will denote elasticity of λ to changes in variable p by $e(p)$.

Effects of Phylogeny and Body Size

We used a nested ANOVA (Stearns 1983, 1984; Miles and Dunham 1992), with order as the main effect and family nested within order, to evaluate the phylogenetic effects on the pattern of elasticities. Proportion of variation attributable to phylogeny was estimated, and the absolute values of residuals were examined to investigate the pattern of the relative importance with phylogenetic effects removed (Stearns 1983, 1984; Promislow and Harvey 1990; Miles and Dunham 1992). Other methods are available

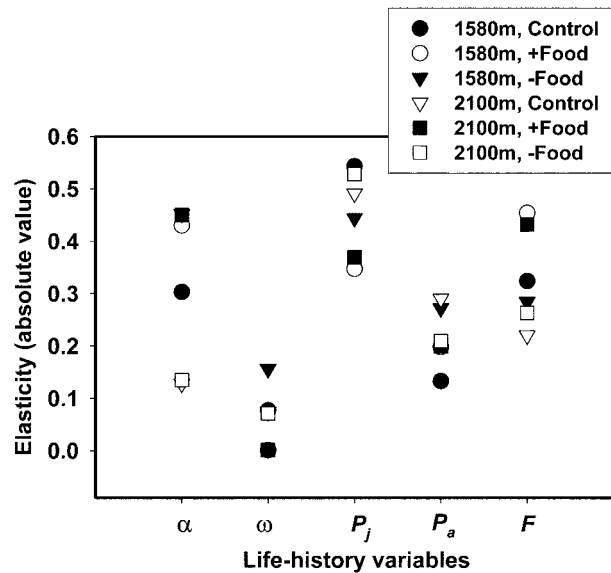


Figure 4: Pattern of elasticities in two control and two experimental populations of Columbian ground squirrels (*Spermophilus columbianus*). Experimental populations received supplemental food ad lib. during 1981–1983 (+Food); these populations were then monitored until 1986 without further supplementation (-Food). Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility. Data from Dobson and Oli (2001).

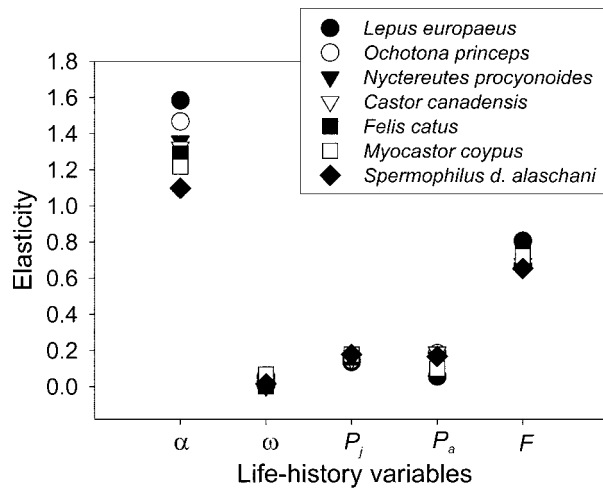


Figure 5: Elasticity of population growth rate (λ) to changes in five life-history variables in *Lepus europaeus* (Lagomorpha: Leporidae), *Ochotona princeps* (Lagomorpha: Ochotinidae), *Nyctereutes procyonoides* (Carnivora: Canidae), *Castor canadensis* (Rodentia: Castoridae), *Felis catus* (Carnivora: Felidae), *Myocastor coypus* (Rodentia: Myocastoridae), and *Spermophilus d. alaschani* (Rodentia: Sciuridae). Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility.

for evaluating phylogenetic effects in comparative analysis (e.g., phylogenetically independent contrasts: Felsenstein 1985; phylogenetic autocorrelation: Cheverud et al. 1985; phylogenetic generalized linear model: Martins and Hansen 1997; for reviews, see Miles and Dunham 1992, 1993; Rohlf 2001), but these require a well-supported phylogeny, which is currently not available for species included in this study. In the absence of a well-supported phylogeny, a nested ANOVA was the only feasible option for evaluating the phylogenetic influence on the pattern of elasticities. We chose to limit our analyses to the family level because $\geq 75\%$ of variation in life-history traits of mammals occurs among families (Stearns 1983; Promislow and Harvey 1990).

To remove the effects of body size on elasticities, we regressed $e(p)$ on log-transformed body mass. Absolute values of residuals were then analyzed to investigate the pattern of elasticities with effects of body size removed. Finally, we used a nested ANCOVA, with log-transformed body size as a covariate, to remove phylogenetic and body size effects simultaneously; absolute values of residuals were then analyzed to investigate the pattern of elasticities with phylogenetic and body size effects removed. However, original elasticity values were used to test theoretical predictions regarding the relative importance of life-history variables to λ , because these predictions were made independent of phylogeny or body size.

Test of Predictions

To test the prediction that α should have the largest relative influence on λ (Cole 1954; Lewontin 1965), we ranked absolute values of $e(p)$ for each population in a descending order such that a life-history variable with the largest relative influence on λ would receive a rank of 1, and the variable with the smallest relative influence on λ would receive a rank of 5 (Pfister 1998). We then compared the relative frequency at which absolute values of $e(p)$ ranked first (largest relative influence on λ), second, third, fourth, and fifth (smallest relative influence on λ). The prediction that the pattern of elasticities should depend on values of λ was tested by examining the relationship between λ and $e(p)$. Additionally, we ranked $e(p)$ for each population as above and compared the relative frequencies of elasticity ranks in increasing ($\lambda > 1.0$) and relatively stable/declining ($\lambda \leq 1.0$) populations with the pattern predicted by Meats (1971). We examined the relationship between the λ/P_a ratio and $e(p)$ to test the prediction that the pattern of elasticities should depend on the λ/P_a ratio (Caswell and Hastings 1980). We also compared the relative frequency of elasticity ranks in populations with $\lambda/P_a > 1.25$ with those with $\lambda/P_a \leq 1.25$, because Caswell and Hastings (1980) make specific predictions about the pattern of relative importance for high and low values of the ratio.

To test the prediction that the pattern of elasticities should be determined by α and λ (Stearns 1992), we

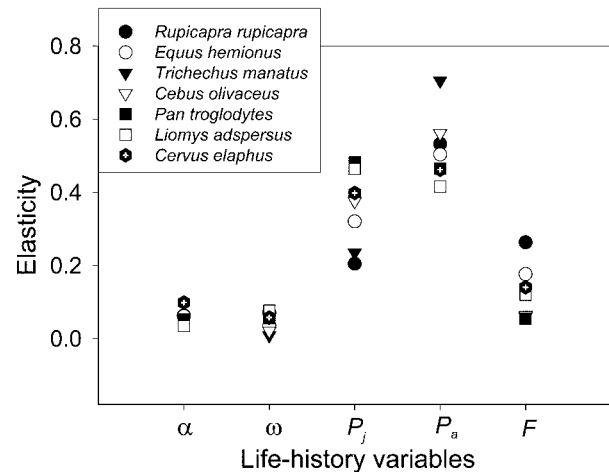


Figure 6: Elasticity of population growth rate (λ) to changes in five life-history variables in *Rupicapra rupicapra* (Artiodactyla: Bovidae), *Equus hemionus* (Perissodactyla: Equidae), *Trichechus manatus* (Sirenia: Trichechidae), *Cebus olivaceus* (Primates: Cebidae), *Pan troglodytes* (Primates: Pongidae), *Liomys adspersus* (Rodentia: Heteromyidae), and *Cervus elaphus* (Artiodactyla: Cervidae). Life-history variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility.

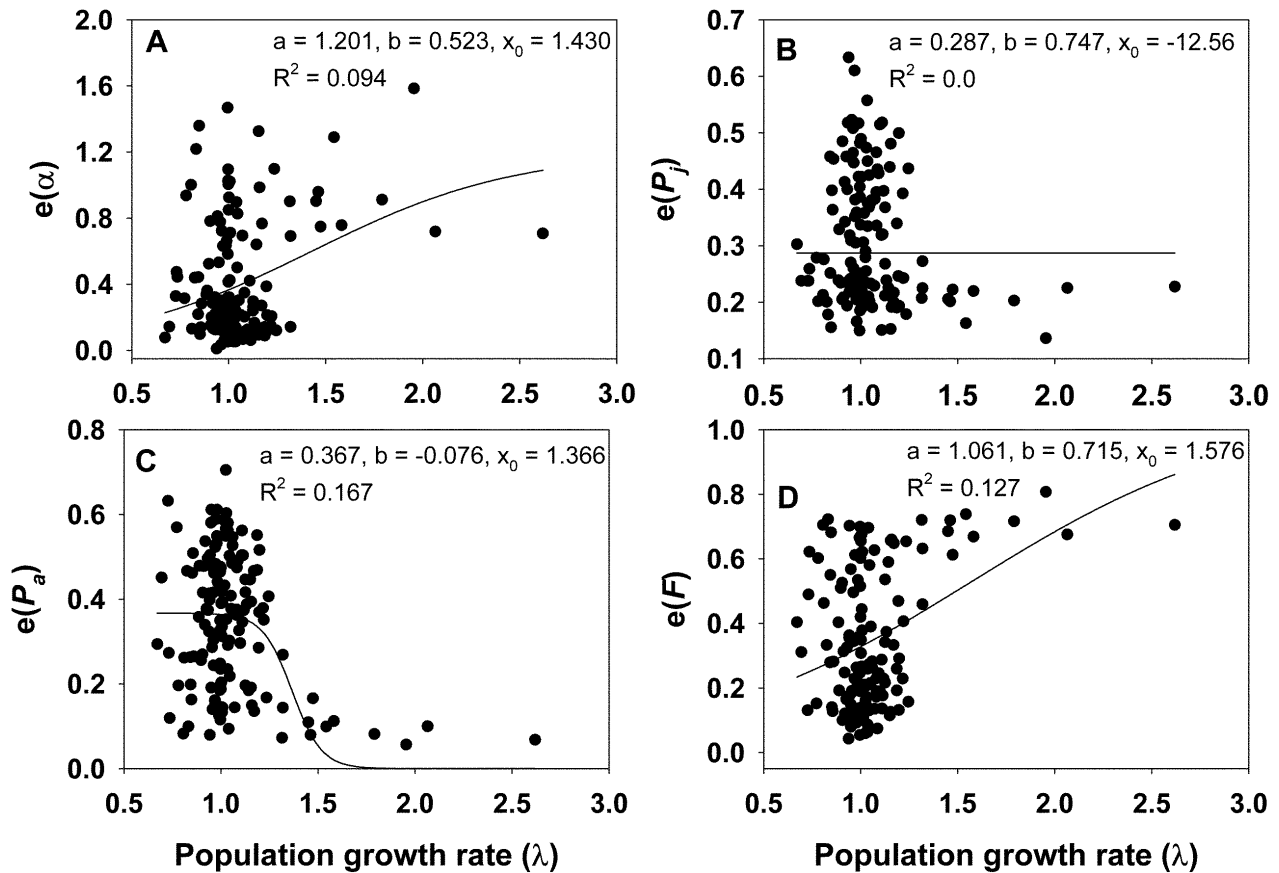


Figure 7: Relationship between population growth rate (λ) and elasticity of λ to changes in (A) age at maturity, $e(\alpha)$; (B) juvenile survival, $e(P_j)$; (C) adult survival, $e(P_a)$; and (D) fertility, $e(F)$. A three-parameter nonlinear regression model of the form $Y = a\{1 + \exp[-(X - x_0)/b]\}$ was fitted; estimates of the three parameters (a , b , and x_0) and the coefficient of determination (R^2) are also given ($N = 142$).

grouped populations into four qualitative categories on the basis of values of α and λ : low λ , early maturity ($\lambda \leq 1.0$ and $\alpha = 1$); low λ , late maturity ($\lambda \leq 1.0$ and $\alpha > 1$); high λ , early maturity ($\lambda > 1.0$ and $\alpha = 1$); and high λ , late maturity ($\lambda > 1.0$ and $\alpha > 1$). We then compared observed patterns of ranks of absolute values of $e(p)$ with those predicted by Stearns (1992). Additionally, we calculated the λ/α ratio and examined the relationship between this ratio and $e(p)$.

We used the F/α ratio to quantify the magnitude of reproduction relative to the onset of reproduction, and we examined the relationship between this ratio and elasticity of λ to changes in life-history variables. Additionally, we classified each population in the sample in one of the following four categories on the basis of the onset and magnitude of reproduction: early maturity, high fertility ($\alpha = 1$ and $F > 0.60$); early maturity, low fertility ($\alpha = 1$ and $F \leq 0.60$); late maturity, high fertility ($\alpha > 1$ and $F > 0.60$); and late maturity, low fertility ($\alpha > 1$ and $F \leq$

0.60). The relative magnitudes of elasticities among these four categories were examined for patterns.

Results

Life-history data were compiled for 142 populations of mammals, representing 110 species, 33 families, and 11 orders. Rodentia was the most represented order, with 42 populations of 27 species, followed by Artiodactyla (29 populations of 27 species) and Carnivora (27 populations of 20 species; see appendix in the online edition of the *American Naturalist*). Ranges of values of life-history variables were as follows: α , 15 d to 15 yr; ω , 84 d to 60 yr; P_j , 0.111 to 0.969; P_a , 0.232 to 0.978; and F , 0.068 to 1.77. Body mass ranged from 4.20 g to 2,770 kg, and λ ranged from 0.67 to 2.62 (see appendix in the online edition of the *American Naturalist*; table 1). Thus, the sample used in this study represented mammals of diverse size and life histories in both increasing and declining populations.

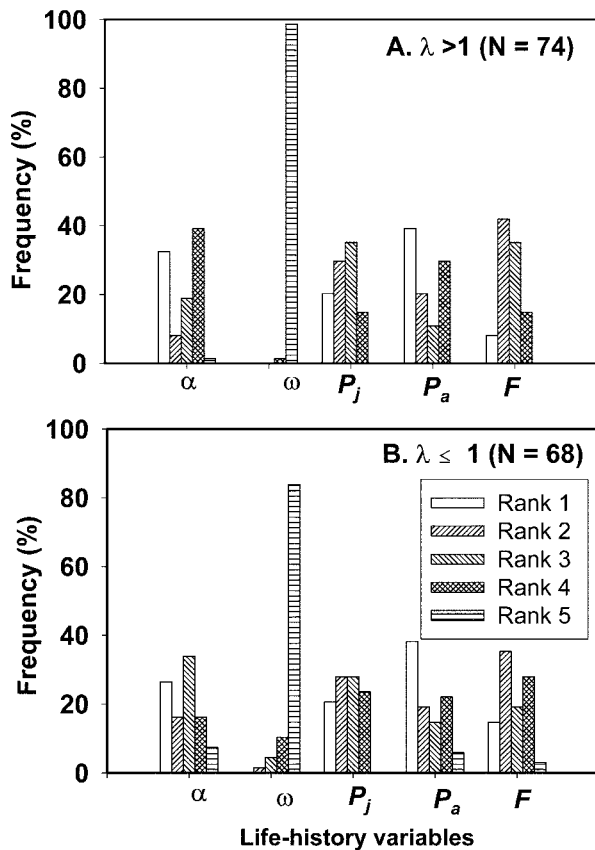


Figure 8: Frequency distribution (%) of ranks of elasticity of population growth rate (λ) to changes in age at maturity (α), age at last reproduction (ω), juvenile survival (P_j), adult survival (P_a), and fertility (F) in (A) increasing populations ($\lambda > 1.0$; $N = 74$) and (B) stable/declining populations ($\lambda \leq 1.0$; $N = 68$). For each population, absolute values of $e(p)$ were ranked in a descending order such that a life-history variable with the largest relative influence on λ would receive a rank of 1, and a life-history variable with the smallest relative influence on λ would receive a rank of 5.

Among sampled populations, mean of $e(\alpha)$ was the highest, closely followed by that of $e(F)$ and $e(P_a)$; mean of $e(\omega)$ was almost an order of magnitude smaller (table 1). Elasticity of λ to changes in α , P_j , P_a , and F ranked first (i.e., had the largest elasticity) in 29.58%, 20.42%, 38.73%, and 11.27% ($N = 142$), respectively, of populations included in our study; $e(\omega)$ never ranked first and rarely ranked second (fig. 2A). There was, therefore, no single life-history variable with the highest $e(p)$ in the majority of the populations, but $e(\omega)$ was lowest in >90% of populations.

A nested ANOVA indicated significant influence of phylogeny at the level of order ($P < .0001$) and family ($P \leq .003$) on the elasticity of λ to changes in all life-history variables except ω , and it also indicated a significant in-

fluence of order ($P = .0373$) but not family ($P = .178$) on $e(\omega)$. The proportion of variance of $e(\alpha)$, $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ accounted for by the nested ANOVA model ranged from 33.7% ($e(\omega)$) to 67.20% ($e(F)$; table 2). After adjusting for phylogenetic effects, we found that the mean (± 1 SE) absolute values of $e(\alpha)$, $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ were 0.14 ± 0.01 , 0.03 ± 0.003 , 0.06 ± 0.004 , 0.07 ± 0.006 , and 0.09 ± 0.007 , respectively. Elasticity of λ to changes in α , ω , P_j , P_a , and F ranked first in 45.77%, 3.52%, 11.97%, 16.90%, and 21.13% of the populations ($N = 142$), respectively (fig. 2B). Body size also influenced elasticity of λ to changes in several life-history variables and explained $\leq 23.20\%$ of variation in $e(p)$ (table 3). After the body size effect was removed, means of absolute values of $e(\alpha)$, $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ were 0.24 ± 0.02 , 0.04 ± 0.003 , 0.09 ± 0.005 , 0.12 ± 0.007 , and 0.15 ± 0.009 , respectively. Absolute values of elasticity of λ to changes in α , ω , P_j , P_a , and F ranked first in 59.15%, 2.11%, 11.97%, 9.15%, and 17.61% ($N = 142$) of the populations, respectively (fig. 2C). A nested ANCOVA with body mass as a covariate revealed that a substantial proportion of variance of elasticity of λ to changes in α (64.68%), ω (34.75%), P_j (51.93%), P_a (64.09%), and F (71.04%) was associated with phylogeny and body size (table 4). After effects of phylogeny and body size were removed, the mean absolute values of $e(\alpha)$, $e(\omega)$, $e(P_j)$, $e(P_a)$, and $e(F)$ were 0.14 ± 0.01 , 0.03 ± 0.003 , 0.06 ± 0.005 , 0.07 ± 0.005 , and 0.08 ± 0.007 , respectively. Elasticity of λ to changes in α , ω , P_j , P_a , and F ranked first in 48.59%, 3.52%, 8.45%, 23.24%, and 14.79% ($N = 142$) of the populations, respectively (fig. 2D).

All life-history variables were significantly correlated with each other and with body mass ($P < .0001$). Similarly, elasticity of λ to changes in life-history variables were correlated with most life-history variables, with the notable exception of ω ; λ was significantly correlated with P_j , P_a , and F but not with body mass, α , and ω . When effects of both phylogeny and body size were removed, correlation between life-history variables and elasticity of λ to changes in variables other than α and F became weaker and insignificant in most cases (table 5).

To investigate whether the pattern of elasticity is fixed within species or populations, we examined elasticity patterns in five populations of Columbian ground squirrels (*Spermophilus columbianus*) along an elevation gradient (Zammuto 1987). Relative magnitudes of elasticities varied substantially among populations; ranges of absolute values of $e(\alpha)$, $e(F)$, and $e(P_j)$ were 0.32–0.85, 0.30–0.60, and 0.21–0.51, respectively (fig. 3). Reanalyses of recently published life-history data for four populations of Columbian ground squirrels (two control and two experimental populations; Dobson and Oli 2001) revealed a similar intra-specific elasticity pattern. Furthermore, elasticity patterns

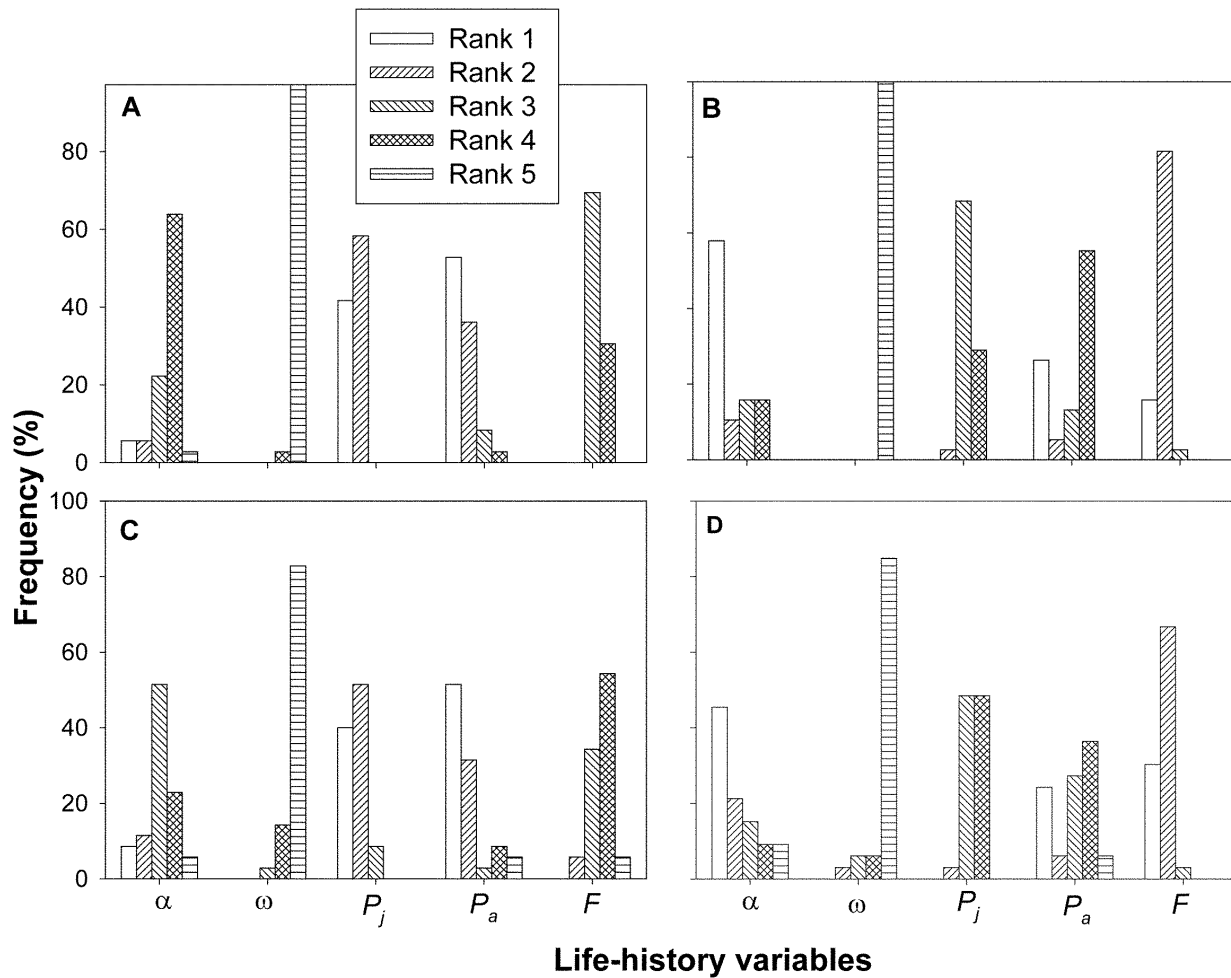


Figure 9: Frequency distribution (%) of ranks of elasticities on the basis of population growth rate and age at maturity (λ - α criteria); (A) high λ -high α ($N = 36$), (B) high λ -low α ($N = 38$), (C) low λ -high α ($N = 35$), and (D) low λ -low α ($N = 33$). Variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility; λ = population growth rate. For each population, absolute values of elasticities, $e(p)$, were ranked in a descending order such that a life-history variable with the largest relative influence on λ would receive a rank of 1, and a life-history variable with the smallest relative influence on λ would receive a rank of 5.

varied within populations depending on abundance of food resources (fig. 4). For example, when supplemental food was being provided at 2,100 m, relative magnitudes of $e(p)$ were $e(\alpha) > e(F) > e(P_j) > e(P_a) > e(\omega)$; after the termination of food supplementation, this pattern changed to $e(P_j) > e(F) > e(P_a) > e(\alpha) > e(\omega)$ (fig. 4).

We also investigated whether distantly related species exhibited similar elasticity patterns. Six distantly related species belonging to three orders and six families exhibited remarkably similar patterns of elasticities, with identical patterns of the relative magnitudes of $e(p)$ (fig. 5). Similar patterns were observed in several other distantly related species, some of which differed in body size by several

orders of magnitude (fig. 6). These results suggest that distantly related species or those that differ in body size by >2 orders of magnitude (e.g., *Equus hemionus* and *Liomys adspersus*; fig. 6) may exhibit remarkably similar elasticity patterns, whereas elasticity patterns can vary substantially within species or populations (cf. figs. 3, 4 and figs. 5, 6).

The correlation between λ and elasticity of λ to changes in most life-history variables was weak and insignificant (table 5), and there was no discernible relationship between them (fig. 7). In both increasing ($N = 74$) and stable/declining populations ($N = 68$), elasticity of λ to changes in P_a ranked first most frequently, followed by

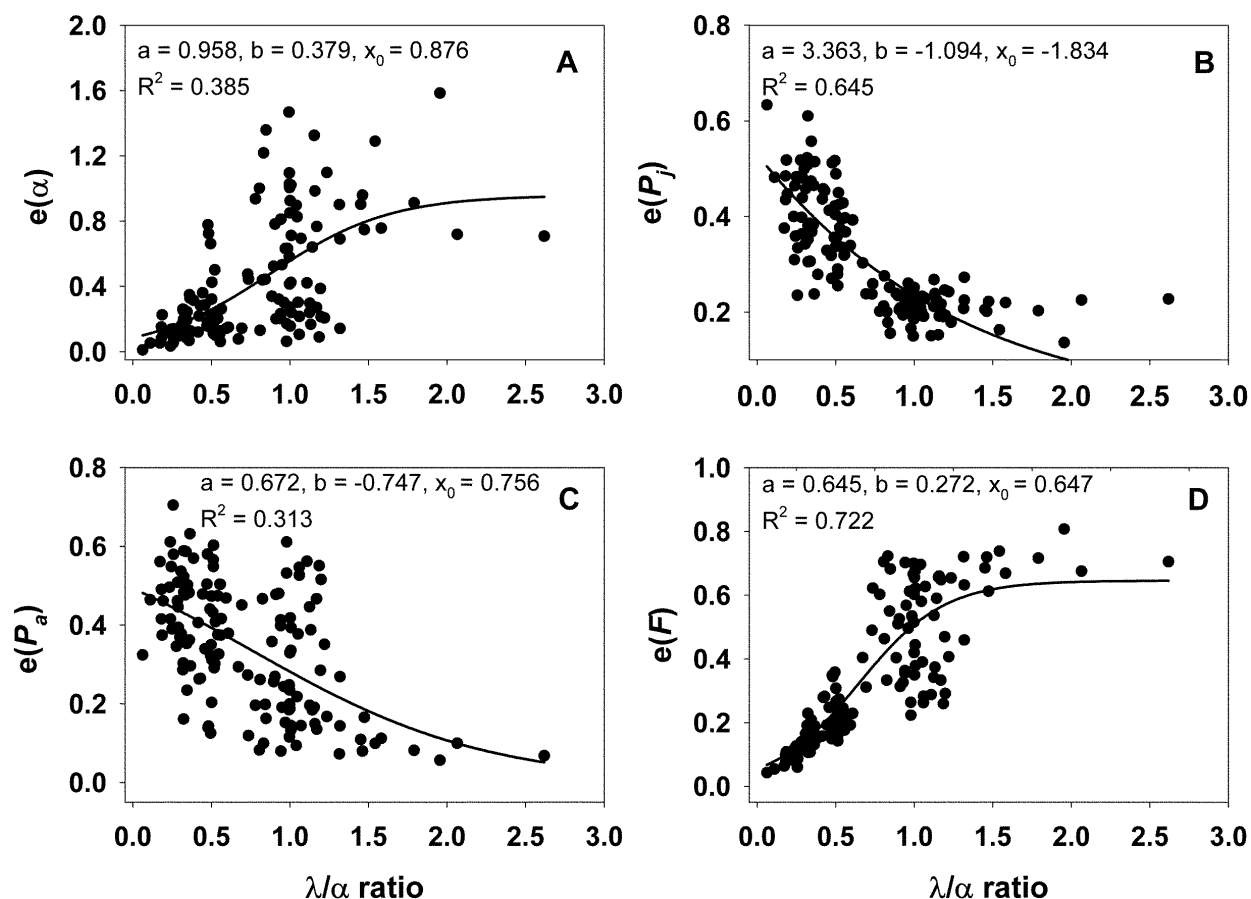


Figure 10: Relationship between λ/α ratio and elasticity of population growth rate (λ) to changes in (A) age at maturity, $e(\alpha)$; (B) juvenile survival, $e(P_j)$; (C) adult survival, $e(P_a)$; and (D) fertility, $e(F)$. A three-parameter nonlinear regression model of the form $Y = a/[1 + \exp\{-(X - x_0)/b\}]$ was fitted; estimates of the three parameters (a , b , and x_0) and the coefficient of determination (R^2) are also given ($N = 142$).

that in α and P_j (fig. 8). No single life-history variable had the largest relative influence on λ in either stable/declining or increasing populations.

Elasticities in four qualitative categories on the basis of values of λ and α were examined to test the prediction that these two variables determine the pattern of elasticities (Stearns 1992). In increasing populations with delayed maturity (high λ , high α), elasticity of λ to changes in P_a ranked first most frequently, followed by that in P_j ($N = 38$), and a similar pattern was evident in near-equilibrium/declining populations with delayed maturity (low λ , high α ; $N = 35$). In near-equilibrium/declining populations with early maturity (low λ , low α), $e(\alpha)$ and $e(F)$ ranked first most frequently in 45.45% and 30.30% ($N = 33$) of the populations, respectively (fig. 9). The λ/α ratio was predictably associated with elasticity of λ to changes in several life-history variables, particularly P_j and F (fig. 10).

In populations with $\lambda/P_a > 1.25$, $e(\alpha)$ ranked first most

frequently (43.16%), followed by $e(P_a)$ (22.11%; $N = 95$), and $e(P_a)$ ranked first most frequently (72.34%; $N = 47$) in populations with $\lambda/P_a \leq 1.25$ (fig. 11). The λ/P_a ratio was predictably associated with elasticity of λ to changes in several life-history variables, particularly P_a and F (fig. 12).

To test the prediction that the relative influence on λ of changes in life-history variables should be determined by the onset (α) and magnitude (F) of reproduction, we examined the pattern of elasticities for four qualitative categories on the basis of the values of α and F . In all populations characterized by early maturity and high F , $e(\alpha)$ always ranked first and $e(F)$ ranked second ($N = 30$). In populations with early maturity and low F , $e(P_a)$ (43.90%; $N = 41$) and $e(F)$ (39.02%) ranked first almost equally; $e(P_j)$ never ranked first. In cases where maturity was delayed and F was high, $e(P_j)$ (42.86%) ranked first most frequently, followed by $e(\alpha)$ (35.71%; $N = 14$); $e(F)$ never ranked first or second. However, when a delayed

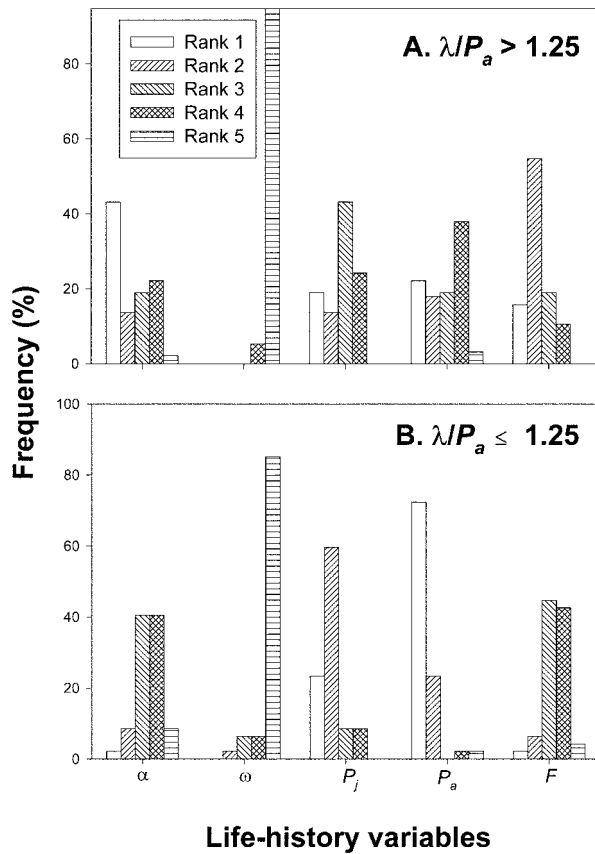


Figure 11: Frequency distribution (%) of ranks of elasticities on the basis of λ/P_a ratio; (A) high ($\lambda/P_a > 1.25$; $N = 95$) and (B) low ($\lambda/P_a \leq 1.25$; $N = 47$). Variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility; λ = population growth rate. For each population, absolute values of elasticities, $e(p)$, were ranked in a descending order such that a life-history variable with the largest relative influence on λ would receive a rank of 1, and a life-history variable with the smallest relative influence on λ would receive a rank of 5.

maturity was associated with low F , $e(P_a)$ (59.65%) and $e(P_j)$ (40.35%; $N = 57$) ranked first most frequently; $e(\alpha)$ and $e(F)$ never ranked first and rarely second.

Because the F/α ratio was predictably associated with $e(p)$ (fig. 13), we also examined the relative magnitudes of $e(p)$ in relation to the F/α ratio. First, in populations with $F/\alpha < 0.15$, survival rates were most influential, with $e(P_a)$ and $e(P_j)$ ranking first in 70.97% and 29.03% of the populations ($N = 31$), respectively. When $e(P_a)$ ranked first, $e(P_j)$ always ranked second and vice versa; elasticity of λ to changes in no other life-history variables ranked first or second. Second, in populations with $0.15 \leq F/\alpha \leq 0.30$, $e(P_a)$ (48.57%) and $e(P_j)$ (48.57%; $N = 35$) still ranked first most frequently. However, elasticity of λ to changes in other variables frequently ranked second,

and $e(F)$ ranked first in one population. Third, in populations with $0.30 < F/\alpha \leq 0.60$, $e(P_a)$ and $e(F)$ ranked first most frequently in 34.88% and 37.21% ($N = 43$) of the populations in this category, respectively. Elasticity of λ to changes in reproductive parameters (α and F) ranked first in 55.81% of populations in this category. Fourth, in populations with $F/\alpha > 0.60$, $e(\alpha)$ ranked first and $e(F)$ ranked second in 100% ($N = 33$) of the populations. Elasticity of λ to changes in P_j or P_a never ranked first or second. Fifth, elasticity of λ to changes in α never ranked first in populations with $F/\alpha < 0.47$. Sixth, elasticity of λ to changes in P_a never ranked first or second in populations with $F/\alpha > 0.54$. Seventh, elasticity of λ to changes in P_j never ranked first in populations with $F/\alpha > 0.42$ (fig. 14).

Discussion

Elasticity Patterns and Evaluation of Theoretical Predictions

The life-history variable with the smallest relative influence on λ was ω ; $e(\omega)$ was the lowest in >90% of the populations examined. No single life-history variable had the largest relative influence on λ in the majority of the populations. Thus, the prediction that α (Cole 1954; Lewontin 1965) or any other single life-history variable should have the largest relative influence on λ was not supported by data. Empirical support for the predicted pattern of the relative importance of life-history variables to λ on the basis of values of λ (Meats 1971), α and λ (Stearns 1992), and the λ/P_a ratio (Caswell and Hastings 1980) was poor at best.

We suggest four possible reasons for the discrepancy between the predicted and observed patterns of the relative importance of life-history variables to λ . First, most theoretical studies that investigated the relative importance of life-history variables to λ were motivated by Cole's (1954) results. Because Cole focused on the relative influence of changes in age at maturity and reproductive rate on λ , most subsequent studies followed Cole's lead and focused on these two variables (e.g., Lewontin 1965; Green and Painter 1975; Caswell and Hastings 1980). Arguably, all life-history variables influence λ to some extent, and the relative influence on λ of changes in all life-history variables must be considered simultaneously, because exclusion of ≥ 1 life-history variables can change the pattern. Second, most of these studies made assumptions that may not hold in mammalian populations. For example, Cole (1954) assumed that mortality does not occur until age ω , and Lewontin (1965) assumed that reproductive rate function has a triangular shape, which are perhaps poor assumptions for many populations of mammals. Third, many of these studies were based on numerical simulations, and some of them used values of life-history vari-

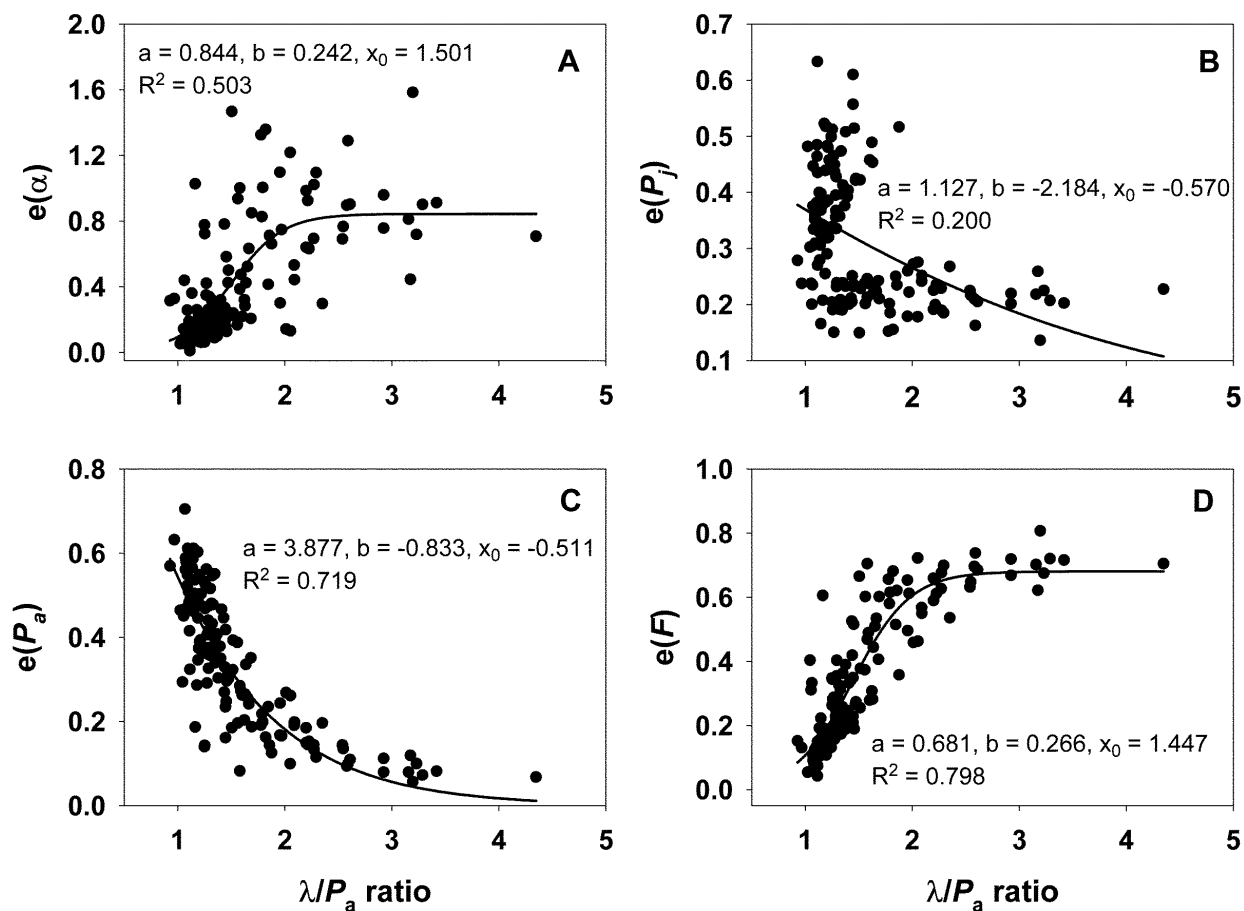


Figure 12: Relationship between λ/P_a ratio and elasticity of population growth rate (λ) to changes in (A) age at maturity, $e(\alpha)$; (B) juvenile survival, $e(P_j)$; (C) adult survival, $e(P_a)$; and (D) fertility, $e(F)$. A three-parameter nonlinear regression model of the form $Y = a/[1 + \exp\{-(X - x_0)/b\}]$ was fitted; estimates of the three parameters (a , b , and x_0) and the coefficient of determination (R^2) are also given ($N = 142$).

ables that are not commonly observed in vertebrate populations. For example, Lewontin (1965) used values of reproductive rate ranging from 100 to 8,000; these values are substantially greater than reproductive rates of most mammals. Finally, demographic techniques that allow simultaneous, analytical quantification of the relative importance of life-history variables to λ were not available at the time most of the theoretical studies considered here were conducted. The lack of adequate demographic models and appropriate analytical techniques precluded rigorous theoretical analyses that could potentially lead to robust predictions. However, strong association between $e(p)$ and metrics such as λ/P_a (Caswell and Hastings 1980) and λ/α (Stearns 1992) ratios suggests that these authors had identified important variables with substantial influence on the pattern of relative importance of life-history variables to λ .

Using a prebreeding census partial life cycle model,

Heppell et al. (2000) investigated the pattern of elasticity of λ to changes in P_j , P_a , and F in 50 populations of mammals. They found that, in “fast” mammals (those that attain sexual maturity early, produce large litters, and have short life spans; Gaillard et al. 1989; Heppell et al. 2000), F has a greater relative influence on λ than do P_j or P_a , whereas survival rates (P_j or P_a) have a greater relative influence on λ in “slow” mammals (those that mature late, produce small litters, and have long life spans). Similar analyses in 49 species of birds revealed that the potential influence on λ of changes in F increased with an increase in clutch size (Sæther and Bakke 2000). However, Heppell et al. (2000) and Sæther and Bakke (2000) did not consider the elasticity of λ to changes in α and ω , nor did they test theoretical predictions regarding the relative importance of life-history variables to λ . To our knowledge, this study is the first to consider simultaneously the relative influence on λ of changes in five important life-history variables (α ,

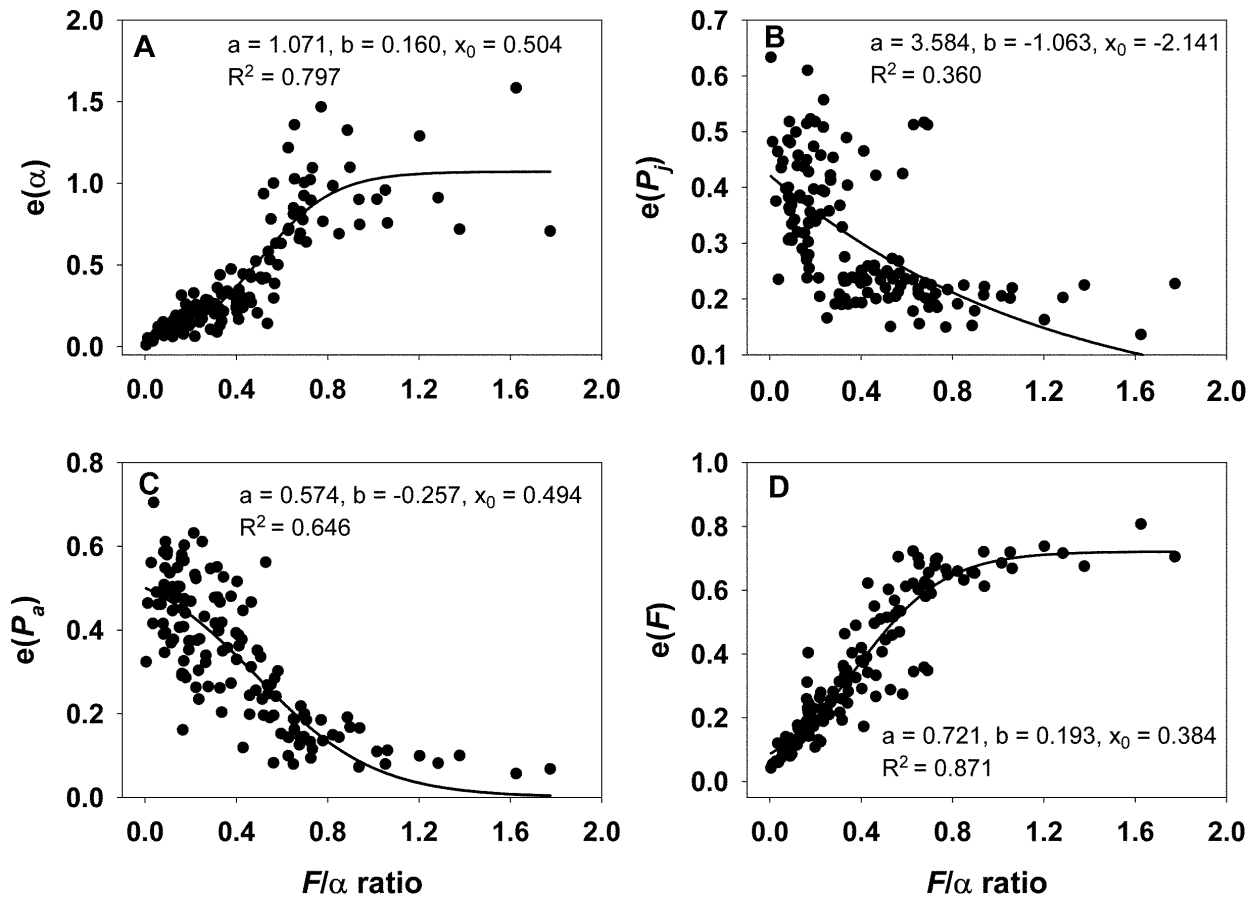


Figure 13: Relationship between F/α ratio and elasticity of population growth rate (λ) to changes in (A) age at maturity, $e(\alpha)$; (B) juvenile survival, $e(P_j)$; (C) adult survival, $e(P_a)$; and (D) fertility, $e(F)$. A three-parameter nonlinear regression model of the form $Y = a/[1 + \exp\{-(X - x_0)/b\}]$ was fitted; estimates of the three parameters (a , b , and x_0) and the coefficient of determination (R^2) are also given ($N = 142$).

ω , P_j , P_a , and F) and to test theoretical predictions regarding the relative importance of life-history variables to λ using empirical data in age-structured populations.

Effects of Onset and Magnitude of Reproduction

When elasticities were examined in relation to onset (α) and magnitude (F) of reproduction, a clear picture emerged. In all populations characterized by early maturity and high reproductive rates ($F/\alpha > 0.60$), λ was overwhelmingly most sensitive to changes in α , followed by F , and relatively insensitive to changes in survival parameters (P_j or P_a). The prediction that α should have the largest relative influence on λ (Cole 1954; Lewontin 1965) was supported for this particular case (see also Levin et al. 1996; Oli et al. 2001, 2002). In all populations characterized by a delayed maturity and low reproductive rates

($F/\alpha < 0.15$), λ was most sensitive to changes in P_j or P_a and relatively insensitive to changes in α and F . In general, as the F/α ratio increased, $e(\alpha)$ and $e(F)$ increased, and $e(P_j)$ and $e(P_a)$ decreased; as the F/α ratio decreased, $e(P_j)$ and $e(P_a)$ increased, and $e(\alpha)$ and $e(F)$ decreased. Thus, analyses based on the F/α ratio clearly revealed situations in which reproductive or survival parameters were most influential.

The pattern of elasticities based on the value of the F/α ratio has an intuitive biological interpretation. Life-history theory predicts that populations that mature early and have large reproductive rates are likely to have low survival rates as a result of trade-offs between somatic and reproductive efforts (Bell 1980; Stearns 1992). In such populations, maturing earlier ensures that a greater proportion of offspring enters the reproductive age class, and it thus influences λ substantially. However, populations that ma-

ture late and have low reproductive rates generally survive better because costs of reproduction in such populations may be low, and a greater proportion of energy may be allocated for somatic efforts (Hirshfield and Tinkle 1975; Roff 1992; Stearns 1992; Oli 1999). In such populations, λ might be increased most rapidly by surviving better each time step.

Effects of Phylogeny and Body Size

The relative influence on λ of changes in life-history variables might be influenced by phylogenetic constraints, by the range of body size of mammalian species, or by both. We examined these possibilities in a preliminary way by making statistical adjustments for order and family effects and by analyzing the residuals of $e(p)$ regressed on body size. We found that a substantial proportion of variation in $e(p)$ was associated with phylogeny and that statistical removal of phylogenetic effects on $e(p)$ accentuated the relative influence of α and F on λ . This may reflect a long evolutionary history of life-history traits, causing elasticity patterns to be generally similar among closely related species. The relative magnitudes of mean $e(p)$, however, were identical to those of unadjusted $e(p)$, indicating that the average pattern of the relative influence of life-history variables to λ had not changed substantially.

Body size had a much more minor, though still significant, influence on elasticities, and removal of the influence of variation in body size appeared to accentuate the relative influence of α and F on λ . Influences of body size on life-history variables are well known for mammals (Western 1979, 1983; Western and Ssemakula 1982; Millar and Zamuto 1983; Stearns 1983), but influences on elasticities were previously untested (but see Heppell et al. 2000). When influences of both body size and phylogeny were statistically removed, the pattern of mean $e(p)$ was again similar to that of unadjusted $e(p)$. Thus, the influences of phylogeny and body size on the relative importance of life-history variables to λ were at best minor.

While the influence of evolutionary history on the pattern of relative importance of life-history variables to λ was interesting, values of $e(p)$ corrected for phylogeny are difficult to interpret. There are several reasons for this. First, it is generally assumed in phylogenetic comparative analyses that traits under investigation are subject to natural selection (Price 1997). Elasticities are not evolutionary traits. Second, most phylogenetic comparative analyses give priority to phylogeny over ecology as a correlate of a trait and thus implicitly treat the two as mutually exclusive, an incorrect assumption (Westoby et al. 1995a, 1995b). Thus, it would be erroneous to conclude that only the proportion of variation in $e(p)$ not explained by phylogeny is associated with current ecological conditions.

Third, elasticity patterns within family or species can be quite diverse, while distantly related taxa may exhibit remarkably similar elasticity patterns (cf. figs. 3, 4 and figs. 5, 6). Finally, patterns of elasticity may change even within populations, depending on current ecological conditions and their influences on life-history patterns (fig. 4; see also Dobson and Oli 2001; Oli et al. 2001).

Elasticity Patterns, "Fast-Slow" Continuum, and F/α Ratio

Several authors have suggested that species of mammals can be placed along a "fast-slow" continuum, with species that mature early and have large litters and a short generation time occupying the "fast" end of the continuum and those with an opposite suite of traits occupying the "slow" end of the continuum (Gaillard et al. 1989; Read and Harvey 1989; Promislow and Harvey 1990; Franco and Silvertown 1997; Heppell et al. 2000). Quantification of the continuum has remained unclear, however, and objective criteria on which to base such a determination are lacking. We suggest that the F/α ratio adequately quantifies the fast-slow continuum. Populations with a high F/α ratio (typically $F/\alpha > 0.60$) occupy the "fast" end of the continuum; in such populations, λ is most sensitive to perturbations in α , followed by F . Populations with a low F/α ratio (typically $F/\alpha < 0.15$) occupy the "slow" end of the continuum; in such populations, λ is most sensitive to perturbations in survival parameters (P_j and P_a), and changes in reproductive parameters are of little consequence. Thus, we have provided an objective criterion for determining the position of a species or a population in the fast-slow continuum and explicitly linked the continuum with elasticity patterns. This link may be used for classifying mammals according to their likely response to perturbations, as suggested by Heppell et al. (2000).

Relevance to Population Ecology

Population regulation underlies many ecological and evolutionary processes and thus serves as a central, unifying concept in ecology (Murdoch 1994; Turchin 1995, 1999; Sinclair 1996). An understanding of the demographic machinery that produces changes in population size is essential for discerning the factors or processes that underlie the dynamics and regulation of biological populations (Dobson and Oli 2001). This is because life-history variables differ substantially with respect to density-dependent responses (e.g., Fowler 1981; Sinclair 1989, 1996; Tinkle et al. 1993; Leips et al. 2000; Coulson et al. 2001) and potential influences on λ (Cole 1954; Enright et al. 1995; Heppell et al. 2000; Sæther and Bakke 2000; this study) and also because dynamical behavior of a population is

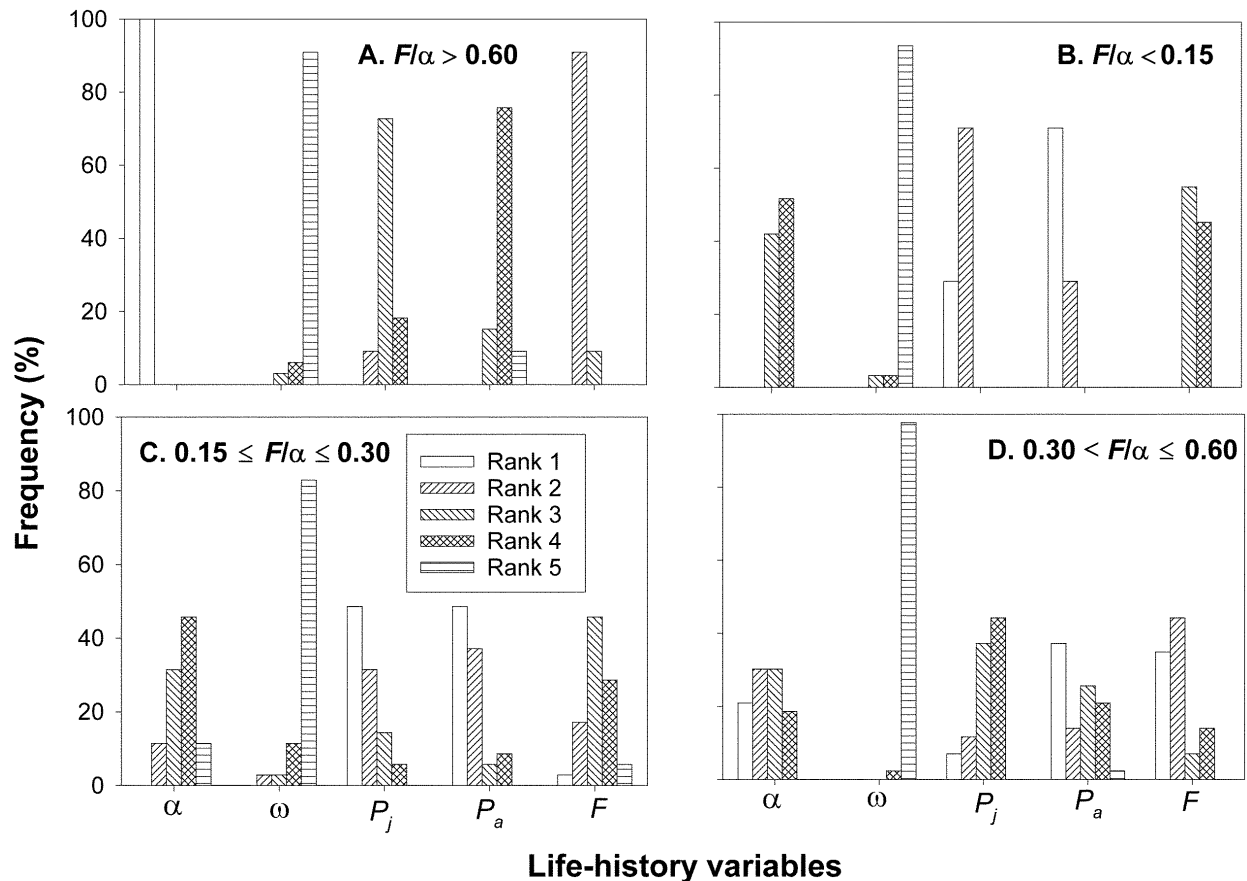


Figure 14: Frequency distribution (%) of ranks of elasticities on the basis of values of F/α ratio; (A) $F/\alpha > 0.60$ ($N = 33$), (B) $F/\alpha < 0.15$ ($N = 31$), (C) $0.15 \leq F/\alpha \leq 0.30$ ($N = 35$), and (D) $0.30 < F/\alpha \leq 0.60$ ($N = 43$). Variables are as follows: α = age at maturity; ω = age at last reproduction; P_j = juvenile survival; P_a = adult survival; F = fertility; λ = population growth rate. For each population, absolute values of elasticities, $e(p)$, were ranked in a descending order such that a life-history variable with the largest relative influence on λ would receive a rank of 1, and a life-history variable with the smallest relative influence on λ would receive a rank of 5.

heavily influenced by demographic origin of density dependence (Higgins et al. 1997; Neubert and Caswell 2000). The wide range of dynamical behaviors exhibited by natural populations (stable, cyclic, or chaotic) suggests that the demographic bases of population regulation can vary among populations, but it is unknown what determines the likely numerical dynamics of a population.

We suggest that numerical dynamics of biological populations are governed by the likely response of λ to changes in life-history variables (quantified by $e(p)$), the response of life-history variables to environmental perturbations, and the demographic origin of density-dependent feedback mechanisms. Specifically, we predict large-scale fluctuations in population size with cyclic or chaotic dynamics if life-history traits with large potential influence on λ exhibit strong density-dependent, plastic responses. How-

ever, numerical dynamics of a population are predicted to be relatively stable if density dependence is weak or if density-dependent life-history traits have little potential influence on λ . In general, if reproductive parameters (α and F) show strong density-dependent responses in populations with $F/\alpha > 0.60$, substantial fluctuations in population size with cyclic or chaotic dynamics may be predicted. For example, many populations of voles (*Microtus* spp., *Clethrionomys* spp.) exhibit cyclic fluctuations in abundance (Krebs et al. 1973; Taitt and Krebs 1985; Lidicker 1988; Boonstra 1994; Krebs 1996; Boonstra et al. 1998). An examination of the problem from a demographic perspective revealed that changes in α are at the core of the demographic machinery that produces large-scale fluctuations in abundance such as those observed in cyclic populations (Oli and Dobson 1999, 2001). These

findings are consistent with results presented here, because cyclic populations of voles are generally characterized by early maturity and high reproductive rates with $F/\alpha > 0.60$, and α exhibits strong density-dependent, phase-related changes (Boonstra 1989, 1994; Gilbert and Krebs 1991; Tkadlec and Zejda 1995; Oli and Dobson 1999).

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Clearly, the pattern of elasticities depends on values of all life-history variables as well as on λ , but our results suggest that general predictions regarding the pattern of relative influence on λ of changes in life-history variables are possible, on the basis of the values of F/α ratio. Although several authors have argued that the pattern of the relative importance of life-history variables to λ depends on the pattern of life history (Roff 1992; Stearns 1992), conditions in which one or the other life-history variable should be most influential were unclear until now. Our results demonstrate that reproductive parameters have the largest relative influence on λ in populations characterized by early maturity and high fertility rates, or when $F/\alpha > 0.60$. In contrast, survival parameters have the largest relative influence on λ in populations characterized by delayed maturity and low reproductive rates, or when $F/\alpha < 0.15$. Thus, our study has answered, at least partially, the question first asked by Cole (1954).

Species of mammals differ greatly in body size, age structure, and many aspects of life history (Western 1979, 1983; Western and Ssemakula 1982; Millar and Zammuto 1983; Read and Harvey 1989; Purvis and Harvey 1995). These differences make interspecific comparison of life histories difficult. Our results suggest that mammalian life history may be conveniently grouped into a few discrete categories according to their likely responses to perturbations in life-history variables, on the basis of values of the F/α ratio. The study of life histories within such a framework would make interspecific comparisons easier and allow predictions regarding likely responses of a population to environmental perturbations, and it might also shed new light on the numerical dynamics and evolution of life histories in age-structured populations. Similar studies in other taxa are needed to elucidate the generality of our predictions regarding the relative importance of life-history variables to λ and numerical dynamics of age-structured populations.

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