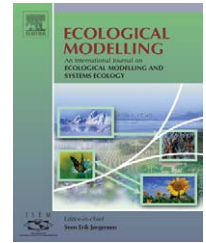


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# Relative importance of avian life-history variables to population growth rate

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## ARTICLE INFO

### Article history:

Received 17 May 2005

Received in revised form

29 March 2006

Accepted 5 April 2006

Published on line 12 June 2006

### Keywords:

Demography

Elasticity analysis

Life history

Matrix population models

Partial life cycle models

## ABSTRACT

Population growth rate is a function of several life-history variables, which differ in their potential influence on population dynamics. Knowledge of the relative importance of these life-history variables can have implications for ecological and evolutionary theory as well as the conservation of endangered species. We used life-history data for 155 populations of birds to estimate asymptotic growth rate ( $\lambda$ ) and elasticity of  $\lambda$  to changes in four life-history variables: age at maturity ( $\alpha$ ), juvenile survival ( $P_j$ ), adult survival ( $P_a$ ), and mean fertility ( $F$ ). Elasticities were used to quantify relative importance, and to test predictions regarding the pattern of relative importance. Neither  $\alpha$  nor any other single life-history variable was most influential in all populations, but  $P_a$  had the largest relative influence on  $\lambda$  in 53.5% of the populations. Several metrics ( $\lambda/\alpha$ ,  $\lambda/P_a$ ,  $F/\alpha$ ,  $m/\alpha$ , and two estimates of generation time:  $\bar{A}$  and  $T$ ) were strongly correlated with elasticities, suggesting that these metrics may be useful predictors of the pattern of relative importance. In general, reproductive parameters ( $\alpha$  and  $F$ ) were most important in populations that matured early and had high reproductive rates, whereas survival parameters ( $P_j$  and  $P_a$ ) were most important in populations that matured late and had low reproductive rates, consistent with earlier research in other taxa. Metrics that require minimal data and have strong predictive power (e.g. the  $m/\alpha$  ratio) should be useful in devising conservation plans for those species that lack detailed demographic data.

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## 1. Introduction

An important goal in population ecology is to estimate the rate at which a population is growing or declining. Because the population growth rate is a function of several life-history variables, changes in these parameters will cause changes in the growth rate (Caswell, 2001; Oli and Armitage, 2004). Questions regarding which life-history variables have the greatest influence on population growth rate, and the overall pattern of influence of such variables (hereafter, pattern of relative importance) have attracted much theoretical interest over

the past 50 years (Cole, 1954; Lewontin, 1965; Meats, 1971; Snell, 1978; Caswell and Hastings, 1980; Stearns, 1992; Oli and Dobson, 2003) and also has the potential to be of considerable conservation importance (Benton and Grant, 1999; Mills et al., 1999; Heppell et al., 2000; Caswell, 2001). In the case of endangered or pest species, knowing which life-history variables have the strongest impact on the population growth rate enables managers to target those parameters to increase the population growth rate of a threatened species (Crouse et al., 1987; Crowder et al., 1994; Fisher et al., 2000; Gerber and Heppell, 2004), to reduce the population growth rate of

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an invasive or pest species (Shea and Kelly, 1998), or to determine sustainable harvest of a population (Citta and Mills, 1999; Caswell, 2001). Measures of the relative importance of life-history variables to population growth rate also can be viewed as selection gradients (Van Tienderen, 2000; Caswell, 2001; Coulson et al., 2003; Forbis and Doak, 2004). Those life-history variables with the greatest influence on growth rate are also expected to experience strong selection pressure (Stearns, 1992; Charlesworth, 1994; Caswell, 2001).

Lamont Cole (1954) was one of the first to investigate the pattern of relative importance of life-history variables on population growth rate. Based on simulation studies, Cole concluded that "... the age at which reproduction begins is one of the most significant characteristics of a species ..." (1954:138). Since Cole (1954), several authors (Lewontin, 1965; Meats, 1971; Snell, 1978; Caswell and Hastings, 1980; Stearns, 1992; Oli and Dobson, 2003) have examined the pattern of relative importance. The earlier studies (e.g., Cole, 1954; Lewontin, 1965) were based on simulations, while later analyses (e.g., Oli and Dobson, 2003) were based on analytical methods using matrix models. Many of the studies mentioned have made theoretical predictions or proposed metrics that allow one to predict the pattern of relative importance using combinations of reproductive and survival parameters, and the population growth rate. However, there is a paucity of empirical studies testing these predictions (see Oli and Dobson, 2003 for an exception).

The pattern of relative importance has been thoroughly investigated in mammalian populations (Oli and Dobson, 2003), but similar analyses on most other taxa are currently lacking. A recent study based on the analysis of 49 avian populations by Sæther and Bakke (2000) concluded that in populations characterized by high reproductive rates, changes in fertility had the greatest impact on the population growth rate, whereas in populations with low reproductive rates, changes in survival (particularly of adults) had the greatest impact on the growth rate. Sæther and Bakke's (2000) work made important contributions to the understanding of patterns of relative importance in avian populations, and formed the basis of our study. However, the authors did not consider the influence of age at maturity on population growth rate, an influential life-history variable (Cole, 1954; Oli et al., 2002), nor did they test any of the theoretical predictions regarding the pattern of relative importance. Our study significantly extends Sæther and Bakke's (2000) findings by examining the relative importance of several life-history variables to population growth rate, including age at maturity, as well as testing several theoretical predictions regarding the pattern of relative importance in avian populations.

We used elasticities (de Kroon et al., 1986, 2000; Caswell, 2001) to quantify the relative importance of four life-history variables: age at maturity ( $\alpha$ ), juvenile survival ( $P_j$ ), adult survival ( $P_a$ ), and fertility ( $F$ ) to the asymptotic population growth rate ( $\lambda$ ) in 155 avian populations representing 113 species from 41 families and 14 orders, making this the most comprehensive study of this type. We tested six theoretical predictions concerning the use of several life-history metrics to predict the pattern of relative importance: (1) age at maturity should have the highest influence on  $\lambda$  (Cole, 1954); (2) the pattern of relative importance of life-history variables to  $\lambda$  should depend

on  $\lambda$  and differ between increasing populations and declining/near equilibrium populations (Meats, 1971; Snell, 1978); (3) the pattern of relative importance should depend on the  $\lambda/P_a$  ratio (Caswell and Hastings, 1980); (4) the pattern of relative importance should depend on  $\lambda$  and  $\alpha$  (Stearns, 1992); (5) the pattern of relative importance should depend on the magnitude of reproduction relative to the onset of reproduction ( $F/\alpha$  and  $m/\alpha$  ratios, where  $m$  is the average fecundity (Oli and Dobson, 2003; Oli, 2004; Oli and Dobson, 2005)); (6) the pattern of relative importance should be determined by generation time (Gaillard et al., 2005). These metrics have the potential to predict the pattern of relative importance even for populations for which data are limited. Therefore, these metrics could serve as useful tools in, for example, recovery efforts for endangered species (populations of which are often characterized by limited data). Finally, we examined the influence of phylogeny and body mass on the elasticities, and investigated the relative importance of life-history variables to  $\lambda$  after statistically removing the effects of phylogeny and body mass.

## 2. Methods

We compiled avian life-history data from published literature (Appendix I). Data based solely on the male segment of the population or from captive populations were not used. If life tables or age-specific survival and at least average fecundity rates were available, age-specific survival probabilities ( $P_i$ ) and fertilities ( $F_i$ ) were estimated using birth-pulse, post-breeding census methods (Caswell, 2001):

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

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

where  $l_i$  is age-specific survivorship (probability at fledging of surviving to age class  $i$ ) and  $m_i$  is age-specific fecundity (the average number of female offspring fledged by each female of age class  $i$ ). We then constructed an age-classified Leslie matrix  $\mathbf{A}$  for each population (Caswell, 2001).

Because age at first ( $\omega$ ) and last reproduction ( $\omega$ ) do not appear explicitly in the age-based Leslie matrix, the sensitivity and elasticity of  $\lambda$  to changes in these two variables cannot be estimated using standard techniques. Thus, we used a post-breeding census partial life-cycle model (Oli and Zinner, 2001a,b) for demographic analyses. The post-breeding census partial life-cycle model is based on two life-history stages: juvenile (pre-reproductive) and adult (reproductive) (Oli and Zinner, 2001a,b). Juveniles take  $\alpha$  time units to reach reproductive maturity, and they survive each time unit with probability  $P_j$ . Once reproduction begins at age class  $\alpha$ , adults survive with a probability  $P_a$  and reproduce with an average fertility  $F$  each time unit until age at last reproduction,  $\omega$ . The characteristic equation for the post-breeding census partial life-cycle model 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 largest real root of Eq. (3) is an estimate of the asymptotic population growth rate,  $\lambda$ . Although some age-specific information is lost (simplified models are likely to overlook complex patterns of demography, especially in long-lived species), the simplified partial life-cycle model allows estimation of the sensitivity and elasticity of  $\lambda$  to changes in all life-history variables, including  $\alpha$  and  $\omega$ ; other advantages of the model are discussed elsewhere (Oli and Zinner, 2001a; Oli, 2003a,b; Oli and Dobson, 2003). Therefore, we used the partial life cycle model of Oli and Zinner (2001a) for demographic analyses of populations for which life tables or estimates of the five life-history variables ( $\alpha$ ,  $\omega$ ,  $P_j$ ,  $P_a$ , and  $F$ ) were available.

We defined  $\alpha$  and  $\omega$  as the first and last age classes with nonzero fertility, respectively. When age-specific data were available,  $m$ ,  $P_j$ , and  $P_a$  were estimated from the age-classified population projection matrix as weighted averages, weighted according to the contribution of each age class to the stable age distribution (Oli and Zinner, 2001a):

$$m = \frac{\sum_{i=\alpha}^{\omega} w_i m_i}{\sum_{i=\alpha}^{\omega} w_i}, \tag{4}$$

$$P_j = \frac{\sum_{i=1}^{\alpha} w_i P_i}{\sum_{i=1}^{\alpha} w_i}, \tag{5}$$

$$P_a = \frac{\sum_{i=\alpha+1}^{\omega-1} w_i P_i}{\sum_{i=\alpha+1}^{\omega-1} w_i}, \tag{6}$$

where  $w_i$  is the  $i$ th entry of the right eigenvector (stable age distribution) corresponding to the dominant eigenvalue of the age-classified projection matrix  $\mathbf{A}$ .  $F$  was then estimated as

$$F = mP_a \tag{7}$$

For a majority of the populations included in our study (86%,  $N=134$  of 155), age-specific data or estimates of  $\omega$  were not available. Thus, we used a reduced-parameter post-breeding census partial life-cycle model that requires only four parameters ( $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$ ) (Oli, 2003a). This model is similar to that in Eq. (3), except that  $\omega$  is ignored. The characteristic equation is:

$$\lambda^{\alpha+1} - \lambda^{\alpha}P_a - P_j^{\alpha-1}F\lambda + P_j^{\alpha-1}FP_a - P_j^{\alpha}F = 0. \tag{8}$$

We used the estimates of life-history variables that were reported by the sampled studies. We estimated  $\alpha$  as the mean age (rounded down) at which females laid their first clutch. Many neotropical migrant passerines exhibit low natal philopatry, and estimates of first year survival can be difficult to obtain. In cases where juvenile survival was not reported ( $N=5$ ), we estimated  $P_j$  as one-half of the reported adult survival rate (May and Robinson, 1985; Holmes et al., 1996). The average fecundity ( $m$ ) was the average number of female fledglings produced per adult female per year. Fertility rate ( $F$ ) was then estimated using Eq. (7).

### 2.1. Quantifying the relative importance

The asymptotic growth rate of a population,  $\lambda$ , was estimated as the largest real root of Eq. (3) or Eq. (8), depending on the availability of estimates of  $\omega$  (or detailed demographic data). We used prospective perturbation analysis (sensitivity and elasticity) to quantify the effect of changes in a parameter on  $\lambda$ . Sensitivity of  $\lambda$  to changes in a variable  $p$  was estimated as the partial derivative of  $\lambda$  with respect to  $p$  (i.e.,  $\partial\lambda/\partial p$ , where  $p$  is the life-history variable in question), and was obtained by implicit differentiation of Eq. (3) or Eq. (8). Elasticity of  $\lambda$  to changes in a variable  $p$  was calculated by multiplying the sensitivity of  $\lambda$  to  $p$  by  $p/\lambda$  (i.e.,  $[p/\lambda][\partial\lambda/\partial p]$ ; Caswell, 2001). Because elasticities are directly comparable among life-history variables and sum to one (excluding  $\alpha$  and  $\omega$ ), we used elasticities to quantify the relative importance of life-history variables to  $\lambda$  (de Kroon et al., 2000; Caswell, 2001; Oli and Dobson, 2003).

### 2.2. Effects of hierarchical taxonomy and body mass

We used Dunning (1992) as a source for avian body masses and as a guide for taxonomy. Taxonomy in Dunning (1992) was based on Clements (1990), which made use of Sibley and Ahlquist (1990). To investigate the effects of hierarchical taxonomy (hereafter, taxonomy) and body mass on elasticity patterns, we used a nested ANCOVA, with order as the main effect, family nested within order, and body mass as a covariate (Stearns, 1983, 1984; Miles and Dunham, 1992; Oli and Dobson, 2003). All elasticity values were  $\log(e)$ -transformed. Absolute values of the residuals were examined to investigate the pattern of elasticities after the effects of taxonomy and body mass were removed. Theoretical predictions regarding the relative importance of life-history variables to  $\lambda$  were tested using original elasticity values, because these predictions were made independent of taxonomy and body mass.

### 2.3. Testing theoretical predictions and evaluating proposed metrics of relative importance

In order to evaluate Cole's (1954) conclusion that age at maturity ( $\alpha$ ) should have the highest relative influence on  $\lambda$ , we examined the relationship between  $\alpha$  and the absolute values of the elasticity of  $\lambda$  to changes in each life-history variable. Therefore, the life-history variable with the largest influence on  $\lambda$  would be ranked first and the parameter with the least influence on  $\lambda$  would be ranked fourth.

The idea that the relative importance of life-history variables to  $\lambda$  depends on  $\lambda$  (Meats, 1971; Snell, 1978) was evaluated by examining the relationship between  $\lambda$  and the elasticities. Additionally, to determine whether the order of relative importance differed between increasing and decreasing/near equilibrium populations, we compared the ranking of absolute values of the elasticities for populations in which  $\lambda > 1$  (increasing) to those in which  $\lambda \leq 1$  (declining/near equilibrium).

Several proposed metrics of the relative importance ( $\lambda/P_a$ ,  $\lambda/\alpha$ ,  $T$  and  $\bar{A}$ , and  $F/\alpha$  and  $m/\alpha$ ) had no obvious cut-off points. Therefore, we examined the relationship between elasticities and the metric of interest to identify situations in which a pattern of elasticities, if any, was apparent. Although the

thresholds were arbitrary, we feel that these values enable us to find such situations, and are based on similar thresholds of a previous analysis (Oli and Dobson, 2003). Caswell and Hastings' (1980) metric of relative importance, the  $\lambda/P_a$  ratio, was evaluated by ranking the absolute values of elasticities for each population as before. We then examined the data for a trend in the relationship between elasticity ranks and  $\lambda/P_a$  ratio.

Stearns (1992) suggested that the relative importance could be determined using  $\alpha$  and  $\lambda$ , and we evaluated this proxy by examining the relationship between the  $\lambda/\alpha$  ratio and the elasticities. The pattern of relative importance in populations with  $\lambda/\alpha < 0.3$  was compared to those characterized by  $\lambda/\alpha > 1.15$ .

We evaluated the magnitude of reproduction relative to the timing of reproduction as a proxy for the relative importance of life-history variables (Oli and Dobson, 2003; Oli, 2004) by examining the relationship between the  $F/\alpha$  and  $m/\alpha$  ratios, and the elasticities. We compared the pattern of relative importance in populations that matured early and exhibited high reproductive rates ( $F/\alpha > 0.6$ ,  $m/\alpha \geq 0.75$ ) to those characterized by delayed maturity and low reproductive rates ( $F/\alpha < 0.15$ ,  $m/\alpha \leq 0.25$ ).

Finally, generation time was evaluated as a proxy for the pattern of relative importance (Gaillard et al., 2005) using two measures of generation time. The first measure of generation time,  $T$ , defined as the time required for the population to increase by a factor of the net reproductive rate ( $R_0$ ), was estimated as (Caswell, 2001):

$$T = \frac{\log R_0}{\log \lambda}, \quad (9)$$

where  $\lambda$  was estimated as described above. The net reproductive rate  $R_0$  was the dominant eigenvalue of the matrix  $R$  (Caswell, 2001):

$$R = FN, \quad (10)$$

where  $F$  is the reproductive matrix consisting of the age- or stage-specific fertility rates on the first row of the matrix and zero elsewhere, and  $N$  is the fundamental matrix defined as (Caswell, 2001):

$$N = (I - T)^{-1}, \quad (11)$$

where  $I$  is the identity matrix and  $T$  is the transition matrix. Entries of the matrix  $T$  ( $t_{ij}$ ) represent the probability that an individual alive in stage  $j$  at time  $t$  is alive in stage  $i$  at time  $t + 1$  (Caswell, 2001). We note that, for age-structured matrix models or partial life cycle models in Eq. (3), the estimate of  $R_0$  obtained from this approach will be identical to that obtained from equation 5.62 of Caswell (2001).

The second measure of generation time,  $\bar{A}$ , was the mean age of the parents of the offspring produced by a population at the stable age distribution and was estimated as the inner product of the left ( $\mathbf{v}$ ) and right ( $\mathbf{w}$ ) eigenvectors (corresponding to the dominant eigenvalue) of the population projection matrix  $A$ , with the first entry of the eigenvectors scaled to be 1. That is,  $\bar{A} = \langle \mathbf{w}, \mathbf{v} \rangle$ , with  $\mathbf{w}(1) = 1$ , and  $\mathbf{v}(1) = 1$ . For age-structured models or partial-life-cycle model in Eq. (3), the

estimate of  $\bar{A}$  obtained in this way will be identical to that computed using equation (5.77) of (Caswell, 2001). We note that  $\bar{A}$  is the inverse of the elasticity of  $\lambda$  to fertility (i.e.,  $\bar{A} = 1/e(F)$ ), and that the sum of the elasticity of  $\lambda$  to all survival terms is  $(1 - 1/\bar{A})$  (Gaillard et al., 2005; Oli and Dobson, 2005).

### 3. Results

We compiled life-history data for 155 avian populations, representing 113 species, 41 families, and 15 orders. Passeriformes was the most represented order, with 40 populations of 32 species, followed by Charadriiformes (28 populations of 16 species), Falconiformes (20 populations of 12 species), and Procellariiformes (16 populations of 14 species). Life-history variables showed substantial variation, and ranged as follows:  $\alpha$ , 1–12 year;  $P_a$ , 0.270–0.987;  $P_j$ , 0.032–0.945;  $F$ , 0.040–2.698. Population growth rate  $\lambda$  ranged from 0.531 to 2.834 and body mass ranged from 7.3 to 34,000 g (Table 1). Therefore, our study included species with diverse life-histories and in various stages of population growth.

The mean (S.E.) elasticity of  $\lambda$  to changes in each life-history variable was as follows: absolute value of  $e(\alpha) = 0.468$  (0.051);  $e(P_a) = 0.437$  (0.019);  $e(F) = 0.314$  (0.021);  $e(P_j) = 0.249$  (0.010) (Table 1). On average,  $e(\alpha)$  was the highest, followed by  $e(P_a)$  and  $e(F)$  (Table 1). The population growth rate was most sensitive to changes in adult survival in most populations, as  $e(P_a)$  ranked first most frequently (53.5%,  $N = 155$ ), followed by  $e(\alpha)$ , 26.5%;  $e(P_j)$ , 11.0% and  $e(F)$  in 9.0% of populations (Fig. 1).

The life-history variables were well correlated with each other, and with body mass and elasticities. Of the metrics of relative importance considered,  $\lambda$  was the least correlated with the elasticities (Table 2). Population growth rate ( $\lambda$ ) was most strongly correlated with  $F$ , but also correlated with  $\alpha$  and  $P_j$ . Values for  $e(P_a)$  and  $e(\alpha)$  were most strongly correlated with  $F$ , while  $e(F)$  was most strongly correlated with  $P_a$  and  $\alpha$  (Table 2).

**Table 1 – Summary statistics for body mass (g), life-history variables, population growth rate ( $\lambda$ ), and elasticities**

Variable	Mean	S.E.	Min.	Max.
Mass (g)	1425.210	269.757	7.300	34000.000
$\alpha$	2.690	0.210	1.000	12.000
$\omega$	13.905	2.165	3.000	50.000
$P_j$	0.500	0.018	0.032	0.945
$P_a$	0.735	0.014	0.270	0.987
$m$	0.934	0.070	0.060	4.305
$F$	0.595	0.037	0.040	2.698
$\lambda$	1.104	0.030	0.531	2.834
Elasticity of $\lambda$ to changes in				
$\alpha$ (absolute value)	0.468	0.051	0.017	4.359
$P_j$	0.249	0.010	0.015	0.537
$P_a$	0.437	0.019	0.005	0.942
$F$	0.314	0.021	0.011	0.980

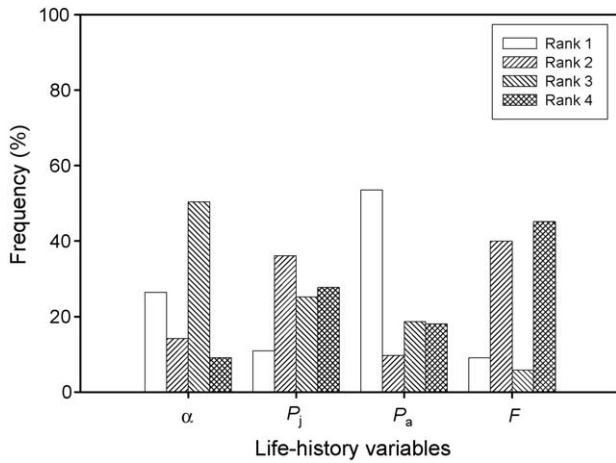
Life-history variables are as follows:  $\alpha$  = age at maturity;  $\omega$  = age at last reproduction;  $P_j$  = juvenile survival;  $P_a$  = adult survival;  $F$  = fertility.  $N = 155$ , except for  $\omega$ , where  $N = 21$ .

**Table 2 – Correlation matrix for body mass (g), life-history variables, population growth rate ( $\lambda$ ), elasticity of  $\lambda$  to changes in four life-history variables, and metrics of relative importance**

	Mass	$\alpha$	$\omega$	$P_j$	$P_a$	F	$\lambda$	$\lambda/\alpha$	$\lambda/P_a$	F/ $\alpha$	m/ $\alpha$	$\bar{A}$	T	$e(\alpha)$	$e(P_j)$	$e(P_a)$	
$\alpha$	0.726 <0.0001																
$\omega$	0.607 0.004	0.387 0.083															
$P_j$	0.529 <0.0001	0.658 <0.0001	0.468 0.033														
$P_a$	0.655 <0.0001	0.665 <0.0001	0.818 <0.0001	0.629 <0.0001													
F	-0.250 0.002	-0.468 <0.0001	0.007 0.977	-0.477 <0.0001	-0.365 <0.0001												
$\lambda$	0.039 0.632	-0.213 0.008	0.433 0.050	-0.229 0.004	-0.014 0.861	0.735 <0.0001											
$\lambda/\alpha$	-0.635 <0.0001	-0.955 <0.0001	-0.185 0.422	-0.656 <0.0001	-0.597 <0.0001	0.639 <0.0001	0.492 <0.0001										
$\lambda/P_a$	-0.443 <0.0001	-0.623 <0.0001	-0.430 0.052	-0.609 <0.0001	-0.728 <0.0001	0.767 <0.0001	0.696 <0.0001	0.766 <0.0001									
F/ $\alpha$	-0.584 <0.0001	-0.873 <0.0001	-0.253 0.269	-0.668 <0.0001	-0.610 <0.0001	0.840 <0.0001	0.537 <0.0001	0.940 <0.0001	0.807 <0.0001								
m/ $\alpha$	-0.634 <0.0001	-0.888 <0.0001	-0.443 0.045	-0.702 <0.0001	-0.723 <0.0001	0.802 <0.0001	0.471 <0.0001	0.934 <0.0001	0.842 <0.0001	0.989 <0.0001							
$\bar{A}$	0.668 <0.0001	0.861 <0.0001	0.564 0.008	0.643 <0.0001	0.742 <0.0001	-0.698 <0.0001	-0.429 <0.0001	-0.899 <0.0001	-0.831 <0.0001	-0.926 <0.0001	-0.951 <0.0001						
T	0.719 <0.0001	0.905 <0.0001	0.721 0.000	0.710 <0.0001	0.817 <0.0001	-0.632 <0.0001	-0.317 <0.0001	-0.901 <0.0001	-0.804 <0.0001	-0.904 <0.0001	-0.944 <0.0001	0.969 <0.0001					
$e(\alpha)$	-0.547 <0.0001	-0.736 <0.0001	-0.205 0.374	-0.748 <0.0001	-0.671 <0.0001	0.872 <0.0001	0.562 <0.0001	0.825 <0.0001	0.867 <0.0001	0.933 <0.0001	0.942 <0.0001	-0.912 <0.0001	-0.891 <0.0001				
$e(P_j)$	0.266 0.001	0.460 <0.0001	0.090 0.699	0.710 <0.0001	0.254 0.001	-0.082 0.311	-0.259 0.001	-0.488 <0.0001	-0.361 <0.0001	-0.328 <0.0001	-0.334 <0.0001	0.318 <0.0001	0.299 0.000	-0.282 0.000			
$e(P_a)$	0.332 <0.0001	0.476 <0.0001	0.650 0.001	0.639 <0.0001	0.635 <0.0001	-0.767 <0.0001	-0.710 <0.0001	-0.639 <0.0001	-0.943 <0.0001	-0.717 <0.0001	-0.746 <0.0001	0.745 <0.0001	0.719 <0.0001	-0.833 <0.0001	0.345 <0.0001		
$e(F)$	-0.660 <0.0001	-0.855 <0.0001	-0.564 0.008	-0.615 <0.0001	-0.738 <0.0001	0.723 <0.0001	0.422 <0.0001	0.889 <0.0001	0.819 <0.0001	0.924 <0.0001	0.947 <0.0001	-1.000 <0.0001	-0.970 <0.0001	0.916 <0.0001	-0.166 0.039	-0.745 <0.0001	

Life-history variables were as follows:  $\alpha$  = age at maturity;  $\omega$  = age at last reproduction;  $P_j$  = juvenile survival;  $P_a$  = adult survival; F = fertility. The absolute value of  $e(\alpha)$  was used and all variables were log(e)-transformed. P values for  $H_0: r = 0$  are given below each correlation coefficient. N = 155 except in the following cases:  $\omega$  (N = 21); T (N = 154; values of T < 0 were treated as missing values);  $\bar{A}$  (N = 151; values of  $\bar{A} > 50$  were treated as missing values).





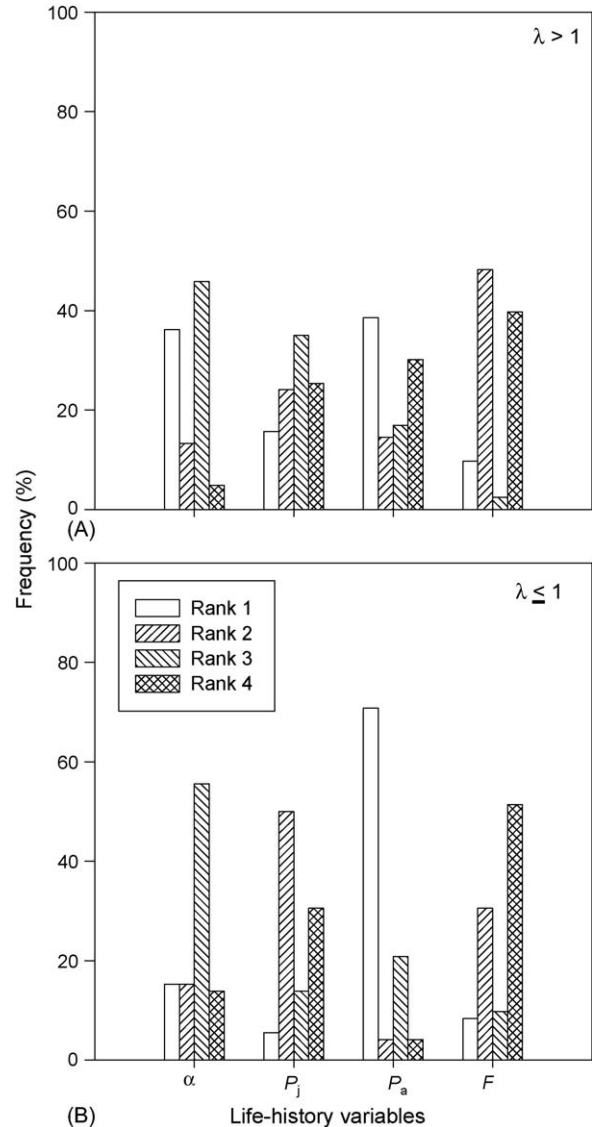
**Fig. 1 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in four life-history variables: age at maturity ( $\alpha$ ), juvenile survival ( $P_j$ ), adult survival ( $P_a$ ), and fertility ( $F$ ). For each population ( $N = 155$ ) we ranked absolute values of the elasticities in descending order such that the life-history variable with the largest relative influence on  $\lambda$  would be ranked first, and the variable with the smallest relative influence on  $\lambda$  would be ranked fourth.**

A nested ANCOVA with body mass as a covariate revealed that a substantial proportion of variance of elasticity of  $\lambda$  to changes in  $\alpha$  (57.1%),  $P_j$  (37.0%),  $P_a$  (66.9%), and  $F$  (79.0%) was associated with taxonomy and body mass (Table 3). After

**Table 3 – Results of nested ANCOVA (with body mass as a covariate) for elasticity of population growth rate ( $\lambda$ ) to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in 155 populations of birds**

Source	d.f.	F	P	R <sup>2</sup>
<i>e</i> ( $\alpha$ ):				
Body mass	1	12.51	0.0006	0.571
Order	14	5.88	<0.0001	
Family (order)	26	1.36	0.1352	
<i>e</i> ( $P_j$ ):				
Body mass	1	0.71	0.4027	0.370
Order	14	1.73	0.0587	
Family (order)	26	1.03	0.4369	
<i>e</i> ( $P_a$ ):				
Body mass	1	15.57	0.0001	0.669
Order	14	9.02	<0.0001	
Family (order)	26	2.01	0.0065	
<i>e</i> ( $F$ ):				
Body mass	1	33.21	<0.0001	0.790
Order	14	10.2	<0.0001	
Family (order)	26	1.31	0.1706	

All variables were log(e)-transformed. Life-history variables are as follows:  $\alpha$  = age at maturity;  $P_j$  = juvenile survival;  $P_a$  = adult survival;  $F$  = fertility. *e*(*p*) = the elasticity of  $\lambda$  to changes in the life-history variable, *p*. Values of R<sup>2</sup> represent the proportion of variation in elasticity of  $\lambda$  to changes in each life-history variable explained by the nested ANCOVA model.

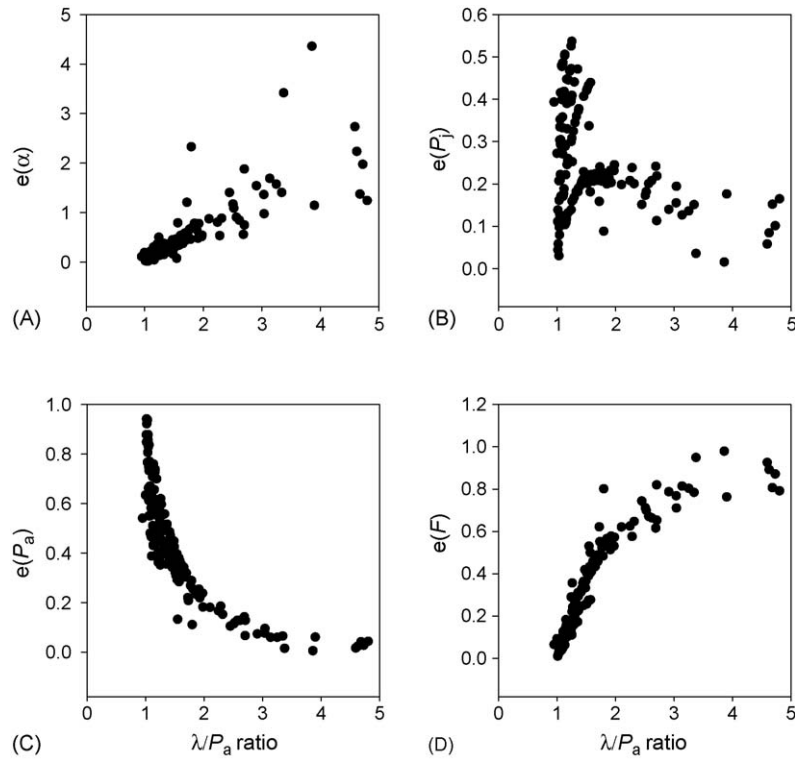


**Fig. 2 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in (A) increasing populations ( $\lambda > 1$ ;  $N = 83$ ) and (B) declining/near equilibrium populations ( $\lambda \leq 1$ ;  $N = 72$ ). For symbol definitions and methods used for ranking, see Fig. 1.**

removing the effects of taxonomy and body mass, elasticity of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$ , ranked first in 10.32%, 16.13%, 34.84%, and 37.42% ( $N = 155$ ) of the populations, respectively.

No single life-history variable was most important in a majority of increasing populations ( $\lambda > 1$ ,  $N = 83$ , Fig. 2); *e*( $P_a$ ) ranked first most frequently (38.6%,  $N = 83$ ) followed by *e*( $\alpha$ ) (36.1%). However,  $P_a$  was most important to  $\lambda$  in a majority of declining/near equilibrium populations ( $\lambda \leq 1$ ,  $N = 72$ ); *e*( $P_a$ ) ranked first most frequently (70.8%).

The  $\lambda/P_a$  ratio was significantly correlated with the elasticity of  $\lambda$  to all life-history variables (Table 2). In general, *e*( $\alpha$ ) and *e*( $F$ ) increased, and *e*( $P_a$ ) and *e*( $P_j$ ) decreased with increasing values of  $\lambda/P_a$  ratio (Fig. 3). Separating the populations into four groups based on values of  $\lambda/P_a$  ratio revealed situations in



**Fig. 3 – Relationship between  $\lambda/P_a$  ratio and elasticity of population growth rate ( $\lambda$ ) to changes in (A) age at maturity,  $e(\alpha)$ ; (B) juvenile survival,  $e(P_j)$ ; (C) adult survival,  $e(P_a)$ ; (D) fertility,  $e(F)$  ( $N = 155$ ).**

which changes in survival or reproductive parameters became more important. For populations in which  $\lambda/P_a > 1.6$  ( $N = 44$ ),  $e(\alpha)$  and  $e(F)$  ranked first most frequently (77.3% and 22.7%, respectively, Fig. 4). In populations with  $\lambda/P_a < 1.15$  ( $N = 46$ ),  $e(P_a)$  ranked first most frequently (91.3%). For populations with a  $\lambda/P_a$  ratio between 1.15 and 1.6, the pattern was less clear (Fig. 4).

We examined the relationship between the  $\lambda/\alpha$  ratio and elasticities to investigate Stearns' (1992) prediction. The  $\lambda/\alpha$  ratio exhibited a predictable association with elasticities (Table 2 and Fig. 5). Again, by grouping the populations based on the  $\lambda/\alpha$  ratio, we were able to find situations in which either reproductive parameters or survival parameters were most important to  $\lambda$ . In increasing populations characterized by early maturity ( $\lambda/\alpha > 1.15$ ;  $N = 32$ ),  $e(\alpha)$  ranked first most frequently (78.1%, Fig. 6). In contrast, growth rates of populations characterized by low growth rate and late maturity ( $\lambda/\alpha < 0.3$ ;  $N = 38$ ) tended to be most sensitive to changes in  $P_a$ ;  $e(P_a)$  ranked first most frequently (78.9%). The pattern of relative importance was less clear for populations characterized by intermediate values of  $\lambda/\alpha$  (Fig. 6).

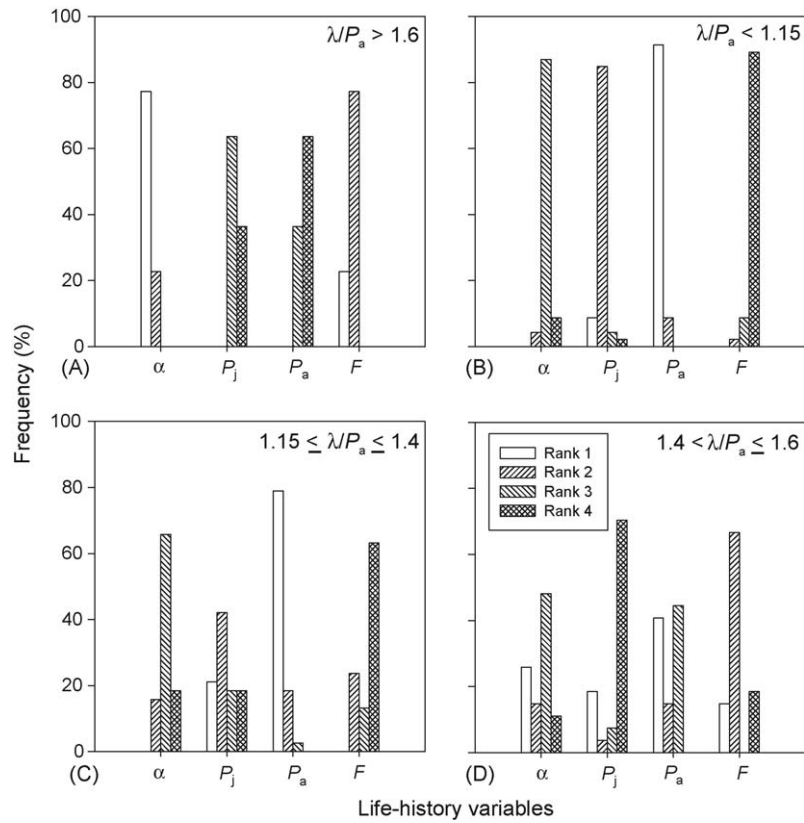
Populations that were characterized by early maturity, high reproductive rates and low survival had short generation times (i.e., small values of  $\bar{A}$  and  $T$ ); the opposite was true for populations characterized by high survival, delayed maturity and low reproductive rates (i.e., large values of  $\bar{A}$  and  $T$ ). The first estimate of generation time,  $\bar{A}$ , was strongly correlated with elasticities (Table 2). Because  $\bar{A} = 1/e(F)$ ,  $\bar{A}$  and  $e(F)$  were perfectly negatively correlated (Table 2 and Fig. 7). In order to find situations in which reproductive or survival parameters were

most important to  $\lambda$ , we grouped the populations by values of  $\bar{A}$  (Fig. 8). In populations with short generation time ( $\bar{A} < 2.5$ ;  $N = 55$ ),  $e(\alpha)$  or  $e(F)$  ranked first most often (74.5% and 25.5%, respectively, Fig. 8). For populations with  $2.5 \leq \bar{A} < 8$ ,  $e(P_a)$  and  $e(P_j)$  ranked first most often (79.5% and 20.5%, respectively,  $N = 49$ ). However,  $e(F)$  and  $e(\alpha)$  ranked second in several populations, and the pattern of relative importance was less clear. Finally, when  $\bar{A} > 8$  (long generation time),  $e(P_a)$  or  $e(P_j)$  ranked first in all cases (86.3% and 13.7%, respectively,  $N = 51$ , Fig. 8).

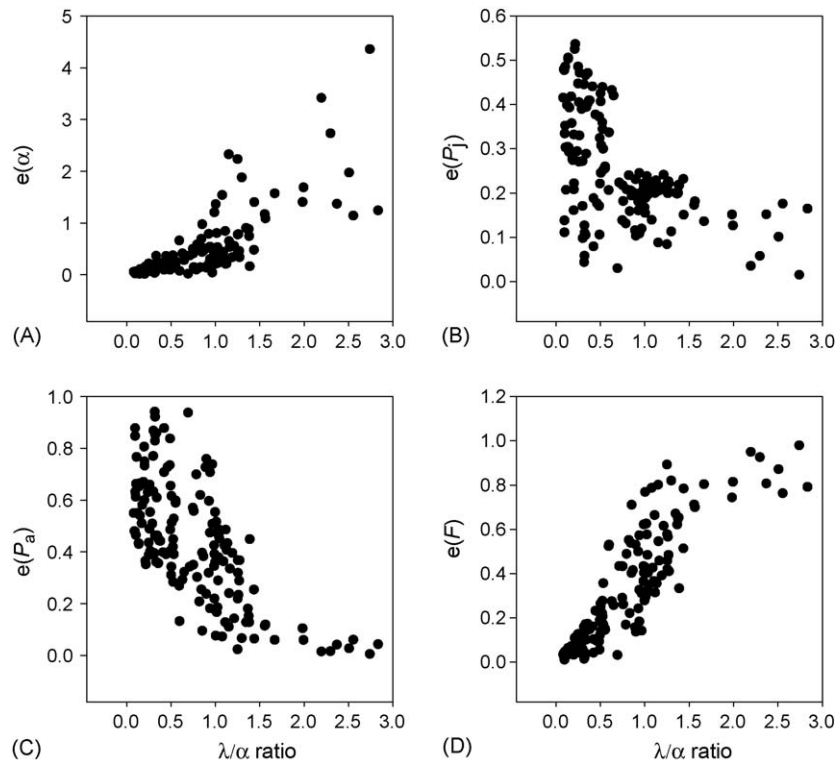
The relationship between  $T$  and elasticities was similar to that between  $\bar{A}$  and elasticities (Table 2 and Fig. 9). When  $T < 2$  ( $N = 37$ ),  $e(\alpha)$  and  $e(F)$  ranked first (81.1% and 18.9%, respectively, Fig. 10). In populations characterized by long generation times ( $T > 6$ ,  $N = 65$ )  $e(P_a)$  and  $e(P_j)$  ranked first most frequently (83.1% and 16.9%, respectively). The pattern of relationship between  $T$  and elasticities was unclear for intermediate values of  $T$ .

Both estimates of generation time exhibited an interesting pattern of relationship with the values of  $e(P_a)$  and  $e(P_j)$  as seen in Figs. 7 and 9. By examining the relationship for each value of  $\alpha$  separately, it became apparent that as  $\bar{A}$  increased,  $e(P_a)$  increased in importance while  $e(P_j)$  decreased in importance (Fig. 7). Thus, the pattern of elasticities was completely determined by  $\bar{A}$  and  $\alpha$  in most populations in our study.

Finally, the  $F/\alpha$  and  $m/\alpha$  ratios were used to evaluate Oli and Dobson's (2003) prediction. The  $F/\alpha$  ratio was strongly correlated with elasticities, especially  $e(\alpha)$  and  $e(F)$  (Table 2 and Fig. 11). In populations in which reproductive output was high and onset of reproduction was early ( $F/\alpha > 0.6$ ,  $N = 36$ ),  $\alpha$  and  $F$  were most important in all cases with  $e(\alpha)$  and  $e(F)$  ranking first in 86.1% and 14.9% of populations, respectively ( $N = 36$ , Fig. 12).



**Fig. 4 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in four ranges of value for  $\lambda/P_a$  ratio; (A)  $\lambda/P_a > 1.6$  ( $N = 44$ ), (B)  $\lambda/P_a < 1.15$  ( $N = 46$ ), (C)  $1.15 \leq \lambda/P_a \leq 1.4$  ( $N = 38$ ), and (D)  $1.4 < \lambda/P_a \leq 1.6$  ( $N = 27$ ). For symbol definitions and methods used for ranking, see Fig. 1.**



**Fig. 5 – Relationship between  $\lambda/\alpha$  ratio and elasticity of population growth rate ( $\lambda$ ) to changes in (A) age at maturity,  $e(\alpha)$ ; (B) juvenile survival,  $e(P_j)$ ; (C) adult survival,  $e(P_a)$ ; (D) fertility,  $e(F)$  ( $N = 155$ ).**



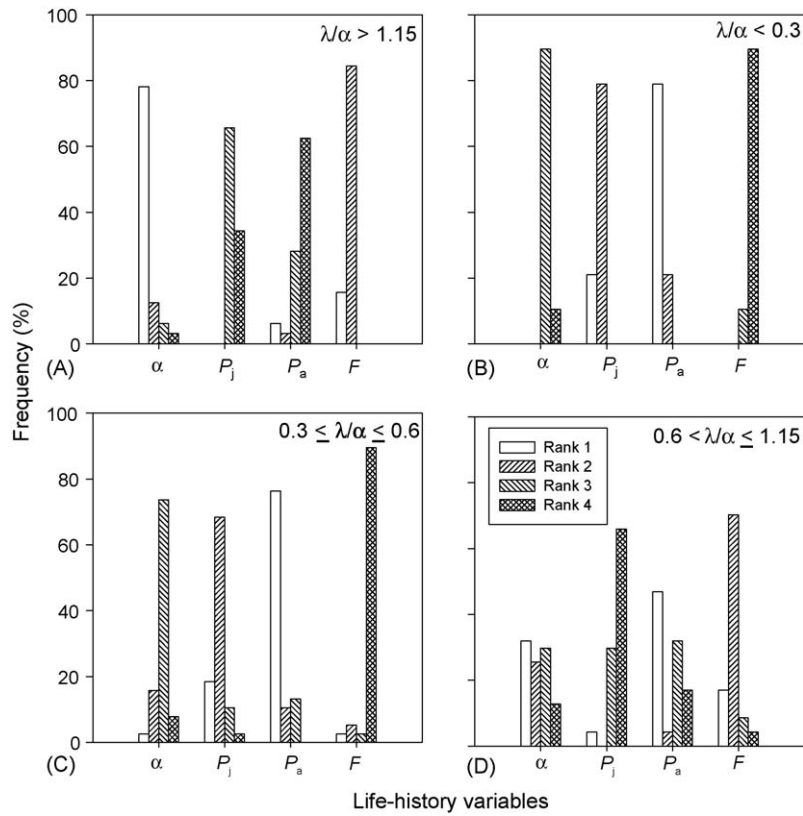


Fig. 6 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in four ranges of value for  $\lambda/\alpha$  ratio; (A)  $\lambda/\alpha > 1.15$  ( $N = 32$ ), (B)  $\lambda/\alpha < 0.3$  ( $N = 38$ ), (C)  $0.3 \leq \lambda/\alpha \leq 0.6$  ( $N = 38$ ), and (D)  $0.6 < \lambda/\alpha \leq 1.15$  ( $N = 47$ ). For symbol definitions and methods used for ranking, see Fig. 1.

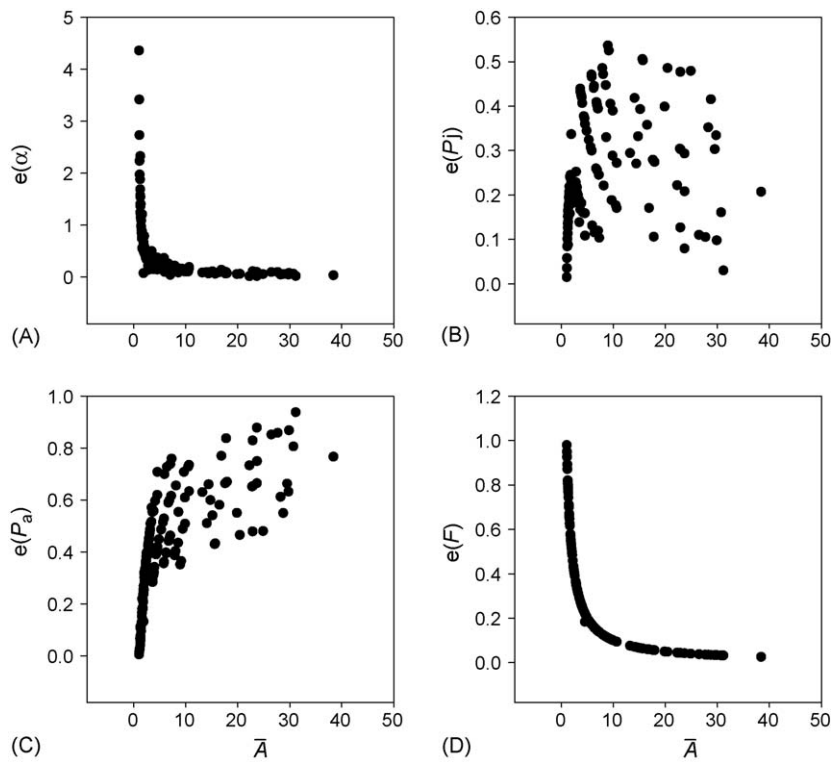
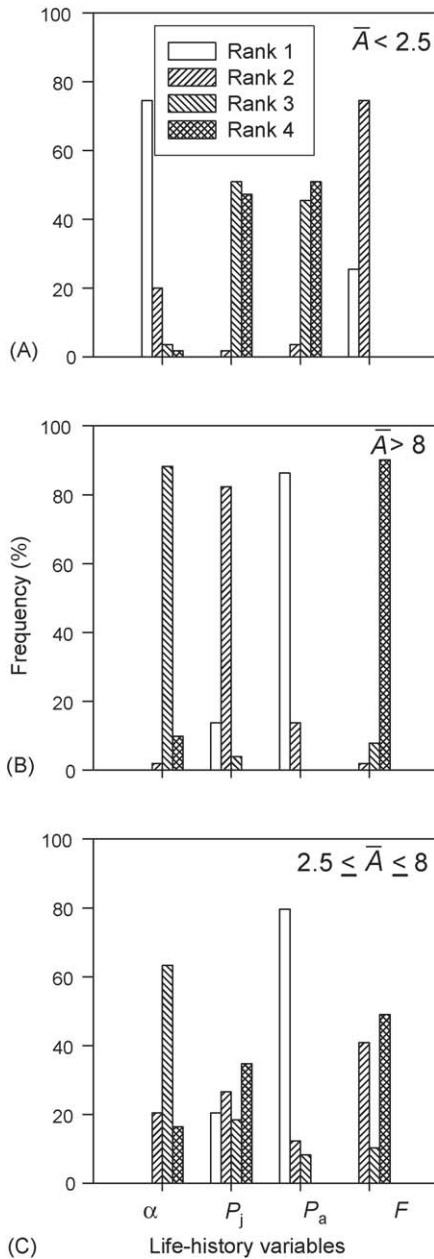


Fig. 7 – Relationship between generation time ( $\bar{A}$ ) and elasticity of population growth rate ( $\lambda$ ) to changes in (A) age at maturity,  $e(\alpha)$ ; (B) juvenile survival,  $e(P_j)$ ; (C) adult survival,  $e(P_a)$ ; (D) fertility,  $e(F)$  ( $N = 151$ ). Values of  $\bar{A} > 50$  ( $N = 4$ ) were excluded.



**Fig. 8 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in three ranges of value for generation time ( $\bar{A}$ ). (A)  $\bar{A} < 2.5$  ( $N=55$ ), (B)  $\bar{A} > 8$  ( $N=51$ ), and (C)  $2.5 \leq \bar{A} \leq 8$  ( $N=49$ ). For symbol definitions and methods used for ranking, see Fig. 1.**

In populations characterized by late maturity and low reproductive output ( $F/\alpha < 0.15$ ,  $N=45$ ), survival was most important in all cases, with  $e(P_a)$  and  $e(P_j)$  ranking first most often (82.2% and 17.8%, respectively,  $N=45$ , Fig. 12). The pattern of relationship between the  $F/\alpha$  ratio and elasticities was less clear for populations with intermediate  $F/\alpha$  values.

One criticism of the  $F/\alpha$  ratio is that it is not just a ratio of the magnitude and timing of reproduction, because  $F$  includes adult survival (Gaillard et al., 2005). Thus, we also examined the relationship between elasticities and the  $m/\alpha$  ratio (Oli, 2004). The ratio of fecundity to age at maturity ( $m/\alpha$ ), was not

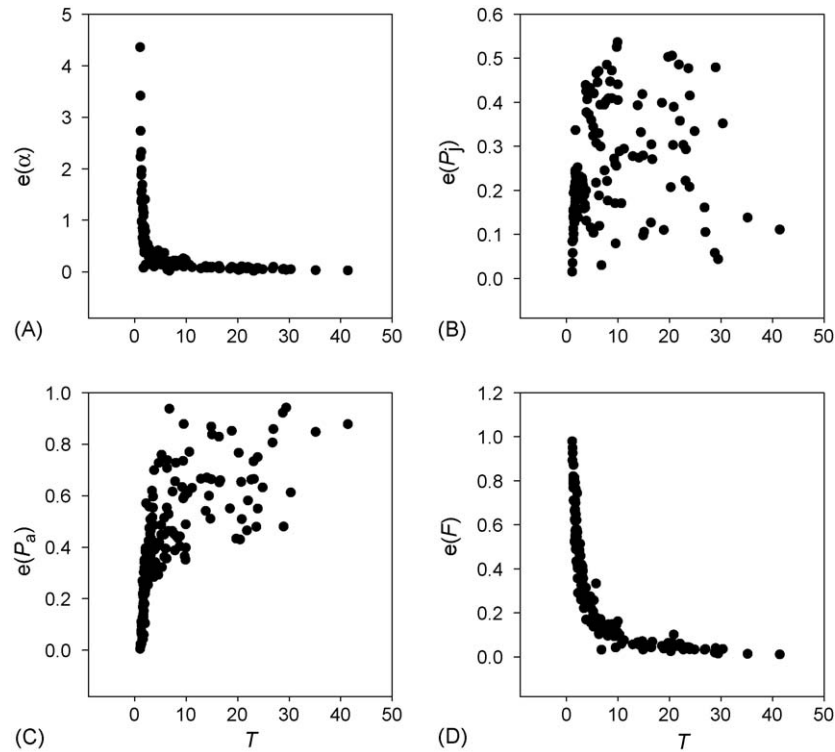
only better correlated with elasticities (Table 2 and Fig. 13), but required less data (estimate of adult survival was not needed). However, the pattern of relationship between elasticities and  $m/\alpha$  ratio was similar to that between elasticities and  $F/\alpha$  ratio (Fig. 14).

When  $m/\alpha \geq 0.75$  (early maturity, high fecundity,  $N=51$ ), reproductive parameters had the greatest influence on  $\lambda$ . If  $e(\alpha)$  ranked first (78.4%),  $e(F)$  ranked second; when  $e(F)$  ranked first (21.6%;  $N=51$ ),  $e(\alpha)$  ranked second (Fig. 14). In populations characterized by  $m/\alpha \leq 0.25$  (late maturity, low fecundity,  $N=57$ ), changes in survival parameters had the greatest potential influence on  $\lambda$  most frequently;  $e(P_a)$  and  $e(P_j)$  ranked first in 84.2% and 15.8% of these populations, respectively.

#### 4. Discussion

Biological populations exhibit a great diversity in patterns of life-history, and such patterns can have substantial population consequences. Cole (1954) unambiguously established that the pattern of life-history determines the population growth rate (and thus, the dynamics of a population), but that life-history variables differ with respect to their potential influences on the population growth rate. Cole's insightful results inspired a series of theoretical studies investigating aspects of the relative importance of life-history variables to population growth rate (Lewontin, 1965; MacArthur and Wilson, 1967; Meats, 1971; Green and Painter, 1975; Snell, 1978; Caswell and Hastings, 1980; Stearns, 1992). The relative importance of life-history variables to population growth rate is frequently interpreted as the selection gradient, and has important implications for the evolution of life-history traits (Benton and Grant, 1999; Van Tienderen, 2000; Coulson et al., 2003; Forbis and Doak, 2004). Additionally, the pattern of relative importance has become an integral part of the formulation and implementation of management plans for the conservation of threatened or endangered wildlife species (Crouse et al., 1987; Crowder et al., 1994; Mills et al., 1999; Caswell, 2000; Fisher et al., 2000; Heppell et al., 2000; Gerber and Heppell, 2004).

With the recent advances in the theory of matrix population models (Caswell, 2001), empirical evaluation of the pattern of relative importance has gained some momentum. Heppell et al. (2000) and Oli and Dobson (2003) recently investigated the pattern of relative importance in mammals. Heppell et al. (2000) found that mammals that matured early and had high reproductive rates tended to be characterized by high fertility elasticities and low adult survival elasticities. Mammals that matured late had low reproductive rates and experienced high adult survival rates were characterized by high adult survival elasticities and low fertility elasticities. Oli and Dobson (2003) made use of a partial life-cycle model (Oli and Zinner, 2001a) that enabled them to investigate the potential influence of changes in age at maturity on the population growth rate. The analysis by Oli and Dobson (2003) supported the results of Heppell et al. (2000) and additionally found that the elasticity of  $\lambda$  to changes in reproductive parameters ( $\alpha$  and  $F$ ) increased as maturation was accelerated (small  $\alpha$ ) and reproductive rate increased (large  $F$ ), while the importance of reproductive parameters ( $\alpha$  and  $F$ ) declined as maturation was delayed (large  $\alpha$ ) and reproductive rate was



**Fig. 9 – Relationship between generation time ( $T$ ) and elasticity of population growth rate ( $\lambda$ ) to changes in (A) age at maturity,  $e(\alpha)$ ; (B) juvenile survival,  $e(P_j)$ ; (C) adult survival,  $e(P_a)$ ; (D) fertility,  $e(F)$  ( $N = 154$ ). Values of  $T < 0$  ( $N = 1$ ) were excluded.**

decreased (small  $F$ ); in the latter situation, survival parameters ( $P_a$  and  $P_j$ ) had the largest relative influence on  $\lambda$ . Additionally, Oli and Dobson (2003) introduced the magnitude of reproduction relative to the onset of reproduction (the  $F/\alpha$  ratio) as a proxy for elasticities and suggested its use in wildlife conservation.

Sæther and Bakke (2000) investigated the variation in life histories and the pattern of relative importance of life-history variables to  $\lambda$  in 49 avian populations. They concluded that the elasticity of  $\lambda$  to changes in adult survival decreased with increasing clutch size, while it increased with an increase in adult survival; only the latter pattern remained after controlling for taxonomy. The elasticity of  $\lambda$  to changes in fecundity increased with an increase in clutch size and decreased strongly with an increase in adult survival; both effects remained after controlling for taxonomy.

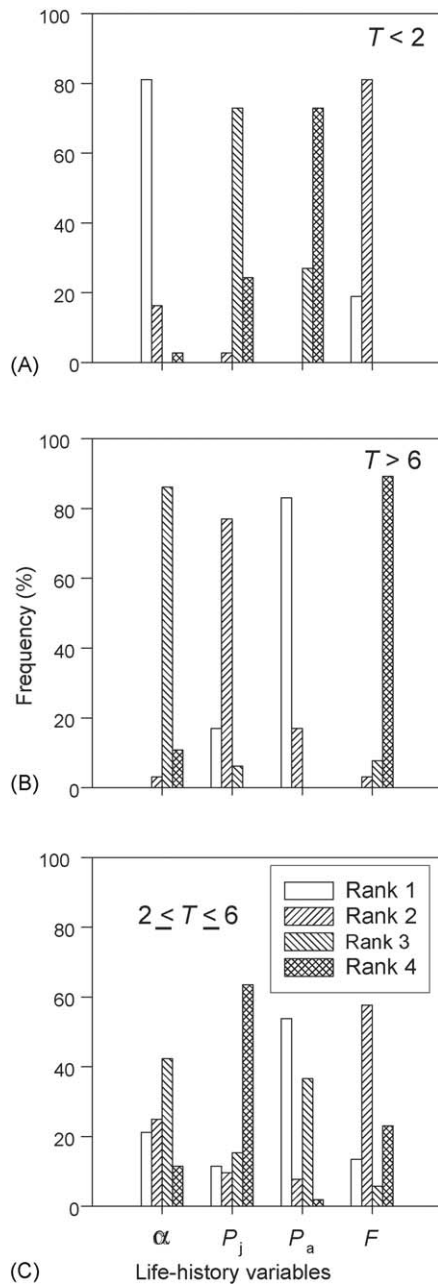
In this study we expanded on the work of Sæther and Bakke (2000) in several ways. First, we tripled the sample size by compiling data for 155 avian populations. Secondly, we examined the relative importance of several life-history variables, including  $\alpha$ , an important life-history variable (Cole, 1954; Lewontin, 1965). Finally, we statistically controlled for the effects of body mass and taxonomy on the elasticity patterns.

Similar to what previous authors have shown in mammals (Heppell et al., 2000; Oli and Dobson, 2003), we found a large range in demography (e.g. some individuals gave birth to just one offspring per attempt, while others gave birth to many). We found adult survival ( $P_a$ ) to have the highest relative influence on  $\lambda$  in a majority of the populations (Fig. 1),

and were therefore unable to support Cole's (1954) prediction that  $\alpha$  should be the most important life-history variable to  $\lambda$ . Although  $e(\alpha)$  ranked first in a majority of populations that matured early ( $\alpha$  at or near 1) and had high reproductive rates, this was not the case when all sampled populations were included. Therefore, Cole's (1954) prediction could not be generalized for all bird species, a conclusion consistent with that of Oli and Dobson (2003) for mammalian populations.

Population growth rate ( $\lambda$ ) was poorly correlated with elasticities, and thus was a poor predictor of the pattern of relative importance. Additionally, no clear pattern of relative importance was found when data were analyzed separately for populations in which  $\lambda > 1$  and those with  $\lambda \leq 1$ . The prediction of Meats (1971) and Snell (1978), that  $\lambda$  should determine the pattern of relative importance and that the pattern should differ between increasing and decreasing/near equilibrium populations, was therefore not supported by data, echoing the findings of Oli and Dobson (2003).

The  $\lambda/P_a$  ratio was well correlated with elasticities, especially  $e(P_a)$ ,  $e(F)$ , and  $e(\alpha)$ . When elasticities were examined for four groups based on the  $\lambda/P_a$  ratio, we were able to find predictable patterns of relative importance, especially at the extreme values of  $\lambda/P_a$  (Fig. 4). This and the strong correlation between  $\lambda/P_a$  and elasticities (Table 2) lead us to support Caswell and Hastings' (1980) prediction that  $\lambda/P_a$  could be used to predict the pattern of relative importance. Caswell and Hastings (1980) concluded that when the  $\lambda/P_a$  ratio was high, there should be strong selection for decreased developmental time, and therefore increased fertility. Our results support their conclusion. Growth rates of populations charac-



**Fig. 10** – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in three ranges of value for generation time ( $T$ ). (A)  $T < 2$  ( $N = 37$ ), (B)  $T > 6$  ( $N = 65$ ), and (C)  $2 \leq T \leq 6$  ( $N = 52$ ). Values of  $T < 0$  were excluded ( $N = 1$ ). For symbol definitions and methods used for ranking, see Fig. 1.

terized by high adult survival (and therefore low  $\lambda/P_a$  ratios) were most sensitive to changes in survival parameters, while growth rates of those with low adult survival (high  $\lambda/P_a$  ratios) were most sensitive to changes in reproductive parameters (Figs. 3 and 4). Our finding, that changes in  $P_a$  became more important to  $\lambda$  with increasing  $P_a$  and decreasing  $F$ , is consistent with the results of previous studies regarding relative importance (Heppell et al., 2000; Sæther and Bakke, 2000; Oli and Dobson, 2003).

Like the  $\lambda/P_a$  ratio, the  $\lambda/\alpha$  ratio was well correlated with elasticities, and had high predictive power regarding the pattern of relative importance (Table 2 and Fig. 5). Populations with early maturity (high  $\lambda/\alpha$ ) showed a marked difference in the pattern of relative importance when compared to populations maturing late (low  $\lambda/\alpha$ ); reproductive parameters were most important when  $\lambda/\alpha$  was high, survival parameters were most important when  $\lambda/\alpha$  was low (Figs. 5 and 6). Stearns' (1992) prediction was generally supported by data when elasticities were analyzed based on the values of the  $\lambda/\alpha$  ratio.

Generation time was strongly correlated with the elasticities, and was also a strong predictor of the pattern of relative importance. Reproductive parameters were most important in populations with short generation times (low values for  $T$  and  $\bar{A}$ ), characterized by early maturity, high reproductive rates, and low adult survival. Populations with long generation times (high  $T$  and  $\bar{A}$  values) were characterized by delayed maturity, low reproductive rates, and high adult survival. In such populations,  $\lambda$  was most sensitive to changes in survival parameters (Figs. 7 and 10). Heppell et al. (2000) found no significant correlation between  $e(P_a)$  and generation time ( $T_c$ —their Eq. (2)), although our analysis shows that  $e(P_a)$  was well correlated with both of our estimates of generation time (Table 2). Additionally, the pattern of relationship between  $T$  and especially  $\bar{A}$  and the life-history variables of interest was striking (Figs. 7 and 9). As Oli and Dobson (2005) also found in mammals, elasticity patterns of birds are primarily determined by  $\bar{A}$  and  $\alpha$ . This pattern is not surprising because  $\bar{A} = 1/e(F)$  and  $e(P_a) + e(P_j) = 1 - \bar{A}$ . Thus, the measures of generation time ( $T$  and  $\bar{A}$ ) were useful in predicting the pattern of relative importance, supporting the prediction of Gaillard et al. (2005).

The  $F/\alpha$  ratio was a good predictor of the pattern of relative importance based on the strong correlation between the ratio and the elasticities. When  $F/\alpha$  was high (early maturity, high reproductive rates) reproductive parameters were most important; when  $F/\alpha$  was low (late maturity, low reproductive rates) survival parameters were most important (Figs. 11 and 12). Sæther and Bakke (2000) found similar results; the importance of fecundity to the population growth increased with increasing clutch size, while the importance of adult survival increased with a reduction in clutch size. Therefore, the prediction of Oli and Dobson (2003), that the ratio of the magnitude and timing of reproduction should determine the pattern of relative importance was supported by data. Oli and Dobson (2003) introduced the  $F/\alpha$  ratio as a simple proxy for elasticity, but it has received recent criticism (Gaillard et al., 2005).

Admittedly, the  $F/\alpha$  ratio includes adult survival ( $F$  is the product of  $m$  and  $P_a$ ), and thus the  $F/\alpha$  ratio is not simply the ratio of magnitude and onset of reproduction. Therefore, we also investigated the pattern of elasticities relative to the  $m/\alpha$  ratio (which does not include  $P_a$  (Oli and Dobson, 2005)). The  $m/\alpha$  ratio was strongly correlated with elasticities, at least as strongly as any other proxy of elasticity, and exhibited a predictable relationship with elasticities (Fig. 13). Thus, the magnitude of reproduction relative to onset of reproduction appears to be a good proxy for elasticities, using either the  $m/\alpha$  or  $F/\alpha$  ratio to quantify it.

Our study was the first to empirically evaluate metrics that have been suggested to quantify relative importance for avian populations. With the exception of  $\lambda$  (Meats, 1971; Snell, 1978),

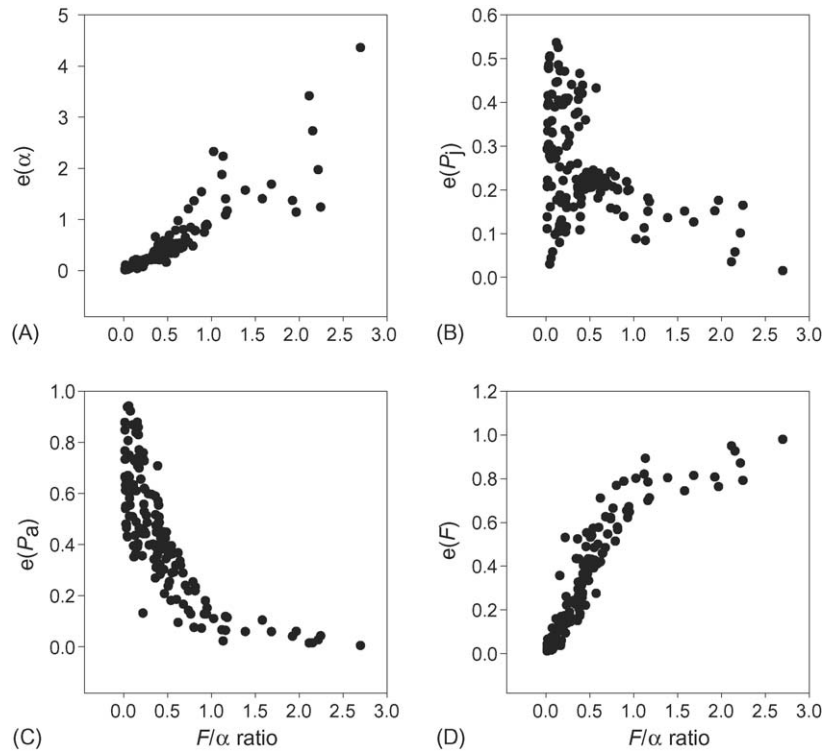


Fig. 11 – Relationship between the  $F/\alpha$  ratio and elasticity of population growth rate ( $\lambda$ ) to changes in (A) age at maturity,  $e(\alpha)$ ; (B) juvenile survival,  $e(P_j)$ ; (C) adult survival,  $e(P_a)$ ; (D) fertility,  $e(F)$  ( $N = 155$ ).

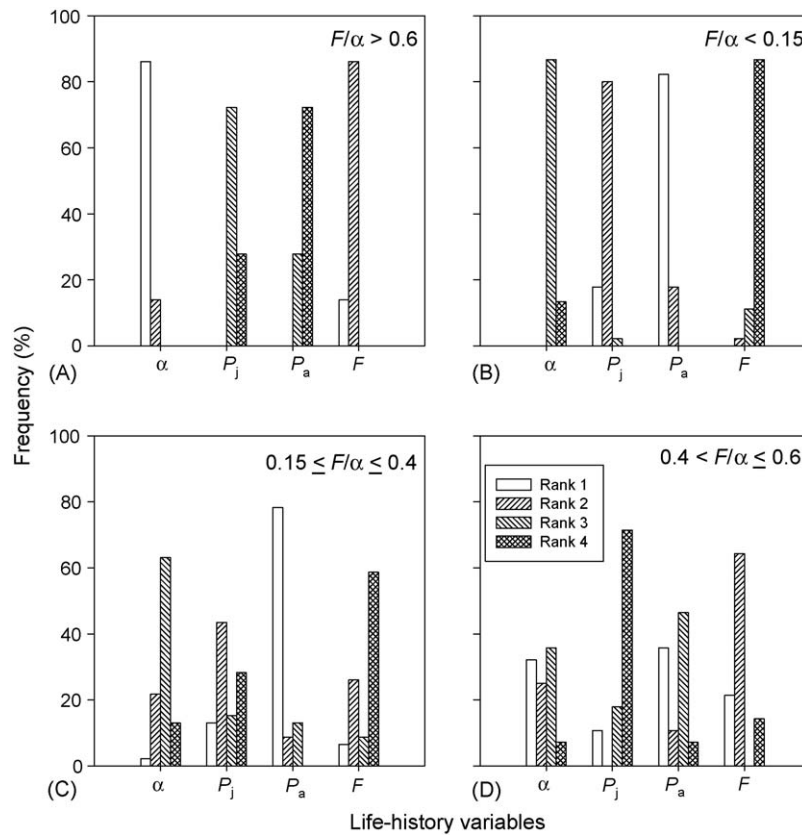


Fig. 12 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in four ranges of value for  $F/\alpha$  ratio; (A)  $F/\alpha > 0.6$  ( $N = 36$ ), (B)  $F/\alpha < 0.15$  ( $N = 45$ ), (C)  $0.15 \leq F/\alpha \leq 0.4$  ( $N = 46$ ), and (D)  $0.4 < F/\alpha \leq 0.6$  ( $N = 28$ ). For symbol definitions and methods used for ranking, see Fig. 1.



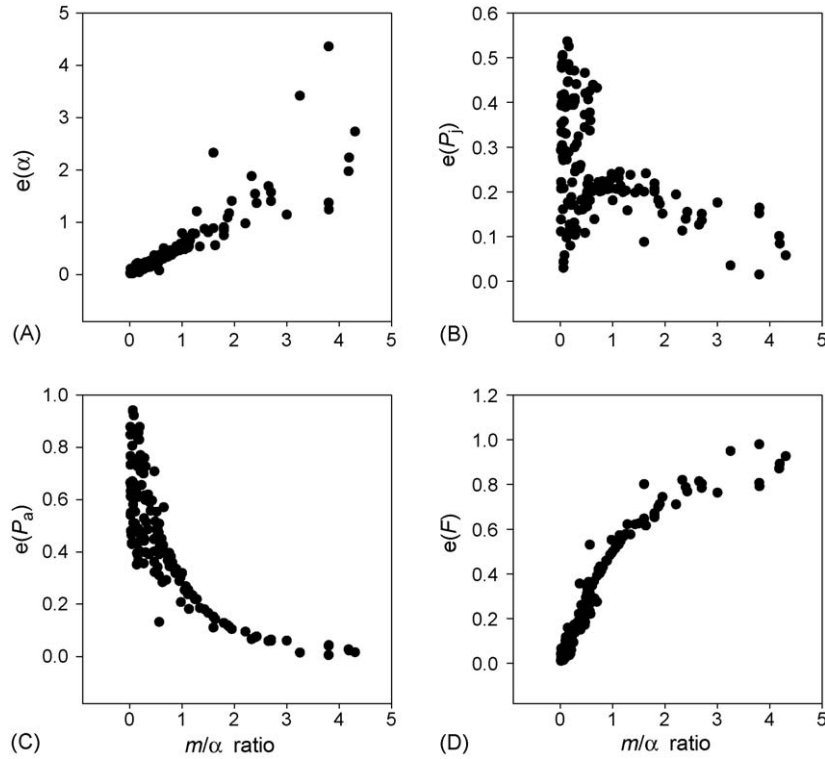


Fig. 13 – Relationship between the  $m/\alpha$  ratio and elasticity of population growth rate ( $\lambda$ ) to changes in (A) age at maturity,  $e(\alpha)$ ; (B) juvenile survival,  $e(P_j)$ ; (C) adult survival,  $e(P_a)$ ; (D) fertility,  $e(F)$  ( $N = 155$ ).

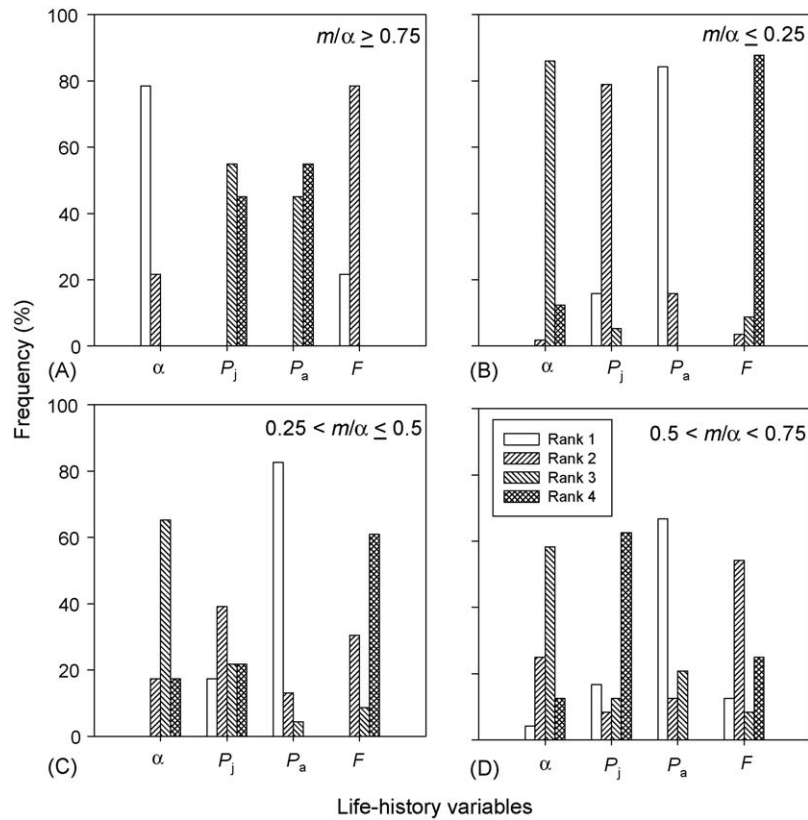


Fig. 14 – Frequency distribution (%) of ranks of elasticity (absolute value) of  $\lambda$  to changes in  $\alpha$ ,  $P_j$ ,  $P_a$ , and  $F$  in four ranges of value for  $m/\alpha$  ratio; (A)  $m/\alpha \leq 0.75$  ( $N = 51$ ), (B)  $m/\alpha \leq 0.25$  ( $N = 57$ ), (C)  $0.25 < m/\alpha \leq 0.5$  ( $N = 23$ ), and (D)  $0.5 < m/\alpha < 0.75$  ( $N = 24$ ). For symbol definitions and methods used for ranking, see Fig. 1.

all of the proposed metrics were strongly correlated with the elasticities and appeared useful in predicting the pattern of relative importance. However, for these metrics to be useful in conservation biology, one must be able to calculate them using minimal demographic data because complete demographic data are seldom available for species of conservation concern (Heppell et al., 2000). For this reason, it is difficult to envision the usefulness of metrics such as  $\bar{A}$  and  $T$ , or those that contain  $\lambda$  (Meats, 1971; Snell, 1978; Caswell and Hastings, 1980; Stearns, 1992; Gaillard et al., 2005), because they require all the data necessary for calculating  $\lambda$  and elasticities. Because the  $m/\alpha$  ratio requires less data than all other proxies of elasticities, and exhibits a predictable relationship with elasticities, this metric promises to be useful in the formulation or implementation of conservation plans for rare or endangered species with minimal demographic data. The  $m/\alpha$  ratio may not be the best proxy for relative importance, but because it can make use of minimal data (typical of threatened species) we feel it is the most useful for species when detailed demographic data are not available. In cases in which demographic data are lacking, managers may benefit from the use of the  $m/\alpha$  ratio for decision making; when estimates of  $m$  are not available,  $\alpha$  alone would be a useful metric because of strong correlation with elasticities. Target populations may be disturbed by unnatural conditions (e.g. introduced predators), and neither the pattern of elasticity nor the ratio of choice would be able to identify which vital rates are being disturbed. However, we feel that ratios, such as those listed above, would still be useful tools in population recovery.

It is important to note that for most populations ( $N = 134$ ) we used the model without age at last reproduction ( $\omega$ ). This model assumes infinite lifespan. It follows that the elasticity of  $\lambda$  to changes in adult survival will be higher than when  $\omega$  is included in the model, especially for populations with high  $P_a$  (Oli, 2003a), however the impact of older age-classes may be trivial because the number of individuals in those age-classes declines for older age-classes. Despite minor methodological differences our results were similar to those for the mammalian populations reported by Oli and Dobson (2003) who used a fully parameterized partial life cycle model including  $\omega$ . Therefore, although the relative importance of  $P_a$  may have been inflated in some cases, we do not believe that ignoring  $\omega$  substantially influenced the pattern of relative importance or our main conclusions.

By statistically controlling for the effects of body mass and taxonomy, we were able to determine the influence of taxonomy and body mass on the pattern of relative importance. Because life-history variables are correlated with body mass (Western, 1979; Western and Ssemakula, 1982; Stearns, 1983; Western, 1983; Stearns, 1984), and species that share a common evolutionary history are likely to possess similar life-history traits (Stearns, 1983, 1984), it was no surprise that a substantial amount of the variation in elasticity patterns could be explained by body mass and taxonomy. When effects of body mass and taxonomy were statistically removed, the pattern of relative importance changed substantially. In a similar study of mammalian populations, Oli and Dobson (2003) found that relative magnitudes of elasticities did not substantially change when effects of body mass and taxonomy were statistically removed. These results suggest that body mass and

taxonomy may influence the pattern of relative importance differently in different taxa.

Elasticities are frequently used for devising strategies for conservation and management of wildlife populations (Crouse et al., 1987; Crowder et al., 1994; Shea and Kelly, 1998; Benton and Grant, 1999; Caswell, 2000; Gerber and Heppell, 2004; Federico and Canziani, 2005) and results of this study can be useful for the conservation of avian populations. For example, 19 of the 21 extant species of albatross are faced with the possibility of extinction (Weimerskirch et al., 1997; Gale, 1998). Our results show that for the 12 populations of albatross sampled, the population growth rate was most sensitive to changes in survival (mean  $e(P_j)$  and  $e(P_a)$ , 0.369 and 0.591, respectively; sum of mean survival elasticities = 0.960). These results suggest that the long-term persistence of these birds can be improved by increasing survival rates, which can be achieved by regulating long-line fishing. On the other hand, in avian species that mature early and have high reproductive rates (e.g. many passerine species), reproductive parameters have the greatest influence on the population growth rate. An endangered species known to mature early and reproduce at a high rate would most likely benefit from efforts to increase the fertility rate of the species, perhaps by the protection of nesting sites.

Cole (1954) introduced one of the earliest forms of the partial life-cycle model, and this model was later revised by others including Lewontin (1965), and Caswell (2001). Recent work has fully developed partial-life cycle models for post-breeding (Oli and Zinner, 2001a; Oli, 2003a) and pre-breeding (Oli and Zinner, 2001b) censusing situations. These partial-life cycle models are useful for situations in which age specific demographic data are unavailable and/or when information regarding the influence of age at first or last reproduction on population dynamics is desired (Oli, 2003b). Our model is the first to apply a simplified partial-life cycle model (Oli, 2003a) to a large, taxonomically diverse data set for avian species. Additionally, this was the first study that used data from avian populations to empirically test several predictions that have been made regarding the pattern of the relative importance of life-history variables to population growth rate.

Our analysis has shown that there is significant variation in the pattern of relative importance for avian populations, but that general predictions can be made based on the life-history patterns. In general, populations that matured early and had high reproductive rates were characterized by population growth rates most sensitive to changes in reproductive parameters. Populations which matured late and had low reproductive rates were likely to be characterized by population growth rates most sensitive to changes in survival parameters. These results support previous studies of birds (Sæther and Bakke, 2000) and mammals (Heppell et al., 2000; Oli and Dobson, 2003), and are most likely applicable to any age-structured population. The theoretical work of several authors has yielded several useful metrics for estimating the pattern of relative importance, but many of these require data that are often unavailable for species of conservation concern. Because the  $m/\alpha$  ratio requires minimal data and has strong predictive power, we suggest that this ratio may be useful for formulating and implementing management strategies for species for which minimal data are available.

## Acknowledgements

Point Reyes Bird Observatory provided unpublished survivorship data for *Ptychoramphus aleuticus*, for which we are grateful. We thank F. Dobson, B. Sandercock, A. Ozgul, G. Hycryshyn, J. Hostetler and one anonymous reviewer for valuable comments on an earlier draft. This research was supported in part by the Department of Wildlife Ecology and Conservation, and School of Natural Resources and the Environment, University of Florida, National Science Foundation grant DEB-0224953 (MKO), and by the Florida Agricultural Experiment Station.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2006.04.001.

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