

## AVIAN LIFE HISTORY VARIATION AND CONTRIBUTION OF DEMOGRAPHIC TRAITS TO THE POPULATION GROWTH RATE

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**Abstract.** A central goal in ecology is to predict population dynamics from demographic information. Based on the asymptotic population growth rate  $\lambda$ , calculated from a projection matrix model as a descriptor of the population dynamics, we analyze published data of 49 species of birds to determine how  $\lambda$  is influenced by variation in different demographic traits. Across species, the mean elasticity of the adult survival rate was significantly larger than the mean elasticity of the fecundity rate. The contribution of the fecundity rate to the population growth rate increased with increasing clutch size and decreasing adult survival rate, while the greatest contribution of adult survival rate occurred among long-lived species that matured late and laid few eggs. This represents a continuum from “highly reproductive species” at one end to “survivor species” at the other end. In addition, a high contribution of adult survival rate was found in some relatively long-lived species with early age at maturity (and a large clutch size) which was assumed to represent a bet-hedging strategy, i.e., producing a large number of offspring in some occasional good years. In a retrospective analysis, interspecific differences in the effects of actual temporal variation in adult survival rate and fecundity rate on the variability of  $\lambda$  were analyzed. These effects are expected to be large when the variance or the sensitivity of the trait is large. Because there was a negative relationship among species, both for the adult survival rate and the fecundity rate between the variability and the sensitivity of the trait, contribution of a trait to the variance in  $\lambda$  decreased with sensitivity. Similarly, within species, less temporal variation was found in traits with high elasticities than in traits with less contribution to  $\lambda$ . In some species, covariance among matrix elements also influenced the contribution of a demographic trait to  $\lambda$ . Monitoring schemes of bird demography should be designed in such a way that temporal variances and covariances among demographic traits can be estimated. Furthermore, it is important in such schemes to include data from a combination of traits that either have large sensitivities or high temporal variation.

**Key words:** birds; demography; elasticity analysis; life history variation; perturbation analysis; population dynamics; population growth rate; projection matrix model; temporal variation.

### INTRODUCTION

There is a strong need in population ecology to develop an empirically based theory for predicting variation in the population growth rate ( $\lambda$ ) (Caughley 1994). One important question to address when developing such a theory is how differences in life history characteristics affect the population responses to temporal variation in demographic traits. Such temporal variation may be due to environmental stochasticity or density-dependent variation (e.g., Sæther 1997, Grant and Benton 2000). Theoretical analyses have shown that the impact of temporal variation in a demographic trait on the population dynamics can be approximated in a projection matrix model (Caswell 1989), by the combined effect of the variance in the trait and the sensitivity of  $\lambda$  to a change in the trait (Caswell 1989,

Brault and Caswell 1993, Wisdom and Mills 1997). Thus, in order to predict the effects on  $\lambda$  of a demographic change, we need information for a wide variety of species on both the magnitude of the temporal variation in different traits, as well as how this variation relates to the sensitivity of the trait.

Our approach is based on perturbation analysis of a projection matrix model (Caswell 1997, 2000, Horvitz et al. 1997). Two approaches can be used to examine the consequences of such demographic perturbations. The purpose of a *prospective* analysis is to compare the effects on  $\lambda$  of a given change in a demographic trait, and such analyses are made by sensitivity (Caswell 1978) or elasticity calculations (de Kroon et al. 1986). Such knowledge is important in many fields of research (Caswell 1997). For instance, in life history theory an essential question is how variation in a demographic rate affects fitness (e.g., Caswell and Werner 1978). Similarly, conservation ecologists often try to predict how variation in the level of protection at different life history stages will influence the population

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growth rate of threatened or endangered species (Menges 1990, Heppell et al. 1994). In *retrospective* analyses, the contribution of actual variation in different demographic traits on the variability of  $\lambda$  is examined. A small contribution is expected when there is low variability in the trait, when the sensitivity is small, or if both occur.

The search for general patterns in the effects of variation in a demographic trait on the population growth rate may be facilitated by the documentation in several taxa of a strong covariation among different life history traits (e.g., Sæther 1988, Charnov 1993). For instance, in birds, the species can be placed along a "slow-fast continuum," where species with a high fecundity rate, but a low survival, are found at one end (Sæther et al. 1996). At the other end of this continuum lie species that mature late, produce few (often a single) offspring, and have a long life expectancy. It is likely that the species' position along this continuum will affect how the population growth rate will respond to a change in a demographic trait. However, few comparative analyses of the relationship between life history characteristics and the impact of different demographic traits on  $\lambda$  have been made. A notable exception is the comparative analysis of life history variation in plants (Silvertown et al. 1993, 1996). Analyzing interspecific differences in the contribution of different life history stages to population growth rates, these studies demonstrated that the species cluster into distinct groups, based on particular combinations of fecundity, growth, and longevity. For instance, high adult mortality was associated with early age at maturity and short life spans (Franco and Silvertown 1996). In contrast, differences among plant species in several reproductive traits were independent of adult survival, which differs from the pattern recorded in several vertebrate taxa (Charnov 1993, Sæther et al. 1996, Heppell et al. 2000). This suggests that there may be large differences among taxa in the relative contribution to population growth by different stages in the life cycle.

Here, we present a comparative analysis of how variation in different demographic traits is likely to affect the population dynamics (summarized by  $\lambda$ ) of birds with different life history characteristics. We do this in three steps. First, by a prospective analysis (Caswell 1997, 2000), we will examine whether interspecific life history differences (e.g., clutch size, age at maturity, or adult survival rate) can be used to predict the contributions of two demographic traits (i.e., fecundity and adult survival rate) to  $\lambda$ . Second, by using long-term avian demographic studies, we will analyze how the contributions to the temporal variance in the population growth rate are related to the sensitivity and the variance of the two traits. More specifically, we will use this retrospective analysis (Caswell 1997, 2000) to examine (1) how the contribution of the fecundity and adult survival rate to the variation in  $\lambda$  differs among species in relation to their life history characteristics,

and (2) whether a relationship between temporal variation and the sensitivity of a demographic trait is present within a species (cf. Pfister 1998). Because species can not be considered as independent data points (see Harvey and Pagel 1991), we analyze the data by a phylogenetic correction, based on a modification of Felsenstein's (1985) independent-contrast method. Third, by an examination of some case studies, we will show that covariation between demographic traits may also affect the contribution of a single trait to the variance in the population growth rate.

## METHODS

### *Interspecific differences in elasticities*

By surveying the literature, we obtained estimates of fecundity rate, age at maturity, and age-specific survival rates. The data and sources, following the taxonomy and classification of Sibley and Monroe (1990, 1993), are readily available (see the Appendix). We managed to obtain data from 49 species, including 27 species from the order Ciconiiformes, 16 species from the order Passeriformes, two species from each of the orders Anseriformes and Strigiformes, and one species each from the orders Coraciiformes and Piciformes.

Estimates of adult survival rate ( $P_{ad}$ ) were based on data from individually color-banded individuals from a single population. Two different types of estimates were available. In 18 cases, the probability of not recapturing or resighting an individual actually present in the population was included into the estimation procedure, as described, for example, by Lebreton et al. (1992). In 28 cases, adult survival rate was estimated as the return rate of breeding birds from one season to the next, which is likely to underestimate the adult survival rate (Martin et al. 1996). However, this bias is probably small compared to the range of the interspecific variation. When data were available for several years, the unweighted mean value was used. In some cases where the data were pooled over years, the survival rate was calculated as the weighted mean of the age-specific adult survival rates.

The modal number of eggs laid in the first clutch was used as an estimator of the clutch size (CS). The fecundity rate ( $F$ ) was estimated as the number of female offspring (assuming an equal sex ratio) produced to fledging at the end of the breeding season, per adult female. For most species, all adult females were assumed to breed each year. However, in several species from the family Procellariidae, the interval between breeding attempts were  $>1$  yr, and were often also dependent on previous breeding success. In such cases, the fecundity rate in year  $t$  (i.e.,  $F_t$ ) is

$$F_t = p_{s,t-1}S_{s,t-1} + p_{u,t-1}S_{u,t-1} + p_{n,t-1}S_{n,t-1}$$

where  $p$  is the proportion of the population and  $S$  is the breeding success, in year  $t$  of a female that was successful (s), unsuccessful (u), or nonbreeding (n) in

year  $t - 1$ , respectively. Furthermore, the modal age when the females first started to breed was used as an estimate of age at maturity ( $k$ ).

The most uncertain estimates were available for the survival rate in the prereproductive period of life. This was related to high natal dispersal rate of birds. Furthermore, juveniles of many long-lived species spend this period of their life away from the breeding area, which makes it difficult to obtain reliable estimates of the return rates. Thus, we used the estimates of the survival rate in the first year of life after fledging (juvenile survival rate,  $P_{\text{juv}}$ ), as presented by the author(s) of each study, and assumed that the survival rate in the rest of the prereproductive period was equal to the adult survival rate  $P_{\text{ad}}$ . However, in order to minimize the effects of bias in the estimates of  $P_{\text{juv}}$ , we also analyzed the data assuming a value of  $P_{\text{juv}}$  that gave a population growth rate  $\lambda = 1$ .

Based on these estimates, we computed the asymptotic population growth rate ( $\lambda$ ) as the dominant eigenvalue of the  $k \times k$  prebirth (Noon and Sauer 1992) Leslie matrix:

$$\begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & FP_{\text{juv}} \\ P_s & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_s & 0 & \cdots & 0 & 0 \\ \vdots & & & \ddots & & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & P_s & P_{\text{ad}} \end{pmatrix} \quad (1)$$

where  $P_s$  is the subadult survival rate after one year of age until maturity, at age  $k$ . In all analyses not involving covariation among traits, it is assumed that  $P_s = P_{\text{ad}}$ . This matrix has been suggested to provide a good description of avian demography (Lebreton and Clobert 1991). The population growth rate  $\lambda$  is determined by the characteristic equation

$$\lambda^k - P_{\text{ad}}\lambda^{k-1} - FP_{\text{juv}}P_s^{k-1} = 0 \quad (2)$$

which was solved numerically. Applying implicit differentiation, we obtain the lower level elasticities (Wisdom and Mills 1997)  $e(T) = \partial \log \lambda / \partial \log T = T(\partial \lambda / \partial T) / \lambda$  of trait  $T$ , holding other traits constant:

$$\begin{aligned} e(F) &= e(FP_{\text{juv}}) = e(P_{\text{juv}}) = \frac{FP_{\text{juv}}P_s^{k-1}}{k\lambda^k - (k-1)P_{\text{ad}}\lambda^{k-1}} \\ &= \frac{1}{k + \frac{1}{\frac{\lambda}{P_{\text{ad}}} - 1}} \end{aligned} \quad (3)$$

where the final equality follows from Eq. 2, as well as

$$e(P_s) = (k-1)e(F) \quad (4)$$

and

$$e(P_{\text{ad}}) = \frac{P_{\text{ad}}\lambda^{k-1}}{k\lambda^k - (k-1)P_{\text{ad}}\lambda^{k-1}} = \frac{1}{k\left(\frac{\lambda}{P_{\text{ad}}} - 1\right) + 1} \quad (5)$$

Matrix entry elasticities are the same as the lower-level elasticities for the matrix elements  $FP_{\text{juv}}$  and  $P_{\text{ad}}$ , whereas the elasticity for each of the elements  $P_s$  is equal to  $e(F)$ . The sum of the elasticities of the matrix elements is equal to 1 (de Kroon et al. 1986, Mesterton-Gibbons 1993):

$$ke(F) + e(P_{\text{ad}}) = 1.$$

#### Analysis of the effects of temporal variation in demographic traits on variation in $\lambda$

We wished to examine the effect of temporal variation of different life history traits on the contribution of adult survival and fecundity rates to the variance in population growth rate. To achieve this end, using a retrospective analysis (Caswell 1997), we only included studies where data on the probability of capture and recapture of recognizable individuals were available for  $\geq 10$  yr within a single population at the breeding site. In this way, we reduced the bias due to a positive relationship between the length of the study period and variance (Pimm 1991). When more than one study was available for a species, we chose the one that had been running for the longest time. However, in most cases, data on temporal variation in the fecundity rate were available for shorter time periods than was the case for the adult survival rate. In order to obtain the longest possible study periods, data on the fecundity rate and adult survival rate in three species (*Parus major*, *Ciconia ciconia*, and *Haematopus ostralegus*) were taken from two different populations. Temporal variation in  $F$  and  $P_{\text{ad}}$  was expressed as the standard deviation of the annual mean values, and the coefficient of variation (cv = standard deviation/mean) was used as a measure of relative variability. In this way, we obtained data (see Appendix for sources) of the species *Anser caerulescens* in the order Anseriformes; *Accipiter nisus*, *Fratercula arctica*, *Haematopus ostralegus*, *Morus bassanus*, *Phalacrocorax aristotelis*, *Pluvialis apricaria*, *Puffinus diomedea*, *Rissa tridactyla*, *Tringa hypoleucos*, and *T. macularia* in the order Ciconiiformes; and *Aphelocoma coerulescens*, *Catharus mustelinus*, *Dendroica discolor*, *Gymnorhinus cyanocephalus*, *Melospiza melodia*, and *Parus major* in the order Passeriformes.

The effects of the temporal variation in a demographic trait  $T$  on the standard deviation (SD) of  $\lambda$  can be approximated, according to Caswell (1989), by using a first order Taylor expansion, by  $SD(\lambda) \approx \sqrt{s(T)^2 \text{var}T}$ , where  $s(T) = \partial \lambda / \partial T$  is the sensitivity of  $\lambda$  to trait  $T$ , the other traits being held constant in the partial differentiation. This approximation has been shown in most cases to be quite accurate (Houllier et al. 1989). However, we assume that the sampling errors

are negligible compared to the interspecific variation. Finally, we also ignore covariation among demographic traits (see Brault and Caswell 1993, Wisdom et al. 2000) because of lack of data. Thus, in each case where sufficient data were available, we computed how the standard deviation in  $\lambda$  was related to temporal variation in the adult survival rate or fecundity rate.

In order to examine the correlation between elasticity and temporal variation in demographic traits within a species, we compared the relative contribution of adult survival rate and the fecundity rate to the population growth rate. We expect the contribution of adult survival rate, relative to fecundity, to decrease when the adult survival rate varies more than the fecundity rate. Since these two traits are measured at different scales, any time dependence in the variance is likely to be less important, so studies lasting  $\geq 5$  yr were included. The elasticity index  $e(T)$  (see Eqs. 3–5) of a matrix element  $T$  was used to compare the relative contribution of the two traits to the growth rate.

#### *The effects of covariation among demographic traits on elasticities*

The analyses presented thus far assume that there is no temporal correlation among the demographic traits. Such covariations will strongly influence the values of the elasticities. For instance, if there is a trade-off between life cycle components (Silvertown et al. 1993), a change in one element of the projection matrix may affect other elements in the opposite direction. Then, the net consequences on the population growth rate, due to variation in a demographic trait, cannot be inferred from the sensitivity or elasticity of a single element (Brault and Caswell 1993, Shea et al. 1994, van Tienderen 1995).

In our database, computation of the correlation coefficients between the annual variation in the elements of the Leslie matrix (Eq. 1) was possible for eight species, where temporal data on all elements included in the projection matrix were available for  $>5$  yr (Table 1). The integrated elasticity of element  $i$  ( $IE_i$ ) was calculated according to van Tienderen (1995) as

$$IE_i = \sum_j r_{ij} e_j cv_j / cv_i \quad (6)$$

where  $r_{ij}$  is the temporal correlation coefficient between element  $i$  and  $j$ , and  $cv_i$  is the coefficient of variation in element  $i$ . Thus, the total contribution to  $\ln \lambda$  is the sum of the direct contribution of the parameter (given by its elasticity) and the indirect contributions through the correlation with other parameters. Note that now the  $IE_i$  values do not sum to unity.

#### *Comparative analyses*

In comparative studies, species' values cannot be considered as statistically independent data points. Closely related species will tend to share more characters through common ancestry than through inde-

pendent evolution (Harvey and Pagel 1991). In order to control for the effects of phylogeny, we used the independent comparison method of Felsenstein (1985) to look for independent evolutionary events. We calculated independent contrasts by identifying a set of independent data points (e.g., the difference between two pairs of species) by the Comparative Analysis by Independent Comparisons (CAIC) software program (Purvis and Rambault 1995), basing the phylogeny of Sibley and Ahlquist (1990) at higher taxonomic levels, and Sibley and Monroe (1990, 1993) for the classification of genera and species. We then tested for a relationship between two variables by correlating the standardized linear contrasts for one variable with those for the other, using regression through the origin (for rationale, see Garland et al. [1992: Appendix 1]), and assuming equal rates of evolutionary change per unit branch length in all branches of the phylogenetic tree.

## RESULTS

### *Elasticities in relation to life history characteristics*

There was a great difference in our data set between the distribution of the elasticities of the fecundity rate  $e(F)$  and the distribution of the elasticities of the adult survival rate  $e(P_{ad})$ . The mean elasticity of the adult survival rate was significantly larger than the mean elasticity of fecundity rate (Fig. 1;  $t = 7.165$ ,  $P < 0.001$ ,  $df = 38$ ). Furthermore, the distribution of  $e(F)$  was skewed against small values, whereas the  $e(P_{ad})$  values were approximately normally distributed around the mean. This difference between the distributions remained when the elasticities were computed, assuming a value of  $P_{juv}$  that gave a population growth rate  $\lambda = 1$ . This suggests that these differences were not due to an effect of biases in the estimates of the juvenile survival rate.

The contribution to the population growth of adult survival differed in relation to the life history characteristics. For species values, the elasticity of adult survival decreased with clutch size (Fig. 2), but this relationship was not significant after accounting for the effects of phylogeny (Fig. 3a). Furthermore,  $e(P_{ad})$  also increased with adult survival rate (Fig. 2) after a phylogenetic correction (Fig. 3b). No significant ( $P > 0.1$ ) relationship appeared between  $e(P_{ad})$  and age at maturity (Fig. 2). The elasticity of fecundity rate ( $e(F)$ ) increased with the clutch size, and decreased strongly with adult survival rate, both before (Fig. 2) and after accounting for the effects of phylogeny (Fig. 3c, d). Furthermore,  $e(F)$  also decreased with age at maturity (Fig. 2), after phylogenetic correction ( $r = -0.47$ ,  $n = 34$ ,  $P < 0.01$ ).

Because interspecific variation in several avian life history traits are correlated with differences in adult survival rate (Sæther 1988, Sæther et al. 1996), a multiple correlation analysis showed that variation in the species values ( $n = 36$ ) of  $e(P_{ad})$  was positively cor-

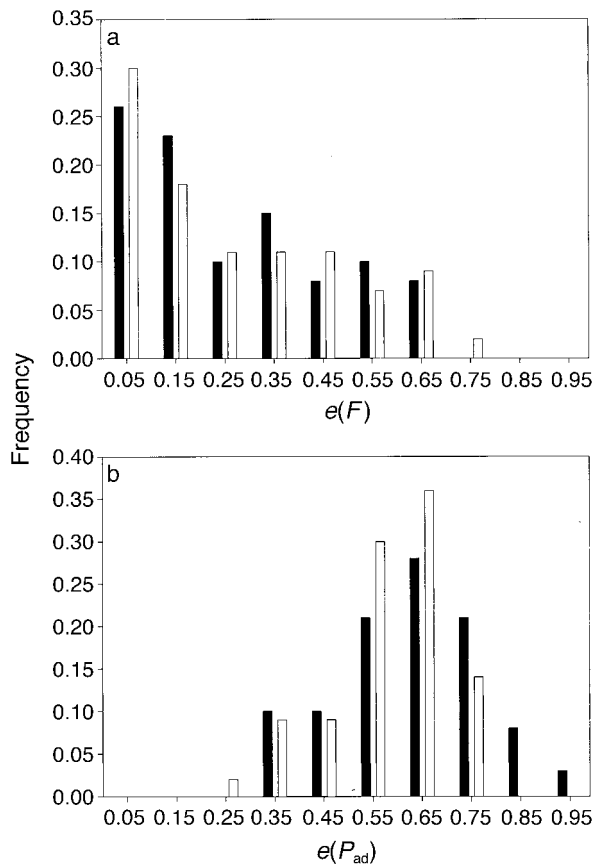


FIG. 1. The distribution among species of the elasticities of (a) the fecundity rate  $e(F)$  and (b) adult survival rate  $e(P_{ad})$ , calculated for the actual asymptotic population growth rate  $\lambda$  (solid bars), and when the juvenile survival rate  $P_{juv}$  is chosen to give  $\lambda = 1$  (open bars).

related with adult survival rate (partial correlation coefficient  $r_p = 0.42$ ,  $P < 0.05$ ). In contrast,  $e(P_{ad})$  decreased with age at maturity ( $r_p = -0.45$ ,  $P < 0.01$ ). The distribution of species in the clutch size–age at maturity plane show that this was due to the high  $e(P_{ad})$  values among species with large clutch sizes and early (2–3-yr-old) age at maturity (Fig. 2). In contrast,  $e(F)$  decreased with adult survival rate ( $r_p = -0.71$ ,  $P < 0.001$ ) and increased with clutch size ( $r_p = 0.34$ ,  $P < 0.05$ ). Thus, the highest elasticities of fecundity occurred among species with high adult mortality and large clutch sizes (Fig. 2). Very similar results were obtained when phylogenetically corrected values were used in the comparisons.

In order to control for the effects of interspecific differences in  $\lambda$ , we computed  $e(F)$  and  $e(P_{ad})$ , assuming a juvenile survival rate that gave  $\lambda = 1$ . After phylogenetic correction, only small changes occurred for the relationship between  $e(F)$  and the two life history traits (Fig. 3c, d). However,  $e(F)$  decreased more strongly (Fig. 3d), and  $e(P_{ad})$  showed a stronger in-

crease with adult survival rate, after accounting for the effects of differences in  $\lambda$  (Fig. 3b).

#### *Sensitivity of the population growth rate to temporal variation in demographic traits*

*Interspecific comparison.*—Retrospective analysis examines the contribution of actual variation in a demographic trait to the variability in  $\lambda$ . This contribution will be related to the variance in the trait, as well as to its sensitivity (see *Methods*). Here we will examine whether the interspecific differences recorded by the retrospective analysis also are present in the prospective analysis. For instance, is the contribution of temporal variation in adult survival rate to the variability in  $\lambda$  larger in long-lived than in short-lived species, as expected from Fig. 3b?

Across species, the sensitivity of the population growth rate to adult survival rate  $s(P_{ad})$  increased with adult survival rate ( $r = 0.71$ ,  $n = 18$ ,  $P < 0.001$ ), whereas there was an insignificant decrease in the sensitivity  $s(F)$  with  $F$  ( $r = -0.21$ ,  $n = 18$ ,  $P > 0.1$ ). However, after phylogenetic correction both relationships were significant ( $r = 0.59$ ,  $n = 15$ ,  $P < 0.05$ ; and  $r = -0.54$ ,  $n = 15$ ,  $P < 0.05$ ; for  $s(P_{ad})$  and  $s(F)$ , respectively).

The standard deviation of adult survival rate decreased with the mean adult survival rate both before ( $r = -0.78$ ,  $n = 18$ ,  $P < 0.001$ ) and after ( $r = -0.75$ ,  $n = 15$ ,  $P < 0.001$ ) phylogenetic correction. Accordingly, the scale-invariant coefficient of variation in adult survival also decreased with adult survival (species values,  $r = -0.87$ ,  $n = 18$ ,  $P < 0.001$ ; after phylogenetic correction,  $r = -0.88$ ,  $n = 15$ ,  $P < 0.001$ ). Such a decrease could be expected from a reduction of the sampling error with increasing survival, for example as a result of a binomial sampling distribution (Lande 1988). However, using a data set of 13 species, where adult survival rate was estimated during each of  $\geq 10$  yr, there was only a slight (and insignificant) decrease in sampling error with adult survival rate ( $r = -0.43$ ,  $P > 0.1$ ). Thus, the decrease in temporal variability with increasing survival rate is likely to be caused by a decrease in environmental stochasticity, or a different pattern of density dependence among long-lived species.

There was a strong positive relationship between the mean fledgling rate and its standard deviation ( $r = 0.92$ ,  $n = 16$ ,  $P < 0.001$ ; after phylogenetic correction,  $r = 0.92$ ,  $n = 15$ ,  $P < 0.001$ ). However, the coefficient of variation in  $F$  was not significantly related to  $F$  ( $r = -0.15$ ,  $n = 16$ ,  $P > 0.1$ ).

For both demographic traits, the standard deviation of the temporal variation decreased with increasing sensitivity after correcting for phylogeny (Fig. 4), but this relationship was significant only when using species values for adult survival rate ( $r = -0.72$ ,  $n = 18$ ,  $P < 0.001$ ). This negative relationship is realized for the two demographic traits in different ways: sensitivity

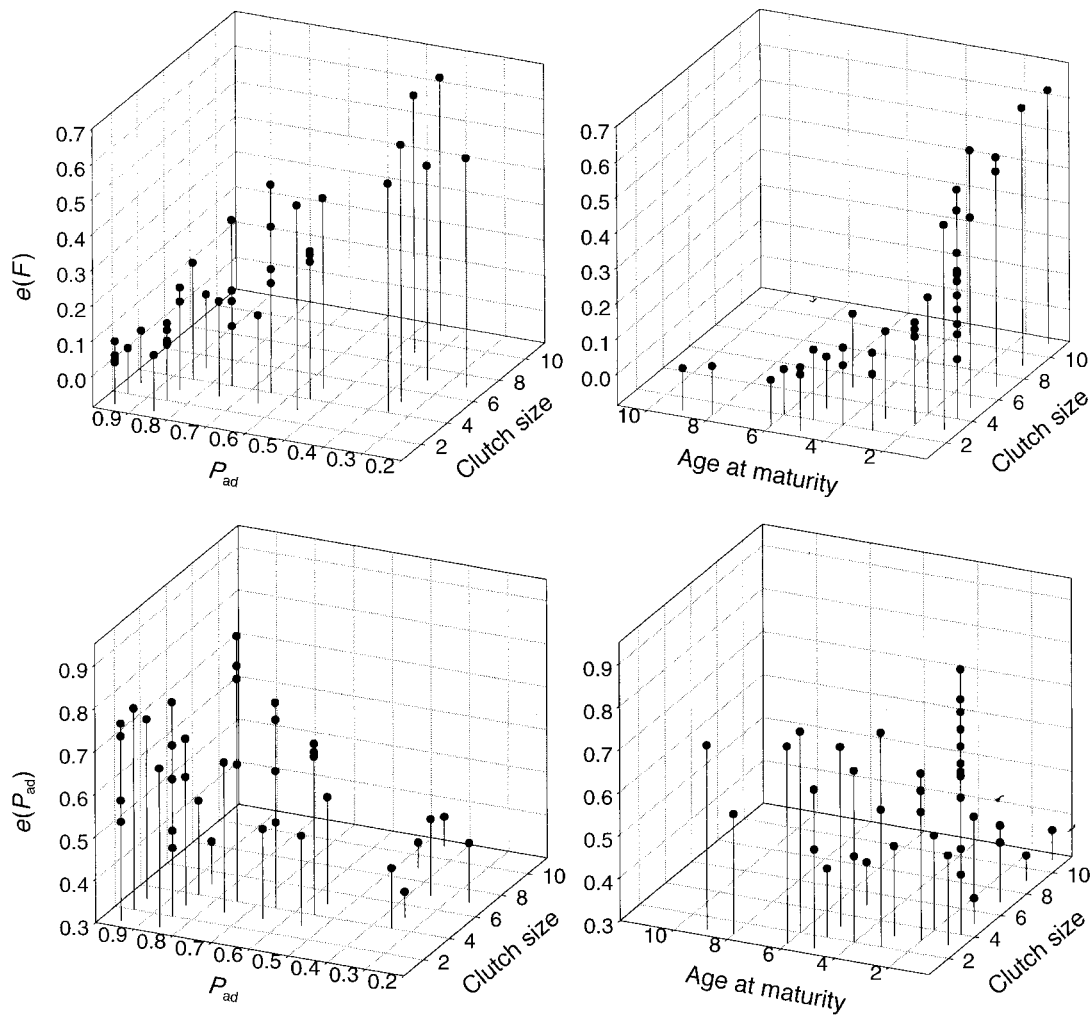


FIG. 2. The distribution of the values of the elasticity of fecundity  $e(F)$  and adult survival rate  $e(P_{ad})$  in relation to clutch size and adult survival rate, or adult survival rate and age at maturity, for 36 species. The correlation coefficients using species' values between  $e(P_{ad})$  and, respectively, clutch size, adult survival rate, and age at maturity are  $r = -0.48$ ,  $P < 0.01$ ;  $r = 0.50$ ,  $P < 0.01$ ; and  $r = 0.10$ ,  $P > 0.1$ . The corresponding correlation coefficients between  $e(F)$  and those three life history traits are  $r = 0.79$ ,  $P < 0.001$ ;  $r = -0.91$ ,  $P < 0.001$ ; and  $r = -0.70$ ,  $P < 0.001$ , respectively.

increases, and standard deviation decreases, with increasing adult survival rate, but the reverse takes place for the fecundity rate.

The contribution of temporal variation in the two demographic traits to the variance in population growth rate  $\lambda$  was related to the species' life history characteristics. For adult survival rate, this contribution decreased with increasing mean adult survival rate both before ( $r = -0.69$ ,  $n = 18$ ,  $P < 0.001$ ) and after correcting for phylogenetic effects (Fig. 5a). In contrast, the impact on  $\lambda$  of temporal variation in fecundity increased with increasing values of  $F$  ( $r = 0.85$ ,  $n = 16$ ,  $P < 0.001$ ). This relationship was also present after correcting for phylogeny (Fig. 5b). A comparison with Fig. 4 shows that these patterns are similar to the relationship between the standard deviation and the mean that was recorded for these two traits. Thus, a general

pattern seems to appear that, across species, the contribution of a trait to the variance in  $\lambda$  is more strongly influenced by the temporal variation than the sensitivity of the demographic trait, and that this contribution decreases with the sensitivity of the trait.

*Within-species comparison.*—The elasticity gives the proportional effects of variation in a demographic trait on the population growth rate  $\lambda$ . Within a species, there was no significant relationship between elasticity and coefficient of variation in either of the two demographic traits ( $r = -0.37$ ,  $P > 0.1$ ; and  $r = -0.11$ ,  $P > 0.1$ ,  $n = 20$  species; for adult survival rate and fecundity rate, respectively). In order to examine whether the variability in a demographic trait was less in those species where the trait had a large contribution to  $\lambda$ , we computed the ratio of  $e(P_{ad})$  to  $e(F)$ . This ratio gives the contribution of  $P_{ad}$  (relative to  $F$ ) to  $\lambda$ . The

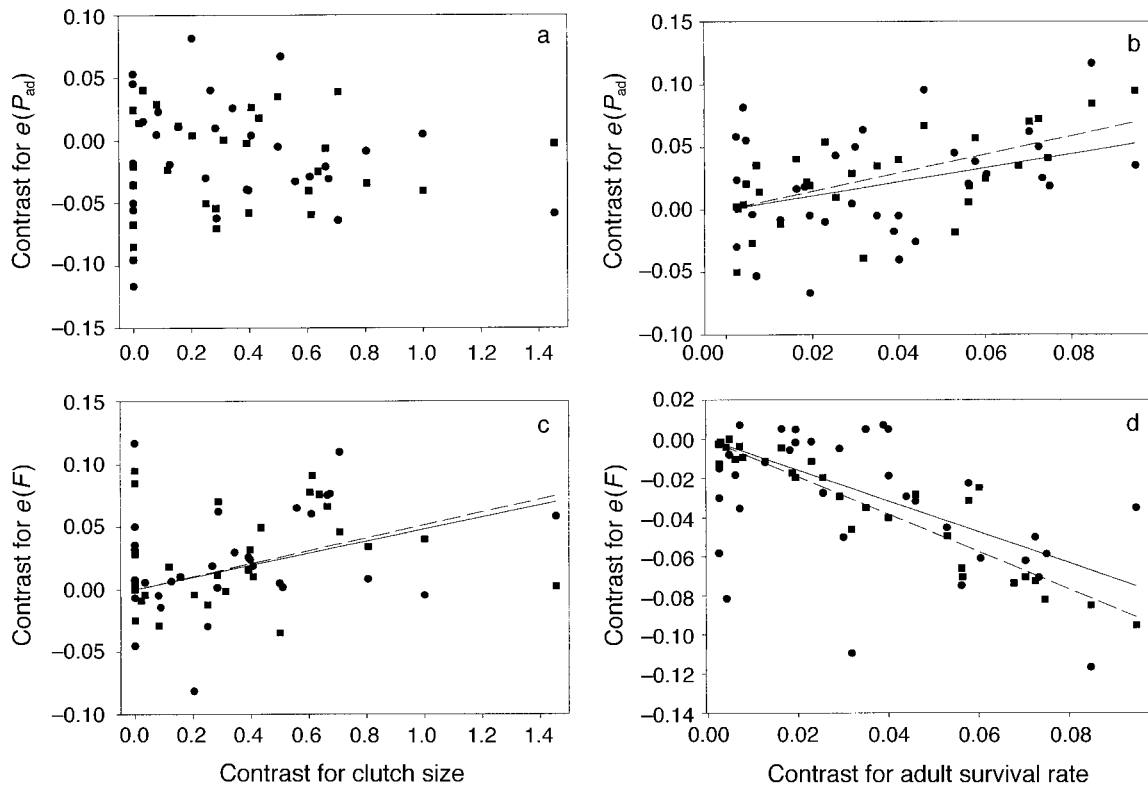


FIG. 3. The relationship between the elasticity of adult survival rate  $e(P_{ad})$  and (a) clutch size ( $r = -0.26$ ,  $n = 33$ ,  $P > 0.1$ ) and (b) adult survival rate ( $r = 0.54$ ,  $n = 34$ ,  $P < 0.001$ ); and the relationship between the elasticity of fecundity rate  $e(F)$  and (c) clutch size ( $r = 0.52$ ,  $n = 33$ ,  $P < 0.01$ ) and (d) adult survival rate ( $r = -0.79$ ,  $n = 30$ ,  $P < 0.001$ ) after phylogenetic correction. In each case, values were calculated for the actual asymptotic population growth rate  $\lambda$  (circles and solid lines) and when the juvenile survival rate  $P_{juv}$  is chosen to give  $\lambda = 1$  (squares and dashed lines). The standardized linear contrasts for each of the variables are given as described in *Methods*. The correlation coefficients when  $\lambda = 1$  are as follows: (a)  $r = -0.25$ ,  $n = 29$ ,  $P > 0.1$ ; (b)  $r = 0.79$ ,  $n = 30$ ,  $P < 0.001$ ; (c)  $r = 0.53$ ,  $n = 29$ ,  $P < 0.01$ ; and (d)  $r = -0.97$ ,  $n = 30$ ,  $P < 0.001$ . The regression lines all pass through the origin.

relative effects of  $P_{ad}$  on  $\lambda$  decreased when the variability of  $P_{ad}$  increased, compared to the variability in  $F$ , both before (Fig. 6) and after phylogenetic correction ( $r = -0.63$ ,  $n = 18$ ,  $P < 0.01$ ). This suggests that the relative contribution of a trait to the population growth rate decreases when the temporal variation in the trait increases.

#### Effects of covariation among demographic traits

Significant correlations between annual variation in the elements were found in five of the eight species listed in Table 1. In general, the correlation coefficients were positive, in particular between  $F$  and  $P_{juv}$  (significant in *Anser caerulescens*, *Melospiza melodia*, and *Aphelocoma coerulescens*). In addition, adult survival rate was significantly positively correlated to juvenile survival rate in *Melospiza melodia*, as well as to sub-adult survival rate in *Gymnorhinus cyanocephalus*. The only significant negative coefficient present in our data was between fecundity rate and juvenile survival rate in *Accipiter nisus*. In this species, the fecundity rate was also negatively correlated to adult survival rate ( $r = -0.64$ ,  $0.05 < P < 0.1$ ).

The covariation between the matrix elements affected the contribution of a parameter to  $\ln \lambda$ . In all but one species, the covariation with other parameters increased the contribution of  $P_{ad}$  (Table 1). The only exception was that, in *Pterichlidon pyrrhonota*, the contribution of adult survival rate was decreased due to a nonsignificant negative correlation with  $F$ . In contrast, a much stronger negative correlation between those two variables was counteracted in *Accipiter nisus* by a strong positive indirect effect of  $P_{juv}$  on  $P_{ad}$ , leading to a large integrated elasticity for adult survival.

#### DISCUSSION

The results of the prospective analysis (Figs. 2 and 3) show that interspecific differences in the contribution of two demographic traits (fecundity rate and adult survival rate) to the asymptotic population growth rate  $\lambda$  show strong life history correlates. Large contributions of the fecundity rate occurred in species with large clutch sizes and high adult mortality rates, whereas the contribution of adult survival rate was highest among species that matured late and laid few eggs. However, in the retrospective analyses, examining the contribu-

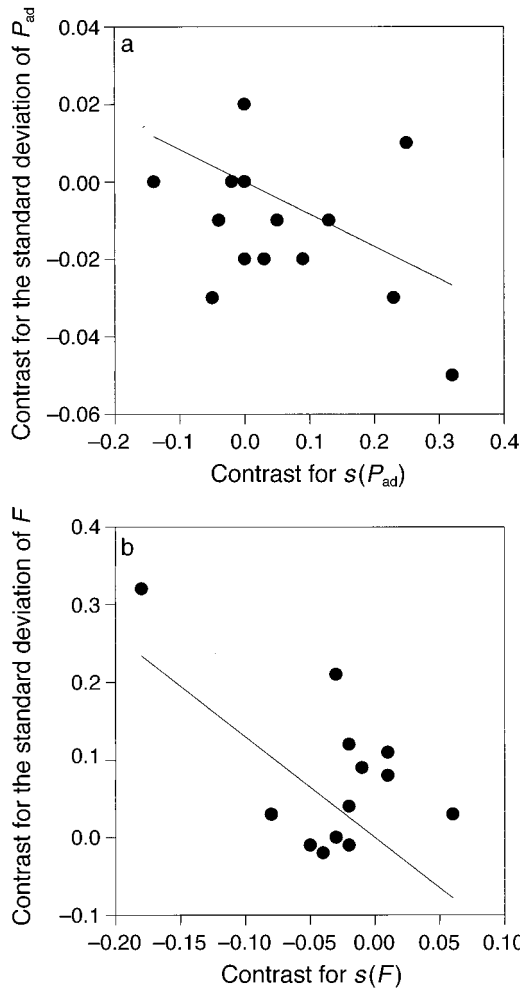


FIG. 4. The relationships between (a) the standard deviation of the adult survival rate ( $P_{ad}$ ), and the sensitivity of the population growth rate to variation in adult survival rate ( $s(P_{ad})$ ) ( $r = -0.55$ ,  $n = 15$ ,  $P < 0.05$ ) and (b) the standard deviation of the fecundity rate ( $F$ ) and the sensitivity of the population growth rate, to variation in the fecundity rate ( $s(F)$ ) ( $r = -0.67$ ,  $n = 15$ ,  $P < 0.01$ ) after phylogenetic correction. The standardized linear contrasts for each of the variables are given as described in *Methods*. The regression lines pass through the origin.

tion of actual temporal variation in the two demographic traits to the variability in  $\lambda$ , a different pattern of life history correlates appeared than in the prospective analysis. The contribution of adult survival rate decreased with increasing adult longevity of the species (Fig. 5a), whereas the largest contribution of the fecundity rate occurred among the highly reproductive species (Fig. 5b). This relationship was due to a negative relationship between the sensitivity of those two traits and their temporal variability (Fig. 4). Furthermore, a negative relationship between elasticity of a demographic trait and its variability was also present within a species (Fig. 6).

The relative contribution to the asymptotic popula-

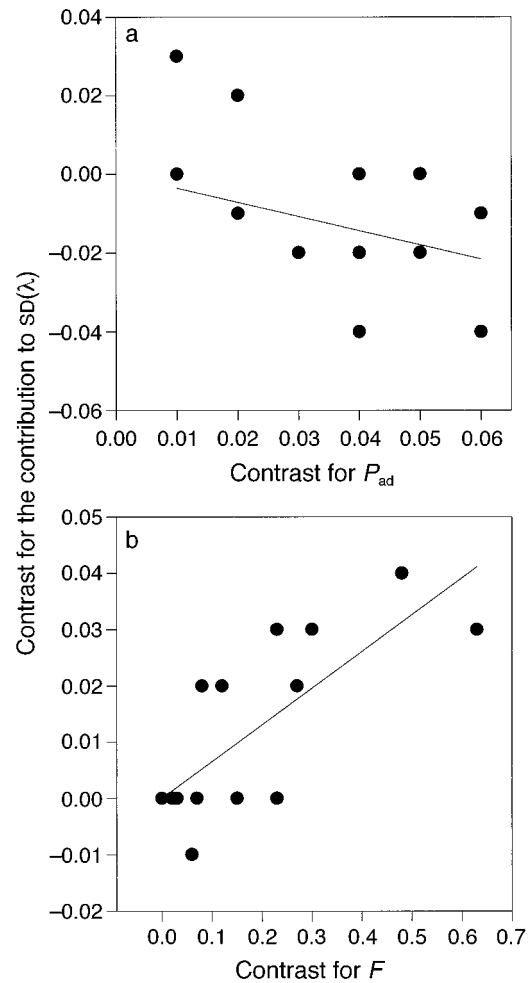


FIG. 5. The relationship between the contribution to the standard deviation of the population growth rate  $\lambda$  and the mean value across years of the contrast for (a) the adult survival rate  $P_{ad}$  ( $r = -0.61$ ,  $n = 15$ ,  $P < 0.05$ ) and (b) the fecundity rate  $F$  ( $r = 0.87$ ,  $n = 15$ ,  $P < 0.001$ ), in birds after phylogenetic correction. The standardized linear contrasts for each of the variables are given as described in *Methods*. The regression lines pass through the origin.

tion growth rate of adult survival is often larger than the contribution of the fecundity rate (Fig. 1), especially among long-lived species (Fig. 3b,d) with small clutches (Fig. 2). The difference between the elasticities of fecundity and adult survival rate also remained when computed for  $\lambda = 1$  (Fig. 1), suggesting that this difference is not related to a bias in the estimates of  $P_{juv}$ . An examination of Eqs. 2–5 shows that the positive relationship between adult survival and its elasticity is precisely defined in the analytical solution of the characteristic equation of the model, and mediated by age at maturity ( $k$ ). The maximal possible value of  $P_{ad}$  is  $\lambda$  (when  $\lambda \leq 1$ ), corresponding to  $FP_{juv}P_s^{k-1} = 0$  (Eq. 2). For these values, we see from Eq. 5 that  $e(P_{ad}) = 1$ . Thus, for long-lived species ( $P_{ad} \approx 1$ ), with a low fecundity rate or low subadult survival rate ( $FP_{juv}P_s^{k-1}$

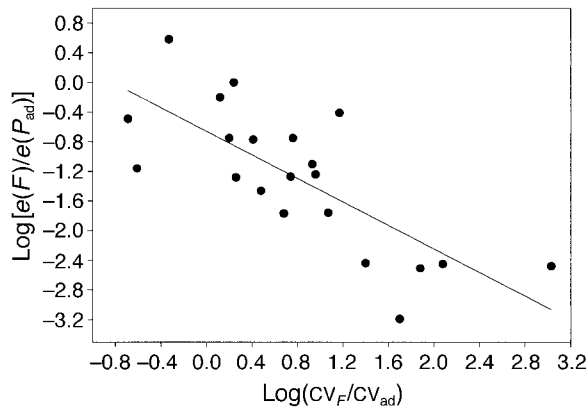


FIG. 6. The relationship within species of the elasticity ratio  $e(F)/e(P_{ad})$  and the ratio of the relative variability of the fecundity rate on the adult survival rate  $CV_F/CV_{ad}$  (logarithmically transformed values;  $r = -0.75$ ,  $n = 20$ ,  $P < 0.001$ ).

$\approx 0$ ),  $e(P_{ad}) \approx 1$ , and  $e(F) \approx 0$ , considering that  $ke(F) + e(P_{ad}) = 1$ . In contrast,  $e(P_{ad}) = 0$ , and  $e(F) = e(FP_{juv}) = 1/k$ , which is the maximal value of  $e(F)$ , again considering that  $ke(F) + e(P_{ad}) = 1$ , when  $P_{ad} = 0$ , and  $FP_{juv}P_s^{k-1}$  attains its maximum  $\lambda^k$  (Eqs. 2, 3, and 5). Thus, for short-lived species with large fecundity rates,  $e(P_{ad}) \approx 0$ .

Overall, our results support previous analyses that suggest the presence of a slow-fast continuum in avian life histories (Sæther 1988). A similar pattern has been suggested in other taxa as well, such as plants (Silvertown et al. 1993, Franco and Silvertown 1996) and mammals (Promislow and Harvey 1990, Purvis and Harvey 1995, Heppell et al. 2000). One end of this continuum is represented by species with a high contribution of the fecundity rate to the population growth rate, which occurs when the adult survival rate is low (Figs. 2 and 3d), the clutch size is large (Figs. 2 and 3c), and the age at maturity is early (Fig. 2). In contrast, the other end consists of species that lay only a single egg, mature at a very high age, and have a high adult survival rate. In those species, a very high contribution

TABLE 1. The direct contributions (elasticities in the diagonals of the effects columns) and indirect contributions of fecundity rate ( $F$ ), juvenile survival rate ( $P_{juv}$ ), survival after the first year of life until age of maturity ( $P_s$ ), and adult survival rate ( $P_{ad}$ ) to the population growth rate  $\lambda$ .

Species	Variable	cv	Contributions to $\lambda$				$IE_i$
			$F$	$P_{juv}$	$P_s$	$P_{ad}$	
<i>Pterichlidon pyrrhonata</i>	$F$	0.34	0.2620	0.0685	...	-0.1139	0.2166
	$P_{juv}$	0.66	0.0180	0.2620	...	-0.0357	0.2443
	$P_{ad}$	0.13	-0.2799	-0.3335	...	0.7380	0.1246
<i>Melanerpes formicivorus</i>	$F$	0.61	0.3800	0.0155	...	0.0607	0.4562
	$P_{juv}$	0.39	0.0371	0.3800	...	-0.0105	0.4066
	$P_{ad}$	0.19	0.3828	-0.0275	...	0.6200	0.9753
<i>Melospiza melodia</i>	$F$	0.47	0.4564	0.3544	...	0.1871	0.9979
	$P_{juv}$	0.46	0.3715	0.4564	...	0.3053	1.1331
	$P_{ad}$	0.37	0.2579	0.4016	...	0.5436	1.2032
<i>Gymnorhinus cyanocephalus</i>	$F$	0.29	0.1626	0.0477	0.0048	-0.1214	0.0937
	$P_{juv}$	0.32	0.0371	0.1626	0.0520	0.1757	0.4274
	$P_s$	0.31	0.0040	0.0564	0.1626	0.4152	0.6383
	$P_{ad}$	0.24	-0.0414	0.0769	0.1674	0.6747	0.8777
<i>Accipiter nisus</i> †	$F$	0.27	0.3164	-0.4133	...	-0.2587	-0.3556
	$P_{juv}$	0.48	-0.1381	0.3164	...	0.1495	0.3288
	$P_{ad}$	0.16	-0.3371	0.5832	...	0.6836	0.9297
<i>Aphelocoma coerulescens</i>	$F$	0.28	0.1962	0.1424	...	0.0371	0.3757
	$P_{juv}$	0.26	0.1696	0.1962	...	0.1230	0.4888
	$P_{ad}$	0.11	0.0782	0.2178	...	0.6076	0.9036
<i>Anser caerulescens</i>	$F$	0.18	0.2310	0.3109	...	-0.0893	0.4526
	$P_{juv}$	0.40	0.0645	0.2310	...	0.0235	0.3190
	$P_{ad}$	0.12	-0.0905	0.1145	...	0.5380	0.5620
<i>Phalacrocorax aristotelis</i>	$F$	0.21	0.1086	...	0.0040	0.0000	0.1126
	$P_s$ ‡	0.76	0.0001	...	0.2172	0.0180	0.2353
	$P_{ad}$	0.13	0.0000	...	0.1958	0.6742	0.8700

Notes:  $P_s$  was only calculated for those species where separate estimates for these age classes were provided by the authors. The indirect contributions between traits  $i$  and  $j$  are  $r_{ij}e_jCV_j/CV_i$ , where  $r$  is the temporal correlation coefficient,  $e$  is the elasticity, and  $CV$  is the coefficient of variation. The indirect contributions denote the contribution of a variable to the population growth through its covariation with other demographic traits. The integrated elasticity of variable  $i$  ( $IE_i$ ) is the sum of the direct and indirect effects. The calculations are made only for the period when data were available for all demographic variables. The species are listed according to increased adult survival rate. The sources are listed in the Appendix.

† The data are for the population in the Rockingham area.

‡ The probability of survival until age 3 (Harris et al. 1994).

of adult survival rate to the population growth rate is found (Figs. 2 and 3b). Sæther et al. (1996) termed these two groups “highly reproductive species” and “survivor species,” respectively. However, an examination of Fig. 2 shows that among species with relatively high survival rates, there is large variation in the contribution of adult survival rate to population growth rate. In particular, high  $e(P_{ad})$  values were found among species (waders, owls, and terns) that have large clutch sizes, but mature early ( $\leq 3$ -yr-old). These species may have large mean or variable recruitment rates. Such a life history strategy may represent an adaptation to a variable environment by securing a large output of offspring in occasional favorable years (Sæther et al. 1996).

The prospective analysis showed that there are large interspecific differences in the proportional effects of a change in different demographic traits, dependent on the species' life history characteristics (Figs. 2 and 3). However, from the retrospective analysis, it was evident that the contribution of a trait to the variance in  $\lambda$  is more strongly influenced by its temporal variation than its sensitivity (Fig. 5). A similar relationship also appeared within a species, where there was an inverse relationship between the relative contribution to the growth rate of a trait (its elasticity) and its relative variability (Fig. 6). However, the correlation between the elasticity and the coefficient of variation for each of them separately was not significant. Accordingly, Pfister (1998) generally found a negative relationship between the contribution of a matrix element to the mean population growth rate and its temporal variance, upon the review of stage-based demographic studies from a wide variety of taxa. Such patterns have also been recorded in comparisons within more restricted taxa. For instance, in the plant species *Calathea ovandensis*, the sensitivity of  $\lambda$  to an element in the projection matrix was negatively correlated with the variability in the element (Horvitz et al. 1997). Furthermore, transitions with high elasticities contributed less to the spatiotemporal variation in  $\lambda$  in the leguminous herb species *Lathyrus vernus* than expected from their elasticity values alone, because smaller variability was found in those traits (Ehrlén and van Groenendael 1998). Similarly, in ungulates (Gaillard et al. 1998), juvenile survival rate has a lower elasticity, but is more variable and has a greater impact on the variation in population growth rate, than does adult survival rate. Thus, a decrease in the contribution of a trait to the variance in the population growth rate with increasing sensitivity may be a common pattern (see also de Kroon et al. [2000]). However, some studies have shown high variability also in sensitive traits (Wisdom and Mills 1997, Crooks et al. 1998, Wisdom et al. 2000).

The inverse relationship between the sensitivity of a trait and its temporal variation, found both in the among-species (Fig. 4) and within-species comparisons (Fig. 6), suggests that a reduction in the variance of

sensitive traits is favored through selection. Accordingly, theoretical analyses have shown that environmental stochasticity is likely to strongly affect the selection pressure acting on a demographic trait (Benton and Grant 1996). Thus, the reduction in the impact on the variance in population growth rate with increasing adult survival (Fig. 5) may be interpreted as the result of an evolution of a bet-hedging strategy (Seger and Brockman 1987) among long-lived species to spread the risk in reproductive investments over several breeding seasons. Accordingly, reduced maternal investment of ungulates during poor reproductive seasons may be one reason for the greater temporal variation recorded in juvenile survival rates, compared to the variation in adult survival rates (J.-M. Gaillard and H. G. Yoccoz, *unpublished manuscript*).

It is important to distinguish between two different approaches that can be taken to demographic perturbation analysis (Caswell 1997, 2000, Horvitz et al. 1997). In prospective analysis, we ask how the population growth rate is functionally related to different demographic traits. They can be used, for example, in conservation ecology, to examine the frequently asked question of how much the population growth rate is changed if a certain management action that affects some vital rate is implemented (Heppell et al. 1994). In contrast, retrospective analyses are concerned with how actual variation in different demographic traits determines the variation in the population growth rate. Our work illustrates that these two types of analyses may give different answers (Brault and Caswell 1993, Horvitz et al. 1997, Wisdom and Mills 1997). For instance, the results of the retrospective analyses (Figs. 4–6) show that demographic traits found in prospective analyses that are functionally related most closely to the population growth rate (Fig. 3) were traits that explained only a small proportion of the variance in  $\lambda$ . This pattern may imply that data on the variance, and not only the mean values of demographic traits, will be crucial in prospective analyses predicting population trends. In particular, changes in the environment that will increase the temporal variance in demographic traits with high sensitivities are likely to have a serious effect on population viability, because this will cause a reduction in the mean population growth rate, and thereby increase the risk of extinction (Lande 1993). Thus, it is important that population studies and monitoring schemes incorporate a collection of data that can be used in retrospective analyses of population responses to temporal variation in demographic traits.

Our retrospective analyses of the impact of variation in different demographic traits on the population growth rate (Figs. 2–6) have ignored the influence of covariation among traits. In those species, where such data were available, large temporal covariation among matrix elements was often recorded (Table 1). These covariations sometimes strongly affected the contribution of the trait to the population growth rate (see

Brault and Caswell 1993, Horvitz et al. 1997, Caswell 2000). Several mechanisms may explain such relationships. Negative correlations may result as a trade-off between life history traits (Silvertown et al. 1993), for instance, through a survival cost of high fecundity rate (but see Shea et al. [1994]). However, such relationships have been difficult to document in birds (Roff 1992). A covariance between two elements may also be due to a common response of two elements to a change in population density. These relationships may be both positive (e.g., both juveniles and adults survive well at low densities) and negative (e.g., high fecundity results in increased juvenile mortality, because of increased intraspecific competition). For instance, in *Melospiza melodia*, the fecundity rate and the adult and juvenile survival rates were closely correlated with population size (Arcese et al. 1992), which may explain the large positive indirect effects on the integrated elasticity in this species (Table 1). Such density-dependent effects make it difficult to use integrated elasticities (Eq. 4) in comparative studies, because the data should be sampled from a similar range of density variation (relative to the carrying capacity [ $K$ ]) for all species. Furthermore, a relationship between two elements may be related to a common response to stochastic variation in the environments or to an ecological perturbation. However, the latter two explanations may not be mutually exclusively. For instance, the high covariation among the elements in the projection matrix of the *Accipiter nisus* population was computed during a period when the population increased rapidly in size, probably due to a large reduction of the pesticide levels in the environment (Wyllie and Newton 1991). Our results show that, whatever the mechanisms, such covariations may affect the contribution of an element to the population growth rate. However, reliable estimates of such indirect effects will require long-term demographic data, which is currently available only for a few species, as well as estimation procedures that include the effects of sampling error in the different elements.

In summary, the results of the elasticity analysis in this, as well as in other studies (Silvertown et al. 1993, 1996, Heppell et al. 2000), have demonstrated that the functional dependence of the population growth rate  $\lambda$  on different demographic traits differ in a predictive way, in relation to the life history characteristics of the species. Following the categorization of Sæther et al. (1996), the population growth rate of “survivor” and “bet-hedging” species is more dependent on variation in adult survival rate than in the case of “highly reproductive” species (Fig. 2). However, the results of the retrospective analysis strongly suggest that the contribution of temporal variation in a demographic trait to the variance in  $\lambda$  (Figs. 5 and 6) is inversely related to the sensitivity of the trait, because it seems to be a common pattern that less sensitive traits are more variable (Fig. 4; Horvitz et al. 1997, Ehrlén and van Gro-

enendael 1998, Pfister 1998, Tombre et al. 1998, de Kroon et al. 2000). A management implication of this is that many monitoring schemes should be designed in such a way that statistically reliable data on the temporal variation in the different demographic traits are obtained. Our results suggest that large environmental variances in sensitive traits of birds should rarely occur and that they should attract particular attention when developing management action plans.

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## APPENDIX

Data on bird fecundity rate, age at maturity, and age-specific survival rates, as well as the sources of those data, are available in ESA’s Electronic Data Archive: *Ecological Archives* E081-005.