Age-Specific Fitness Components and Their Temporal Variation in the Barn Owl

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ABSTRACT: Theory predicts that temporal variability plays an important role in the evolution of life histories, but empirical studies evaluating this prediction are rare. In constant environments, fitness can be measured by the population growth rate λ, and the sensitivity of λ to changes in fitness components estimates selection on these traits. In variable environments, fitness is measured by the stochastic growth rate λ_s, and stochastic sensitivities estimate selection pressure. Here we examine age-specific schedules for reproduction and survival in a barn owl population (*Tyto alba*). We estimated how temporal variability affected fitness and selection, accounting for sampling variance. Despite large sample sizes of old individuals, we found no strong evidence for senescence. The most variable fitness components were associated with reproduction. Survival was less variable. Stochastic simulations showed that the observed variation decreased fitness by about 30%, but the sensitivities of λ and λ_s to changes in all fitness components were almost equal, suggesting that temporal variation had negligible effects on selection. We obtained these results despite high observed variability in the fitness components and relatively short generation time of the study organism, a situation in which temporal variability should be particularly important for natural selection and early senescence is expected.

Keywords: demography, mixed-effects model, population growth, random effects, senescence, stochasticity.

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Classical life-history theory assumes that organisms evolve in an environment that is constant over time (Stearns and Koella 1986; Stearns 1992). Even though this assumption is almost never strictly true, recent theoretical and empirical studies disagree on the importance of taking into account temporal variation. In constant environments, fitness can be measured by the population growth rate λ (or r; Metz et al. 1992), and the sensitivity of λ to changes in fitness components estimates selection pressure on these traits (Lande 1982). In variable environments, fitness is measured by the stochastic population growth rate λ_s, and stochastic sensitivities estimate selection pressure (Tuljapurkar 1982; Tuljapurkar et al. 2003). While some studies find that using the mean environment over time to measure fitness and selection pressure leads to only negligible bias (Cooch and Ricklefs 1994; Benton et al. 1995; Benton and Grant 1999), other studies show that temporal variation can have large effects (Tuljapurkar 1989; Orzack and Tuljapurkar 2001). Usually, temporal variability decreases fitness because it reduces the geometric mean of a fitness component even if its arithmetic mean is unchanged (Gillespie 1977; Stearns 2000; Doak et al. 2005). Furthermore, not all age classes contribute equally to fitness (Charlesworth 1994), and the effect of temporal variation therefore depends on which age classes are affected.

Empirical evidence shows that different age classes are often affected differently by environmental variation (e.g., reviews in Martin 1995; Gaillard et al. 2000). For example, Laaksonen et al. (2002) found that young, but not older, Tengmalm's owls (*Aegolius funereus*) failed to breed in years with low vole abundance, whereas there was little difference among age classes in breeding success when voles were abundant. In six populations of the asp viper (*Vipera aspis*) in Switzerland, juvenile but not adult survival was strongly affected by winter severity (Altwegg et al. 2005). Detailed knowledge of how environmental variation affects age-structured populations is necessary to understand the dynamics of such populations (Coulson et al. 2001; Lande et al. 2003) and to predict how they respond to natural selection (Pfister 1998; Caswell 2001).

Temporal covariation (or the lack of it) between fitness

components therefore presents a further complication. If patterns of covariation between fitness components are ignored, one may obtain wrong inferences about the relative contribution of the different fitness components to observed population growth (Coulson et al. 2005). Doak et al. (2005) recently showed that covariances between fitness components must be considered in temporally fluctuating environments to correctly estimate sensitivities and thus strength of selection (see also Altwegg et al. 2006).

Detailed empirical data on how environmental variation affects fitness components in age-structured populations are rare, and the best examples are from isolated populations of large mammals (e.g., Benton et al. 1995; Clutton-Brock and Coulson 2002). Two types of practical problems have led to a lack of such data. First, obtaining data on all age classes over a sufficiently long time period requires labor-intensive field studies. Second, even if such data can be collected, estimates of temporal variation are usually inflated by sampling variance (Link and Nichols 1994; Stewart-Oaten et al. 1995; Gould and Nichols 1998). Recently developed methods allow the decomposition of the variance in survival estimates into its temporal component and a component due to sampling error (Burnham and White 2002). This method is based on random effects, and the yearly survival rates are treated as realizations of a random variable whose mean and variance can be estimated from the data. To separate temporal variance from sampling variance in reproduction, we suggest using mixed-effects models where time is treated as a random effect and age as a fixed effect. This method allows direct estimation of the temporal variance, and it is available for data with Gaussian errors (Littell et al. 1996; Pinheiro and Bates 2000) and as generalized linear mixed models for data with Poisson or binomial errors (Breslow and Clayton 1993).

We examined age-specific survival and reproduction in female and male barn owls (*Tyto alba*) in western Switzerland and used random-effects methodology to quantify temporal variation in these fitness components. We also examined to what extent fitness components co-vary over time. We then calculated stochastic and deterministic population growth rate sensitivities to evaluate whether temporal variation and covariation of fitness components are important for selection. The barn owl is an ideal organism for studying these questions because its life-history traits are highly variable among years (Altwegg et al. 2003, 2006). Both males and females can be captured at the nest, which ensures that we can estimate these traits and their variance for both sexes. An interesting aspect of barn owl biology is that females do not leave their nests for hunting during incubation until the first chick is about 17 days old (Durant et al. 2004). Females are dependent on being fed by males during this time, and males may thus have a direct influence on clutch size and quality.

Methods

Field Methods

Barn owls were captured and ringed between 1990 and 2004 in the Payerne region in western Switzerland (see Altwegg et al. 2003 for more details about the study population). Most birds were ringed as nestlings. In this study, we also included individuals first encountered as 1-year-old breeding birds because they could be identified by plumage characteristics (i.e., primary and secondary feathers all renewed during last molt; Taylor 1994). We determined the sex of adult birds from breeding behavior and the presence or absence of a brood patch. After 1996, we took blood from all nestlings to determine their sex from blood cell DNA using sex-specific molecular markers (Roulin et al. 1999). Extrapair paternity in the barn owl is rare (Roulin et al. 2004), and we therefore assumed that the male tending a nest was the biological father of all young in that nest.

Estimation of Fitness Components

We used the sample-size-adjusted Akaike Information Criterion (AICc) to select models (Burnham and Anderson 2002). In contrast to null-hypothesis testing, this approach allows a number of alternative hypotheses to be evaluated simultaneously. Each hypothesis is represented by an alternative statistical model, and AICc provides an objective tool to rank these models and thus quantify the evidence for each biological hypothesis (Burnham and Anderson 2002). The best model is the one with the lowest AICc value. The performance of each model relative to the other models in the set is given by the Akaike weight (w). The AICc also provides a framework for drawing inferences from several models (multimodel inference), thus providing parameter estimates that are independent of a particular model structure, and standard errors that take into account model selection uncertainty (see Burnham and Anderson 2002, 2004 for details).

Age-Specific Reproduction. We examined the effect of age on clutch size, which varied between 2 and 13 per nest (mean = median = 6.0; $n = 577$ clutches), mean egg volume within broods (calculated from the length and width, assuming an ellipsoid: volume = $(\pi \times \text{width}^2 \times \text{length})/6$ mm³; $n = 447$ clutches), the number of fledglings produced per nest (range 0–9, mean = median = 4.0; $n = 596$ broods), and the number of eggs that failed to hatch (range 0–9, mean = 0.4, median = 0, $n =$

581 clutches; the sample sizes varied because not all information was available for a few broods). Abandoned clutches were not counted as eggs failing to hatch. Clutch size, egg volume, and the number of fledglings were normally distributed, and we analyzed these data using linear mixed-effects models implemented in procedure "lme" in the program R, version 2.0.1 (R Development Core Team 2003; see also Pinheiro and Bates 2000). For the number of eggs failing to hatch, the errors followed a Poisson distribution, and we used generalized linear mixed models with a log link function implemented in procedure GLMM in R (with add-on library "lme4"; Venables and Ripley 2002). In procedure lme, we used maximum likelihood to fit the models, whereas procedure GLMM provides penalized quasi-likelihood estimation followed by optimization of the second-order Laplacian approximation to the marginal log likelihood.

The fixed effects in our models were breeding attempt (first clutch, second clutch, and replacement clutch; laying date had no additional effect on all response variables) and representations for the age of each parent. We considered six different representations of age: (1) no age effect; (2, 3) linear and quadratic relationships between age and reproduction; (4) a linear relationship, but one allowing for different reproductive success in the first year; (5) different reproduction for three age classes, 1, 2–5, and >5 years; and (6) different reproduction for all ages. The choice of these representations was motivated by earlier studies on age-specific reproduction in birds (Forslund and Pärt 1995). The statistical models assume homogenous residuals, and this assumption was potentially violated because of the following factors. We had repeated observations for most males and females, but the pairs rarely stayed together in subsequent breeding seasons, and nest boxes were often used by different birds each year. Finally, average breeding success varied strongly among years. Therefore, we included the random effects year (15 levels), female identity (288 levels), male identity (249 levels), and nest box (100 levels). It was not possible to account for all four random effects in a single statistical model, and so we ran models with one random effect at a time. Then we used multimodel inference based on AICc to estimate fixed effects (and their confidence intervals) that are independent of the structure of the random-effects model (Burnham and Anderson 2002). Multimodel inference yields a weighted average of the estimates for the fixed effect, weighting each estimate by the Akaike weight (w) of the corresponding random-effect model. We then calculated unconditional (i.e., not dependent on a particular structure of the random-effect model) standard errors for the estimates of the fixed effects, following Burnham and Anderson (2002, 2004). The estimates of temporal variance were taken from the model with year as a random effect.

Probability of Producing a Second Clutch. Some pairs produced a second clutch (46 of 591 broods), and we used logistic regressions to examine whether the probability of producing a second clutch depended on the parents' age and varied over the years. The years were treated as random effects, and the model was fitted as a generalized linear mixed model using procedure glmmPQL in R (with add-on library MASS; Venables and Ripley 2002) rather than procedure GLMM because the model using the latter failed to converge. Procedure glmmPQL uses penalized quasi-likelihood rather than maximum likelihood, and we could therefore not apply model selection based on AICc. For this reason, and because the data were sparse (few second clutches observed), we examined only a linear effect of the female and male parents' ages and their interaction with year.

Survival. We used capture-mark-recapture methods to estimate local survival and recapture rates for the period 1990–2004 (Lebreton et al. 1992) and thus accounted for the fact that not all individuals were captured each year. In total, 3,252 individuals were ringed either as nestlings or as 1-year-olds, of which 341 were recaptured at least once. We examined age-specific survival and recapture rates using the same representations for the age effect as in our analysis of reproduction. In addition, we accounted for lower survival rates of nestlings (age 0) and considered senescence in terms of lower survival after age 9 years, which was the oldest age for which we had large sample sizes. We further examined differences between the sexes and years in survival and recapture rates. For the years 1996–2003, the sex of each fledgling was known. The sex ratio among these nestlings was close to 1 : 1 (809 males : 806 females and no significant variation among years; $\chi^2 = 9.9$, df = 7, $P = .20$). We therefore assumed an equal sex ratio over the rest of the study period and assigned the birds with unknown sex in equal proportions to each sex for each year (Nichols et al. 2004).

We used random-effects models incorporated in the program MARK (White and Burnham 1999; Burnham and White 2002) to estimate the temporal variance of survival rates. MARK uses the method of moments, which is known to perform well with 15 years of data (Burnham and White 2002).

Capture-mark-recapture methods make the assumption of equal survival and recapture rates among individuals, which we tested using the goodness-of-fit test provided by the program RELEASE (Burnham et al. 1987). This test showed that a general time-dependent model accounting for differences between the sexes and lower survival of nestlings fitted our data well ($\chi^2 = 75.79$, df = 84, $P = .70$; age effect is accounted for by omitting test 3SR for birds ringed as nestlings). All models were fitted by

Table 1: Summary of model selection for the effects of female and male age on several components of reproduction in Swiss barn owls

Model and factors	K	Clutch size ΔAICc	Clutch size w	Egg volume ΔAICc	Egg volume w	Number of fledglings ΔAICc	Number of fledglings w	Eggs failing to hatch ΔAICc	Eggs failing to hatch w
Females:									
1. Constant	5	**0**	**.365**	5.35	.033	4.577	.035	**0**	**.411**
2. Linear	6	1.738	.153	7.298	.012	**0**	**.349**	1.05	.243
3. Linear + quadratic	7	.31	.313	3.132	.099	2.008	.128	3.033	.09
4. Linear, first year different	7	3.412	.066	.408	.385	1.586	.158	2.358	.126
5. Three age classes: 1, 2–5, 6+	7	2.552	.102	**0**	**.472**	.438	.28	2.326	.129
6. All ages different	16	16.512	.000	13.43	.001	15.639	.000		
7. Linear × year	8					4.049	.046		
8. Three age classes × year	12					8.933	.004		
Males:									
1. Constant	5	23.637	.000	2.586	.175	2.393	.114	13.91	.001
2. Linear	6	6.026	.028	3.516	.11	3.45	.067	5.102	.061
3. Linear + quadratic	7	1.686	.244	**0**	**.637**	1.384	.189	3.893	.112
4. Linear, first year different	7	**0**	**.568**	5.4	.043	**0**	**.378**	**0**	**.783**
5. Three age classes: 1, 2–5, 6+	7	2.544	.159	5.732	.036	2.042	.136	5.798	.043
6. All ages different	19	13.489	.001	10.97	.003	16.785	.000		
7. Linear, first year different × year	9					3.109	.08		
8. Linear + quadratic × year	9					4.763	.035		

Note: We evaluated six different representations for the age effects (see "Methods"). The table shows for each model the number of parameters (K), the difference in sample-size-adjusted Akaike Information Criterion between the current and the best (in boldface) model (ΔAICc), and the Akaike weight (w). The table shows linear mixed-effects models (generalized linear mixed models with Poisson errors and log link function in the case of eggs failing to hatch), with the best-supported random effect. The random effects were female identity for clutch size and egg volume, year for the number of fledglings, and male identity for eggs failing to hatch. The other random effects were poorly supported (next-best random effect: ΔAICc = 15.6, 251.0, 10.0, and 8.6 for the four components of reproduction). For number of fledglings, we also show two models exploring the interaction between age and year (models 7 and 8). For eggs failing to hatch, the data were insufficient to fit model 6. Each model also accounted for differences among breeding attempts.

maximum likelihood using MARK, version 3.2 (White and Burnham 1999).

Age-Specific Probability of First Reproduction. We used a two-state extension of the same capture-mark-recapture methods to estimate the age-specific probability of first reproduction. The two states were "immature" for individuals marked as nestlings that had not yet reproduced and "breeder" after they started reproducing. The transition probability from the immature to the breeder state is the probability of first-time reproduction (α). All individuals that were marked as breeding adults remain in the breeder state until they die. This model has been described by Lebreton et al. (2003) for multiple sites and is based on the work of Clobert et al. (1994).

For these models, we used extensions of the best models for survival and recapture rates, from the analysis of age-specific survival. In order to reach numerical convergence, this approach requires defining an upper age at which all remaining immatures become breeders (Pradel and Lebreton 1999). We therefore varied this age threshold and examined at which age all individuals have reproduced at least once (full reproduction), that is, the age at which

$\alpha = 1$ for each sex. Then we tested whether α varied over time and estimated the temporal variance in α, using the random-effects approach as outlined above.

Comparing Variability among Different Fitness Components. We used coefficients of variation (CVs) to compare the variability in fitness components that were measured on a ratio scale without upper limit (clutch size, egg volume, number of fledglings, and number of eggs failing to hatch). All other fitness components were measured as rates, and CV is not suitable for comparing their variability because their maximum variance is $p(1 - p)$ for a rate p (e.g., survival). Instead, we compared the variability among these rates by the ratio of the observed variance (σ^2) to the maximum possible variance (i.e., $\sigma^2/p(1 - p)$; Gaillard and Yoccoz 2003; Morris and Doak 2004). Thus, the variability of rates cannot be compared to the variability of the other fitness components, but we know of no way such a comparison could be fairly made.

Stochastic Sensitivities

We used a population matrix model with three stages and a prebreeding census with a projection interval of 1 year
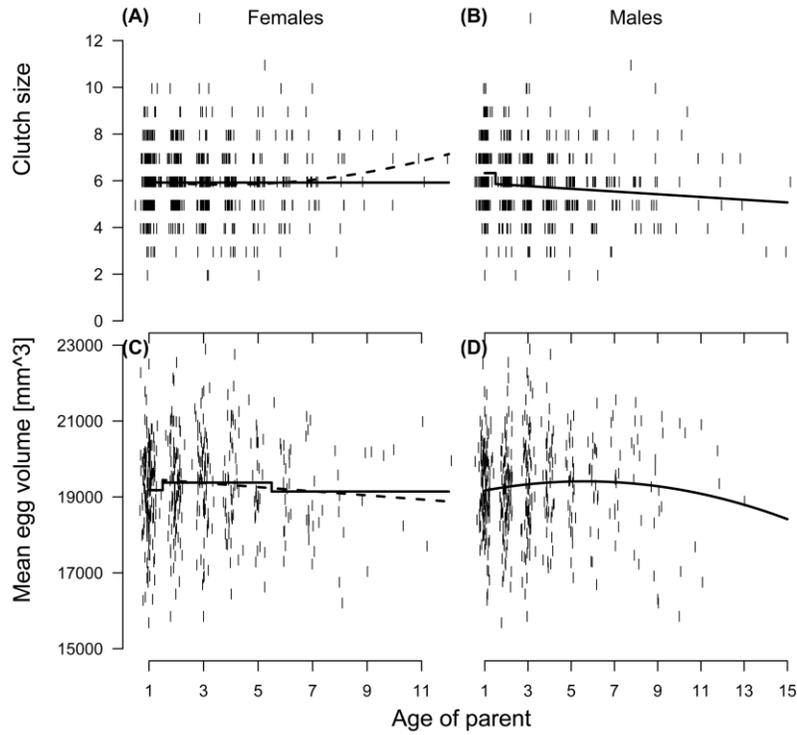
Figure 1: Clutch size (*A*, *B*) and egg volume (*C*, *D*) in relation to age of the female (*A*, *C*) and male parent (*B*, *D*). All observations are plotted with a small random offset to facilitate interpretation. The solid and dashed lines show predictions of the best and second-best (in cases where model selection resulted in a competing model with ΔAICc < 1) models, respectively. The model-averaged (across different random effects; see "Methods") equations for the best-fitting models were *A*, $5.92(\pm 0.14$; 95% confidence interval; *solid line*) and $6.09(\pm 0.32) - 0.14(\pm 0.18) \times \text{age} + 0.02(\pm 0.02) \times \text{age}^2$ (*dashed line*); *B*, age class 1: $6.33(\pm 0.30)$, other ages: $5.94(\pm 0.30) - 0.06(\pm 0.06) \times \text{age}$; *C*, egg volume: age class 1: $19{,}177(\pm 174)$, age class 2: $19{,}377(\pm 160)$, age class 3: $19{,}141(\pm 264)$ (*solid line*), and age class 1: $19{,}182(\pm 196)$, other ages: $19{,}529(\pm 246) - 54(\pm 54) \times \text{age}$ (*dashed line*); *D*, $19{,}052(\pm 226) + 127(\pm 98) \times \text{age} - 11(\pm 10) \times \text{age}^2$.

to estimate the sensitivities of the stochastic population growth rate ($\log \lambda_s$) to changes in the fitness components (Caswell 2001). These sensitivities are equivalent to selection gradients (Lande 1982; Van Tienderen 2000). The three stages were yearlings, second-year birds that had not reproduced, and adults; the number of individuals in each age class at time t is given by the vector $\mathbf{n}_t$. The transition matrix $\mathbf{A}_t$ is based on females and describes how the population vector changes through time, that is, $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$. The transition matrix at time t is parameterized with 11 fitness components: j, juvenile survival rate; y, yearling survival rate; a, adult survival rate; $F1y$, number of fledglings produced by 1-year-old owls in their first breeding attempt; $F2y$, number of fledglings produced by 1-year-old owls in their second breeding attempt; $F1$, number of fledglings produced by adult owls in their first breeding attempt; $F2$, number of fledglings produced by adult owls in their second breeding attempt; pj, probability that a 1-year-old owl conducts a second brood; p, probability that an adult owl conducts a second brood; $\alpha 1$, probability that

an owl starts to reproduce when 1 year old; and $\alpha 2$, probability that an owl starts to reproduce when 2 years old:

$$\mathbf{A}_t =$$

$$\begin{bmatrix} \alpha 1_t \left(\dfrac{F1y_t + pj_t F2y}{2} \right) j_t & \alpha 2_t \left(\dfrac{F1_t + p_t F2_t}{2} \right) j_t & \left(\dfrac{F1_t + p_t F2_t}{2} \right) j_t \\ (1 - \alpha 1_t) y_t & 0 & 0 \\ \alpha 1_t y_t & a_t & a_t \end{bmatrix}.$$

$$(1)$$

We parameterized matrix $\mathbf{A}_t$ with the shrunken (corrected for sampling variance) estimates of the fitness components and used simulations to estimate the sensitivity of λ_s to changes in each fitness component (Morris and Doak 2002). Some of the juveniles and a few older birds emigrated from our study area (Altwegg et al. 2003), and the estimated apparent survival rates therefore underes-
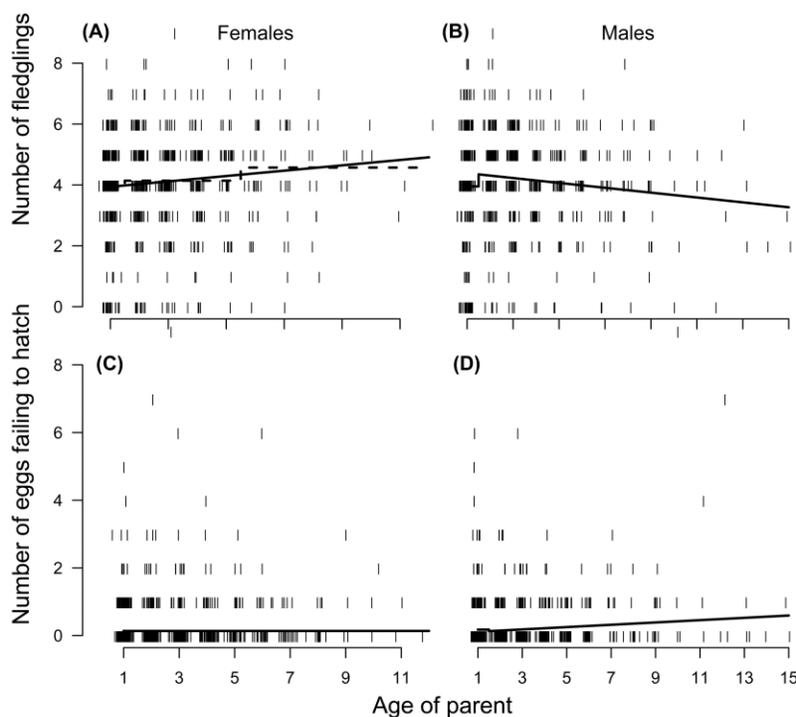
Figure 2: Number of fledglings per nest (*A*, *B*) and number of eggs failing to hatch (*C*, *D*) in relation to age of the female (*A*, *C*) and male parent (*B*, *D*). The solid and dashed lines show predictions of the best and second-best (in cases where model selection resulted in a competing model with ΔAICc < 1) models, respectively. *A*, 3.85(± 0.30; 95% confidence interval) + 0.09(± 0.06) × age (*solid line*), and age class 1: 3.89(± 0.32), age class 2: 4.14(± 0.30), age class 3: 4.57(± 0.48) + 0.09(± 0.06) × age (*dashed line*). *B*, age class 1: 3.95(± 0.36), other ages: 4.45(± 0.36) − 0.07(± 0.06) × age. *C*, *D*, Generalized linear mixed models with a log link function and Poisson-distributed errors: *C*, −2.0(± 0.44) + 0.36(± 0.42) × age and *D*, age class 1: −1.74(± 0.42), other ages: −2.21(± 0.54) + 0.36(± 0.42) × age. These equations are on the log scale. See figure 1 for additional details.

timated true survival. True survival estimates are needed in the sensitivity analysis; otherwise, the population growth rate (fitness) is underestimated. We obtained true survival rates by including data on owls recovered dead and duplicated the analysis of Altwegg et al. (2003), using data collected up to the end of February 2005.

First, we created matrix $\mathbf{A}_t$ by randomly selecting one of the 14 study years with probability 1/14 and by using the estimated fitness components of this year in the transition matrix. By doing so, we retained the correlation structure among fitness components. There were no significant temporal autocorrelations in any of the fitness components, and we therefore did not consider such correlations, despite their potential importance in other cases (Tuljapurkar and Haridas 2006). We started the simulations with a population vector of $\mathbf{n}_0 = 1$. This vector was left-multiplied 1,010,000 times by $\mathbf{A}_t$. After discarding the first 10,000 steps to eliminate transient dynamics, we calculated the stochastic population growth rate from total population size N as

$$\log \hat{\lambda}_s = \frac{1}{1,000,000} \sum_{i=10,001}^{1,010,000} \log\left(\frac{N_{i+1}}{N_i}\right). \tag{2}$$

At the next step, we changed the mean of each fitness component by 0.01 (note that the variance of the fitness component remains unchanged) and repeated the above step to calculate the altered stochastic population growth rate ($\log \hat{\lambda}_s^{\text{alt}}$). While doing so, we retained exactly the same sequence of the 1,010,000 different environments. The sensitivity of the stochastic population growth rate to changes in the fitness component a_i was then calculated as

$$S(a_i) = \frac{\hat{\lambda}_s^{\text{alt}} - \hat{\lambda}_s}{0.01}. \tag{3}$$

These steps were repeated for each of the 11 fitness components. In addition, we repeated the analysis, but this time we did not retain the correlation structure among fitness components. Comparing the results of the two ap-

Table 2: Temporal variance of fitness components in a Swiss barn owl population

Fitness component	Mean	SD	95% CI for SD	CV	P_{max}
Clutch size	5.972	.306	.174–.540	.0513	
Egg volume (mm^3)	19,279	32.442	.0004–2,478,644	.0017	
Number of fledglings	4.008	.324	.178–.589	.0809	
Eggs failing to hatch	−.9	.016	<.0001–1,615,091	.0513	
Probability of producing second clutch	−3.149	2.173	1.259–3.751		.0960
Juvenile survival: females[a]	.041	.018	.0002–.040		.0078
Juvenile survival: males	.074	.038	.021–.073		.0213
Yearling survival: females[a]	.458	.116	.068–.214		.0543
Yearling survival: males	.578	.116	.072–.206		.0552
Adult survival: females[a]	.658	.108	.067–.189		.0514
Adult survival: males	.720	.097	.061–.170		.0468
Proportion breeding as yearlings	.693	.275	.193–.460		.356

Note: These estimates show among-year variance components only and are thus not affected by sampling variance. The table shows estimated mean, standard deviation (SD), 95% confidence interval (CI) for the SD, and coefficient of variation (CV). To compare the variation in traits measured on the [0, 1] scale, we computed the proportion of the maximum possible variance (P_{max}) as $SD^2/mean \times (1 - mean)$; see Morris and Doak (2004). Note that variation is not comparable between fitness components measured as rates and those measured on a scale without upper limit. The estimates for the probability of producing a second clutch are on the logit scale, and those for the number of eggs failing to hatch are on the logarithmic scale, but P_{max} and CV were calculated from back-transformed estimates.

[a] For the population matrix model, we used true instead of local survival rates, with means of 0.180 (juveniles), 0.543 (yearlings), and 0.768 (adults). The difference between true and local survival rate is due to emigration from the study area, which was highest in juveniles (Altwegg et al. 2003).

proaches, we assessed the effect of the correlation among the fitness components on the sensitivities. Finally, we compared these estimates to a deterministic analysis, using mean values for each fitness component (Caswell 2001).

Results

Fitness Components

Age-Specific Reproduction. Model selection showed that clutch size did not vary with female age (table 1; fig. 1*A*). On the other hand, clutch size decreased with increasing male age (table 1; fig. 1*B*). Mean egg volume was lower in young and old individuals of both sexes, compared to individuals aged 2–5 years (table 1; fig. 1*C*, 1*D*). Model selection further showed that the number of fledglings produced per nest increased with female age and was higher for males aged 2–5, compared to yearling or old males (table 1; fig. 2*A*, 2*B*). The number of eggs failing to hatch was independent of female age (table 1; fig. 2*C*), increased with male age, and was slightly but significantly increased for yearling males, compared to 2-year-old ones (table 1; fig. 2*D*). These analyses were performed for both parents separately in order to keep the number of models small. However, there was a loose association between the ages of both parents ($r = 0.24$, $n = 596$ pairs), and so we examined age-specific reproduction in each sex while keeping the best-supported age effects for the other sex in the models. Model selection resulted in the same rankings of all models for both sexes as in the separate analyses.

Of the random effects, female identity explained the most variation in clutch size (SD = 0.67, residual SD = 1.23) and egg volume (SD = 1,100.1, residual SD = 511.2), whereas year explained the most variation in the number of fledglings (SD = 0.32, residual SD = 1.65), and male identity explained the most variation in the number of eggs failing to hatch (SD = 1.01, residual SD = 0.84).

The number of fledglings was slightly more variable among years than clutch size or number of eggs failing to hatch, and egg volume was least variable (table 2). The age-specific pattern stayed constant over time for both sexes: models 7 and 8 (table 1), which allow for an interaction between age-specific production of fledglings and year, were poorly supported by the data. Similarly, we found no evidence for an interaction between age and reproduction in the other traits (results not shown).

Probability of Producing a Second Clutch. The probability of producing a second clutch varied among the years of our study (table 2) and increased with the age of both parents (by a factor of 1.20 [95% confidence interval (CI) = 1.02–1.42] per year for females, $P = .024$, and 1.13 [95% CI = 1.03–1.23] per year for males, $P = .004$). The age effects varied only slightly among years (SD = 0.18, 95% CI = 0.07–0.46 for females and SD = 0.10, 95% CI = 0.04–0.27 for males), showing that older individuals consistently had a higher probability of producing a second clutch than younger ones.

Table 3: Results of model selection: age-specific survival of barn owls in the Payerne region between 1990 and 2004

Model	K	Deviance	AICc	ΔAICc	w
1. Constant	18	1,012.965	3,273.321	39.762	.0000
2. Linear	19	999.708	3,262.083	28.525	.0000
3. Linear + quadratic	20	986.202	3,250.598	17.039	.0001
4. Three age classes: 0, 1, 2+	19	984.871	3,247.246	13.688	.0004
5. Four age classes: 0, 1, 2–5, 6+	20	984.719	3,249.114	15.556	.0002
6. Five age classes: 0, 1, 2–5, 6–8, 9+	21	982.428	3,248.845	15.286	.0002
7. All ages up to 12 years different	29	977.4685	3,260.092	26.534	.0000
8. As 4, no sex effect	18	1,001.610	3,261.966	28.407	.0000
9. As 4, age × sex	21	982.946	3,249.363	15.804	.0001
10. As 4, age × time: 0 vs. older	**32**	**944.840**	**3,233.559**	**.000**	**.4010**
11. As 4, age × time	45	935.216	3,250.452	16.893	.0001
12. As 5, age × time	59	922.115	3,266.106	32.547	.0000
13. As 6, age × time	73	906.353	3,279.304	45.746	.0000
14. As 10, recapture: linear	32	944.8737	3,233.592	.034	.3944
15. As 10, recapture: linear + quadratic	33	944.4323	3,235.184	1.626	.1779
16. As 10, recapture: all ages different	43	938.3575	3,249.503	15.944	.0001
17. As 10, recapture: age + time	45	923.8358	3,239.072	5.513	.0255
18. As 10, recapture: age × time	58	911.1407	3,253.07	19.512	.0000

Note: We first evaluated seven different representations for the age effects (models 1–7) and then examined whether the age-specific patterns in survival differed between the sexes (model 9) or varied over time (models 10–13). The best-supported model is shown in boldface. All models except 8 allowed for differing survival between the sexes, and all models allowed for variation in survival over time. Models 1–13 allow for lower recapture rates of juveniles (age 0), whereas models 14–18 explore different age effects on the recapture rate, using the best-supported survival model. The models are capture-mark-recapture models fitted by maximum likelihood using the program MARK. Deviance is the difference in $-2 \log$ (likelihood) between the current and the saturated model, the saturated model being the one with the number of parameters equal to the sample size. See table 1 note for more details, including definitions of K and AICc.

Age-Specific Survival and Recapture. Model selection favored model 10 (table 3), whose age structure allowed for different survival rates among three age classes, juveniles (0 years old), yearlings (1 year old), and adults (fig. 3). Furthermore, juvenile survival varied over time independently of the other age classes (fig. 4). Allowing survival of other age classes to vary independently resulted in a worse model (models 11–13, table 3), showing that these other age classes varied synchronously over time (fig. 4). Males survived better than females (model 8, in which omitting the sex effect was poorly supported; table 3), but the age pattern in survival was similar in both sexes (model 9 was poorly supported; table 3). Juvenile survival varied less among years than yearling and adult survival (table 2). We found no evidence for reduced survival at old ages and thus no survival senescence. Our failure to find senescence could be a result of poor-quality individuals dying early, which would lead to an increase in average intrinsic fitness with age. Toward testing this hypothesis, we examined whether survival depended on a measure of individual quality, clutch size. We used the estimated individual clutch size predicted from the mixed model with male and female identity as random effects and entered it as an individual covariate into the survival analysis. This measure of individual quality did not explain a significant amount of variation in survival (Δdeviance = 0.14, df = 1, P = .71), and variation among individuals in the clutch sizes they produced was thus unrelated to subsequent survival.

We further examined whether years with high survival led to greater reproductive success in terms of number of fledglings produced, by modeling survival as a function of estimated year effect on the number of fledglings from the analysis of reproduction (above). However, this model was poorly supported by the data (AICc = 3,257.0, K = 19, ΔAICc = 23.4), showing that reproduction and survival were uncorrelated over time.

Model selection was essentially tied for models 10 and 14 (table 3), showing that the recapture rate either was lower for juveniles and then constant with age (model 10) or kept increasing over the entire life span (model 14). The data did not allow a distinction between these two hypotheses because the difference in AICc between these two models was small. The maximum-likelihood estimates for the recapture rates were 0.70 (CI = 0.59–0.78) for juveniles and 0.84 (CI = 0.80–0.87) for adults. However, there was no evidence for temporal variation in recapture (model 17) or for an interaction between time and age on recapture (model 18). As we had access only to breeding birds, of which most were captured, the recapture rates
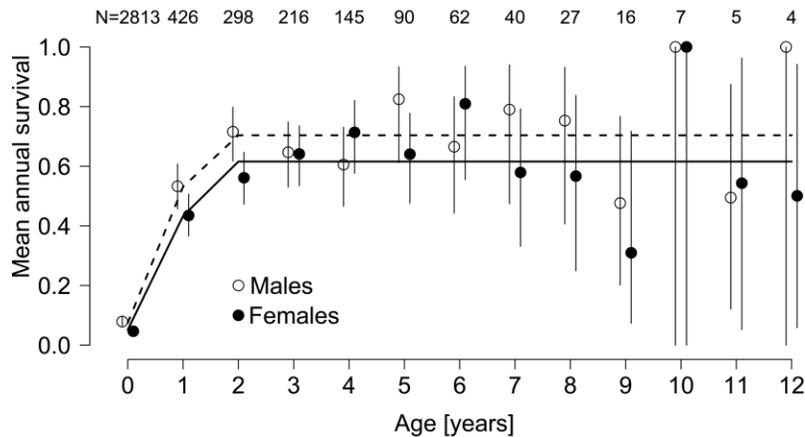
Figure 3: Age-specific local survival of female and male barn owls in western Switzerland. The symbols show survival rates obtained from the most flexible model with respect to age and sex but ignoring variation among years. The lines show the best-fitting models, averaged over the years of our study. Vertical lines show 95% confidence intervals. The sample sizes given at the top are numbers of individuals known to be alive at each age. Two males are known to have survived to age 15.

can give information about the probability of breeding in a given year (Schaub et al. 2004). It therefore appears that the breeding probability of adults was constant across time and higher than in 1-year-old birds (see also below), unless such variation was masked by variation in the probability of detecting breeding pairs, which seems unlikely.

Age-Specific Probability of First Reproduction. The best-supported model suggested that all females bred by age 5 years and that all males bred by age 2 years (fig. 5; model 1, table 4). However, models 2 and 3, corresponding respectively to the hypotheses that all females bred by age 4 and all males bred by age 3, were also well supported by the data. We could not, therefore, clearly distinguish between these hypotheses, but we considered the model with the fewest parameters (model 2, table 4) for further modeling.

In the next step, we examined temporal variation in the age of first reproduction and whether the probability of reproducing as a yearling depended on juvenile survival. Model selection did not favor the model allowing for unconstrained temporal variation in age at first reproduction (models 5–7, table 5). Even so, this model showed substantial among-year variation in the proportion of owls breeding as yearlings, after correction for sampling variance (table 2). Part of this variation is because we did not observe any recruits in 1991 of nestlings ringed in 1990, and the probability of starting to reproduce at age 1 for this year was thus estimated to be 0. Excluding 1991 yielded a slightly smaller estimate of variability for this trait (SD = 0.168, 95% CI = 0.070–0.365, P_{max} = 0.191). There was strong evidence of positive covariation between

juvenile survival and probability of reproducing as a yearling (model 1; table 5). Thus, in years with high juvenile survival, more barn owls started to reproduce as yearlings than in years with low juvenile survival.
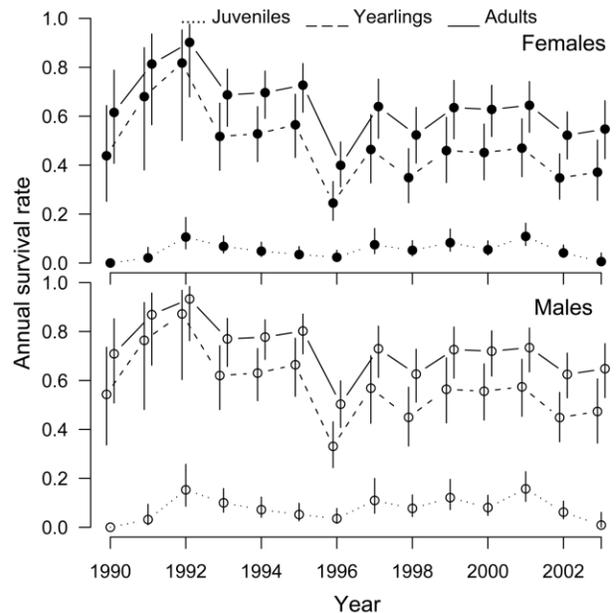
Figure 4: Annual local survival rate of three age classes in a Swiss barn owl population. The error bars show 95% confidence intervals. The estimates are from model 10, table 3.
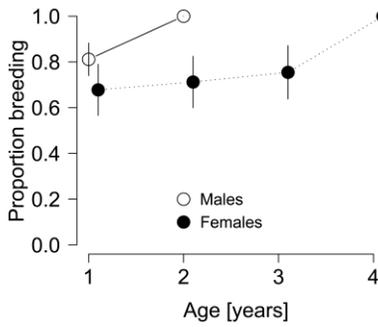
Figure 5: Cumulative probability of starting breeding for young barn owls in western Switzerland. The estimates are from model 2, table 4. Error bars show standard error.

Stochastic Sensitivities

Retaining the observed correlations between fitness components, we estimated that the population increased by 1.84% each year ($\log \lambda_s = 0.0184$). Without these correlations, the stochastic growth rate was 1.79%, and the deterministic growth rate using mean values for all fitness components was 2.72%. The population growth rate was clearly more sensitive to changes in survival than to changes in fitness components associated with reproduction (fig. 6). Juvenile survival achieved the highest sensitivity, followed by adult and yearling survival. Among fitness components associated with reproduction, population growth was most sensitive to variation in the probability of starting reproduction at the age of 1 year and of adults producing second broods. Population growth was rela-

tively insensitive to changes in the number of fledglings raised per brood. The correlation among the fitness components had virtually no effect on the sensitivities, and the stochastic estimates were almost identical to the deterministic ones (fig. 6). Sensitivities are equivalent to selection gradients (Van Tienderen 2000). Apparently, temporal variation in these fitness components had little effect on the strength of selection.

Discussion

Using mixed-effects models and capture-mark-recapture methods, we examined age-specific reproduction and survival in Swiss barn owls. This large data set enabled us to estimate these fitness components for each sex separately and with high precision even for old ages. The 15-year study period permitted estimates of temporal variance in these fitness components and searches for interactions between age and year in their effects on fitness components. Overall, we found that males had a longer reproductive life span than females. Females tended to start reproduction later (fig. 5) and had lower survival rates (fig. 3). We found that most fitness components were variable over the years of our study. Yet this variability appeared unimportant for the strength of selection on these fitness components.

Age Effects

Survival, the number of fledglings produced per brood, and the probability of producing a second clutch were

Table 4: Results of model selection: age of full reproduction in male and female barn owls

| | Age at full breeding (years) | | | | | | |
Model	Males	Females	K	Deviance	AICc	ΔAICc	w
1	**2**	**5**	**36**	**817.406**	**3,224.229**	**.00**	**.237**
2	2	4	35	819.988	3,224.775	.55	.181
3	3	5	37	816.264	3,225.125	.90	.152
4	4	5	38	814.762	3,225.662	1.43	.116
5	3	4	36	818.940	3,225.763	1.53	.110
6	4	4	37	817.515	3,226.376	2.15	.081
7	5	5	39	814.762	3,227.702	3.47	.041
8	5	4	38	817.515	3,228.415	4.19	.029

Note: The structure of the underlying model for survival is the same as that of model 10 in table 3, except that the recapture probability is kept constant with age. The best-supported model is shown in boldface. We previously found a lower recapture rate in yearlings because not all of them were breeding yet and so could not be captured. In the multistate models used here, only the breeding individuals can be recaptured, and thus recapture rate need not be age dependent. We tested all combinations of age of full reproduction up to 5 years in males and females (25 models), but we present only the eight best models here. See table 3 note for more details and table 1 for definitions of K and AICc.

Table 5: Results of model selection: temporal variation in the probability of starting reproduction at age 1 year, given our previous result that all females reproduce by age 4 and all males reproduce by age 2

Model	Source of effect on breeding at age 1	K	Deviance	AICc	ΔAICc	w_i
1	**Juvenile survival**	**34**	**816.316**	**3,219.067**	**.00**	**.587**
2	Sex + juvenile survival	35	815.455	3,220.242	1.18	.326
3	Constant	34	821.172	3,223.923	4.86	.052
4	Sex	35	819.988	3,224.775	5.71	.034
5	Year	44	808.023	3,231.178	12.11	.001
6	Sex + year	45	807.982	3,233.093	14.03	.001
7	Sex × year	58	796.616	3,248.512	29.44	.000

Note: We examined the effects of year, sex, and juvenile survival on the probability of starting breeding at age 1 year. The best-supported model is shown in boldface. Note that model 4 is the same as model 2 in table 4. See table 3 note for more details and table 1 for definitions of K and AICc.

lower for yearling female and male barn owls than for 2-year-old individuals. This is consistent with earlier studies showing lower success of young birds (reviewed by Sæther 1990) and has been attributed to lower experience, lower effort, or a higher proportion of lower-quality individuals in this age group (Wiebe and Martin 1998). We cannot distinguish between these hypotheses. However, we found no evidence that individuals with low reproductive success die earlier, as may be expected if there were large heterogeneity in individual quality. This result shows that heterogeneity in reproduction was not directly related to heterogeneity in survival. It would be desirable to estimate heterogeneity in survival directly (Hougaard 1991), but methods are currently lacking to do this in the face of imperfect detection (Cam et al. 2002; Cooch et al. 2002).

Beyond 2 years of age, the number of fledglings produced increased with female age and declined with male age (fig. 2A, 2B). This decline with male age was partly due to a decrease in clutch size and an increase in the number of eggs failing to hatch with increasing age of the father. Clutch size is potentially controlled by the female, and we thus expected it to be related to female charac-

teristics rather than those of the male partner. This was true for variation among individuals because female identity was the random effect explaining the most variation in clutch size. The dependence of clutch size on male age is thus unexpected at first glance. In barn owls, however, females start incubating and are fed by the male while completing the clutch, and clutch size would thus directly reflect the ability of the male to feed his mate (Epple 1985; Durant et al. 2004). Furthermore, females of several bird species are known to adjust clutch size to characteristics of their mates (Petrie and Williams 1993; Michl et al. 2005). Interestingly, in our study, yearling males had larger clutches than 2-year-old ones. Yet they produced fewer fledglings. The only component of reproduction that decreased at old age in both sexes was egg volume (fig. 1C, 1D). However, the relationship between egg size and offspring performance is not clear (Bize et al. 2002; Christians 2002; Krist et al. 2004); this may therefore not be indicative of a senescent decline in fitness. On the other hand, the number of eggs that failed to hatch increased with male age, and this may be due to lower fertility of older males.
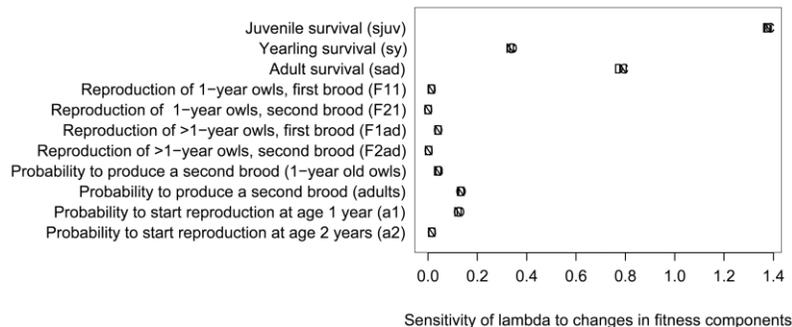
Figure 6: Sensitivity of the population growth rate ($\log \lambda$ and $\log \lambda_s$) to changes in fitness components. The symbols show estimates for the stochastic analyses where correlations between fitness components were retained (*C*) or where these correlations were not retained (*N*) and the deterministic analysis (*D*).

This is the strongest evidence for senescent decline of fitness components in our study population.

Senescence is a decrease in reproductive value with age (Partridge and Barton 1996), and a decrease in either survival, reproduction, or both at late age is well documented from natural populations (Promislow 1991; Ricklefs 1998; Loison et al. 1999; Bondurianski and Brassil 2002; McElligott et al. 2002). In this sense, we did not find strong evidence for senescence in our study population. The decline in reproduction with male age was accompanied by an increased probability of producing second clutches. This may indicate a change in allocation rather than true senescence among males.

Life-history theory predicts an earlier onset of senescence for organisms with higher adult mortality (Charlesworth 1994; Stearns et al. 2000), and a recent review confirmed this prediction for birds (Bennett and Owens 2002). Bennett and Owens's comparative data showed that for birds with 30%–40% adult mortality, as we found here for the barn owl, fecundity senescence starts at age 5–7 years, on average. Our failure to find evidence for senescence was thus not due to small sample sizes among old birds. Barn owls in our study area may, in fact, senesce later than expected from adult mortality. Recent models no longer predict a clear relationship between adult mortality and onset of senescence if interactions between intrinsic and extrinsic mortality occur (Williams and Day 2003; see also Reznick et al. 2004). One possibility is that their lifestyle, aerial hunting at night, exposes barn owls to an environment where even slightly degenerative changes greatly reduce survival, and therefore selection against senescent decline remains strong even at old ages (Williams et al. 2006).

Temporal Variation in Fitness Components

Comparing variability of fitness components is not straightforward. Fitness components that are measured as rates have a maximum possible variance determined by their mean, and we therefore scale these estimates by their theoretical maximum variance (Morris and Doak 2004). Among these fitness components, the probability of breeding at age 1 was the most variable, followed by the probability of producing second clutches (table 2). Among the survival rates, adult and yearling survival was more variable than juvenile survival. Our estimates for temporal variance in survival were comparable to those found for other birds where random-effects methodology was used (Franklin et al. 2002; Loison et al. 2002). Several studies showed that those fitness components that are most closely linked to overall fitness and population dynamics are the least variable ones (Pfister 1998; Sæther and Bakke 2000; Ehrlén 2003; Gaillard and Yoccoz 2003; Morris and Doak

2004). In agreement with these studies, we found that the population growth rate was more sensitive to changes in the less variable survival rates than to changes in the more variable reproductive traits (fig. 6).

The remaining components of reproduction (clutch size, egg volume, number of fledglings, and number of eggs failing to hatch) do not have a theoretical upper limit to their variability, and we compared them by their coefficients of variation. The number of fledglings produced was slightly more variable than clutch size (table 2). For the other two traits, our estimates are imprecise, but the temporal variability in these traits was probably low. Our analysis showed that female identity explained much more of the variation in clutch size and egg volume than time and that male identity accounted for a large proportion of the variation in the number of eggs failing to hatch.

Interaction between Age and Time

The age effects on survival and reproduction were consistent over time in our study, and a year with poor survival or reproduction was thus generally a poor year for all age classes (fig. 4). For survival, the only exception was juveniles, who suffered from low survival in some years that were good for yearlings or adults. This result is not affected by variation in juvenile emigration, because we found the same pattern in an earlier study accounting for variation in emigration rates (Altwegg et al. 2003). Interestingly, the proportion of owls starting to breed as yearlings was higher after years with good juvenile survival. In general, however, the temporal variation in reproduction was unrelated to the variation in survival. These results thus suggest three suites of fitness components that vary relatively independently: reproduction (most variable), juvenile survival, and survival of older age classes (least variable). The effect of environmental variation on population dynamics thus appears to be "buffered" to some degree because the environment affected different fitness components in different ways. A longer-term study suggested, however, that fitness components can become more correlated during extreme environmental events, such as long periods of snow cover, when all parts of a population are affected equally (Altwegg et al. 2006).

Temporal Variation and Selection

Even though we found considerable temporal variation and covariation in and among most of the fitness components we examined, the effect of this variation on fitness and long-term population dynamics was relatively small. Correlations between fitness components had only small effects on the population growth rate and its sensitivity to variation in each component (fig. 6), and the sensitivities

differed little between the stochastic and deterministic time-invariant analyses. The sensitivities are equivalent to selection gradients (Lande 1982), and we therefore found no evidence that temporal variation changed the strength of selection. However, the deterministic analysis yielded a substantially higher (by 50%) estimate of the population growth rate than the stochastic analyses, thus showing that temporal variation in fitness components decreased overall fitness. This is expected because population growth rate is essentially a geometric mean, and variance decreases its magnitude. As in our study, Benton et al. (1995) found that environmental variation affected selection and population dynamics little in a red deer population. The shorter the life span of the species, the more environmental variation affects selection (Benton and Grant 1996) and selects for iteroparity (Orzack 1997). Benton et al. (1995) therefore explained the small effect of variation on their red deer population by the fact that these animals already live long (mean survival rate >0.9 for most age classes) and are very iteroparous. Our results suggest that the same may apply for species with relatively short life spans.

Acknowledgments

Literature Cited

Altwegg, R., A. Roulin, M. Kestenholz, and L. Jenni. 2003. Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*. Journal of Animal Ecology 72:391–399.

Altwegg, R., S. Dummermuth, B. R. Anholt, and T. Flatt. 2005. Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. Oikos 110:55–66.

Altwegg, R., A. Roulin, M. Kestenholz, and L. Jenni. 2006. Demographic effects of extreme winter weather on the barn owl. Oecologia (Berlin) 149:44–51.

Bennett, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds. Oxford University Press, Oxford.

Benton, T. G., and A. Grant. 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. American Naturalist 147:115–139.

———. 1999. Optimal reproductive effort in stochastic, density-dependent environments. Evolution 53:677–688.

Benton, T. G., A. Grant, and T. H. Clutton-Brock. 1995. Does environmental stochasticity matter? analysis of red deer life-histories on Rum. Evolutionary Ecology 9:559–574.

Bize, P., A. Roulin, and H. Richner. 2002. Covariation between egg size and rearing condition determines offspring quality: an experiment with the alpine swift. Oecologia (Berlin) 132:231–234.

Bonduriansky, R., and C. E. Brassil. 2002. Rapid and costly ageing in wild male flies. Nature 420:377.

Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association 88:9–25.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

———. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. Journal of Applied Statistics 29:245–264.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monographs 5:1–437.

Cam, E., W. A. Link, E. G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:96–105.

Caswell, H. 2001. Matrix population models. Sinauer, Sunderland, MA.

Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge.

Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews 77:1–26.

Clobert, J., J. D. Lebreton, D. Allaine, and J. M. Gaillard. 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. II. Longitudinal models. Biometrics 50:375–387.

Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1285–1298.

Cooch, E. G., and R. E. Ricklefs. 1994. Do variable environments significantly influence optimal reproductive effort in birds? Oikos 69:447–459.

Cooch, E. G., E. Cam, and W. Link. 2002. Occam's shadow: levels of analysis in evolutionary ecology: where to next? Journal of Applied Statistics 29:19–48.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, et al. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Coulson, T., J.-M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74:789–801.

Doak, D. F., W. F. Morris, C. Pfister, B. E. Kendall, and E. M. Bruna. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. American Naturalist 166:E14–E21.

Durant, J. M., J. P. Gendner, and Y. Handrich. 2004. Should I brood or should I hunt: a female barn owl's dilemma. Canadian Journal of Zoology 82:1011–1016.

Ehrlén, J. 2003. Fitness components versus total demographic effects: evaluating herbivore impacts on a perennial herb. American Naturalist 162:796–810.

Epple, W. 1985. Ethologische Anpassungen im Fortpflanzungssystem

der Schleiereule (*Tyto alba* Scop., 1769). Ökologie der Vögel 7:1–95.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds: hypotheses and tests. Trends in Ecology & Evolution 10:374–378.

Franklin, A. B., D. R. Anderson, and K. P. Burnham. 2002. Estimation of long-term trends and variation in avian survival probabilities using random effects models. Journal of Applied Statistics 29:267–287.

Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. American Naturalist 111:1010–1014.

Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. Ecology 79:2531–2538.

Hougaard, P. 1991. Modelling heterogeneity in survival data. Journal of Applied Probability 28:695–701.

Krist, M., V. Remes, L. Uvirova, P. Nadvornik, and S. Bures. 2004. Egg size and offspring performance in the collared flycatcher (*Ficedula albicollis*): a within-clutch approach. Oecologia (Berlin) 140:52–60.

Laaksonen, T., E. Korpimäki, and H. Hakkarainen. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. Journal of Animal Ecology 71:23–31.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63:607–615.

Lande, R., S. Engen, and B.-E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lebreton, J. D., J. E. Hines, R. Pradel, J. D. Nichols, and J. A. Spendelow. 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. Oikos 101:253–264.

Link, W. A., and J. D. Nichols. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. Oikos 69:539–544.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, NC.

Loison, A., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and J.-M. Julien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539–2554.

Loison, A., B.-E. Sæther, K. Jerstad, and O. W. Røstad. 2002. Disentangling the sources of variation in the survival of the European dipper. Journal of Applied Statistics 29:289–304.

Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist 35:340–348.

McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). Proceedings of the Royal Society B: Biological Sciences 269:1129–1137.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define "fitness" for general ecological scenarios? Trends in Ecology & Evolution 7:198–202.

Michl, G., J. Torok, P. Peczely, L. Z. Garamszegi, and H. Schwabl. 2005. Female collared flycatchers adjust yolk testosterone to male age, but not to attractiveness. Behavioral Ecology 16:383–388.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, MA.

———. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contribution to fitness. American Naturalist 163:579–590.

Nichols, J. D., W. L. Kendall, J. E. Hines, and J. A. Spendelow. 2004. Estimation of sex-specific survival from capture-recapture data when sex is not always known. Ecology 85:3192–3201.

Orzack, S. H. 1997. Life-history evolution and extinction. Pages 273–302 *in* S. Tuljapurkar and H. Caswell, eds. Structured-population models in marine, terrestrial, and freshwater systems. Chapman & Hall, New York.

Orzack, S. H., and S. Tuljapurkar. 2001. Reproductive effort in variable environments, or environmental variation is for the birds. Ecology 82:2659–2665.

Partridge, L., and N. H. Barton. 1996. On measuring the rate of ageing. Proceedings of the Royal Society B: Biological Sciences 263:1365–1371.

Petrie, M., and A. Williams. 1993. Peahens lay more eggs for peacocks with larger trains. Proceedings of the Royal Society B: Biological Sciences 251:127–131.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences of the USA 95:213–218.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York.

Pradel, R., and J. D. Lebreton. 1999. Comparison of different approaches to the study of local recruitment of breeders. Bird Study 46(suppl.):74–81.

Promislow, D. E. L. 1991. Senescence in natural populations of mammals: a comparative study. Evolution 45:1869–1887.

R Development Core Team. 2003. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reznick, D. N., M. J. Bryant, D. Roff, C. K. Ghalambor, and D. E. Ghalambor. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. Nature 431:1095–1099.

Ricklefs, R. E. 1998. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. American Naturalist 152:24–44.

Roulin, A., A.-L. Ducrest, and C. Dijkstra. 1999. Effect of brood size manipulations on parents and offspring in the barn owl *Tyto alba*. Ardea 87:91–100.

Roulin, A., W. Muller, L. Sasvari, C. Dijkstra, A. L. Ducrest, C. Riols, M. Wink, et al. 2004. Extra-pair paternity, testes size and testosterone level in relation to colour polymorphism in the barn owl *Tyto alba*. Journal of Avian Biology 35:492–500.

Sæther, B.-E. 1990. Age-specific variation in reproductive performance of birds. Pages 251-283 *in* D. M. Power, ed. Current ornithology. Plenum, New York.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004. Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology 85:2107–2113.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

———. 2000. Daniel Bernoulli (1738): evolution and economics under risk. Journal of Biosciences 25:221–228.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893–913.

Stearns, S. C., M. Ackermann, M. Doebeli, and M. Kaiser. 2000. Experimental evolution of aging, growth, and reproduction in fruitflies. Proceedings of the National Academy of Sciences of the USA 97:3309–3313.

Stewart-Oaten, A., W. W. Murdoch, and S. J. Walde. 1995. Estimation of temporal variability in populations. American Naturalist 146: 519–535.

Taylor, I. R. 1994. Barn owls: predator-prey relationships and conservation. Cambridge University Press, Cambridge.

Tuljapurkar, S. 1982. Population dynamics in variable environments. III. Evolutionary dynamics of *r*-selection. Theoretical Population Biology 21:141–165.

———. 1989. An uncertain life: demography in random environments. Theoretical Population Biology 35:227–294.

Tuljapurkar, S., and C. V. Haridas. 2006. Temporal autocorrelation and stochastic population growth. Ecology Letters 9:324–334.

Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. American Naturalist 162:489–502.

Van Tienderen, P. H. 2000. Elasticities and the link between demographic and evolutionary dynamics. Ecology 81:666–679.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(suppl.):120–139.

Wiebe, K. L., and K. Martin. 1998. Age-specific patterns of reproduction in white-tailed and willow ptarmigan *Lagopus leucurus* and *L. lagopus*. Ibis 140:14–24.

Williams, P. D., and T. Day. 2003. Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. Evolution 57:1478–1488.

Williams, P. D., T. Day, Q. Fletcher, and L. Rowe. 2006. The shaping of senescence in the wild. Trends in Ecology & Evolution 21:458–463.