Pattern of variation in avian population growth rates

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A central question in population ecology is to understand why population growth rates differ over time. Here, we describe how the long-term growth of populations is not only influenced by parameters affecting the expected dynamics, for example form of density dependence and specific population growth rate, but is also affected by environmental and demographic stochasticity. Using long-term studies of fluctuations of bird populations, we show an interaction between the stochastic and the deterministic components of the population dynamics: high specific growth rates at small densities r_1 are typically positively correlated with the environmental variance σ_e^2 . Furthermore, θ , a single parameter describing the form of the density regulation in the theta-logistic density-regulation model, is negatively correlated with r_1 . These patterns are in turn correlated with interspecific differences in life-history characteristics. Higher specific growth rates, larger stochastic effects on the population dynamics and stronger density regulation at small densities are found in species with large clutch sizes or high adult mortality rates than in long-lived species. Unfortunately, large uncertainties in parameter estimates, as well as strong stochastic effects on the population dynamics, will often make even short-term population projections unreliable. We illustrate that the concept of population prediction interval can be useful in evaluating the consequences of these uncertainties in the population projections for the choice of management actions.

Keywords: population growth rates; environmental stochasticity; demographic stochasticity; density regulation; population variability; comparative analysis

1. INTRODUCTION

Studies on population growth rates (i.e. how fast population size changes) go back several hundred years, at least to the 16th century when the potential for exponential growth of populations was realized (Caswell 2001). Since then, factors affecting variation in population growth rates have been the major focus for human demography and a major part of population ecology. Although ecologists have dealt with this problem for a long time, surprisingly few generalizations have appeared that allow us to predict variation in population growth rates within and among natural populations. A major reason for this may be difficulties in separating out the relative contribution of density-dependent and density-independent factors on the population growth rate (see reviews in Sinclair 1979; Caughley 1994; Turchin 1995).

The purpose of the present study is to summarize how stochastic effects affect the long-term growth rate of populations with no age structure. We will then extend some recent work (Sæther *et al.* 2002), using data on fluctuations of bird populations, where stochastic factors as well as parameters characterizing the expected dynamics are being separately estimated. We suggest many characteristics of avian population dynamics are closely associated to variation in the specific population growth rate because

of the presence of covariation between differences in the expected dynamics and the stochastic component of the fluctuations in population size. Finally, we strongly emphasize that reliable population projections, for example for use in population viability analysis, will not only require estimates and modelling of the expected dynamics as well as the stochastic components, but also assessment of the effects on the predictions of uncertainties in parameter estimates.

2. STOCHASTIC POPULATION GROWTH RATES

To illustrate the importance of stochastic effects on population dynamics, we consider a simple model describing density-independent growth in a random environment $N(t+1) = \lambda(t)N(t)$ (Lewontin & Cohen 1969). Here $N(t)$ is population size in year t , and $\lambda(t)$, the population growth rate in year t , is assumed to have the same probability distribution each year with mean $\bar{\lambda}$ and variance σ_λ^2 . If the population size is sufficiently large to ignore demographic stochasticity, the environmental stochasticity is $\sigma_e^2 = \sigma_\lambda^2 = \text{var}(\Delta N/N|N)$, where ΔN is the change in population size between t and $t+1$. Population ecologists commonly analyse population fluctuations on the natural-log scale (Royama 1992) so that $X(t+1) = X(t) + r(t)$, where $X(t) = \ln N(t)$ and $r(t) = \ln \lambda(t)$. If E denotes the expectation, the growth rate during a period of time t , $(X(t) - X(0))/t$, has mean $s = Er$ and variance $\text{var}(r)/t = \sigma_r^2/t$. For long time intervals the mean slope of the trajectories on log scale all approaches the constant s , which is called the stochastic population growth rate. This leads to the

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Figure 1. Simulation of five populations growing density independently in a random environment, with parameters $r = 0.06$, $\sigma_r^2 = 0.05$ and initial population size $N_0 = 20$. Solid line shows the population growth in a constant environment and the dashed line the expected long-run growth.

approximation $s \approx \ln \bar{\lambda} - \sigma_r^2/2$ and $\sigma_r^2 \approx \sigma_{\lambda}^2/\bar{\lambda}^2 = \sigma_e^2/\bar{\lambda}^2$ for the mean and the variance, respectively (Lande *et al.* 2003). As expected, we see by simulating this model that all sample paths are after some time below the trajectory for the deterministic model (figure 1). Stochastic effects reduce the mean growth rate of a population on the logarithmic scale by *ca.* $\sigma_r^2/2$, compared with one in a constant environment.

Demographic stochasticity is caused by random fluctuations in individual fitness, which are independent among individuals, giving $\text{var}(\Delta N/N|N) = \sigma_e^2 + \sigma_d^2/N$ (Engen *et al.* 1998; Sæther *et al.* 1998), where σ_d^2 is called the demographic variance. It produces a similar reduction in the stochastic growth rate s as the environmental variance σ_e^2 , given by

$$s \approx \ln \bar{\lambda} - \frac{\sigma_e^2}{2} - \frac{\sigma_d^2}{2N} \quad (2.1)$$

(Lande 1998).

We see that at small population sizes demographic variance creates a deterministic decrease in the long-term growth rate in addition to causing random fluctuations in population size so that $\text{var}(\Delta N/N) = \sigma_e^2 N^2 + \sigma_d^2 N$. However, for population sizes of $N \gg \sigma_d^2/\sigma_e^2$ environmental stochasticity constitutes the major contribution to stochastic variation in the rate of population growth.

One of the few general patterns in ecology is the dependence of population growth rates on population size (Turchin 1995). In the density-dependent case, the population growth rate at population size N is $r_N = E(\Delta N/N|N) = E[(\lambda - 1)|N]$ on an absolute scale, and $s_N = E(\Delta \ln N|N) = E(r|N)$ on a logarithmic scale. To quantify the effects of density dependence on the population growth rate we use the theta-logistic model (Gilpin & Ayala 1973),

$$E\left(\frac{\Delta N}{N} \middle| N\right) = r_0 \left[1 - \left(\frac{N}{K} \right)^\theta \right], \quad (2.2a)$$

where r_0 is the mean specific growth rate of the population at $N = 0$, K is the carrying capacity and θ specifies the density regulation. We can also formulate (2.2a) as

Figure 2. The expected change in population size N from time t to $t + 1$, conditioned on N ($E(\Delta N|N)$) as function of relative population size (to the carrying capacity K) for different values of θ in the theta-logistic model. Other parameters are $r_1 = 0.1$ and $K = 100$.

$$E\left(\frac{\Delta N}{N} \middle| N\right) = r_1 \left[1 - \frac{N^\theta - 1}{K^\theta - 1} \right] \quad (2.2b)$$

(Sæther *et al.* 2000), where r_1 is the mean specific growth rate of the population at $N = 1$. We can then describe a wide variety of density regulation functions by varying only one parameter θ (figure 2). For instance, for $\theta = 0$ we get the Gompertz form of density regulation, whereas $\theta = 1$ gives the logistic model (figure 2).

The dynamic consequences of variation in r_1 are strongly dependent on the density regulation function (figure 3a,b). For a given r_1 , the variability decreases with increasing θ . Similarly, an increase in r_1 also reduces population variability if θ is kept constant. This is due to the inverse of the rate of return to the equilibrium at the carrying capacity being

$$\gamma = r_0 \theta = r_1 \theta / (1 - K^{-\theta}). \quad (2.3)$$

Thus, for a given θ , γ will increase with r_1 and the population will return to equilibrium more rapidly (May 1981).

One advantage of the theta-logistic model is that it has relatively well understood statistical properties (Gilpin *et al.* 1976; Sæther *et al.* 1996, 2000; Diserud & Engen 2000). This allows us to calculate approximately the stationary distribution of population size. The variance of this distribution using the diffusion approximation (Karlin & Taylor 1981) is

$$\sigma_N^2 = \frac{K^2 \Gamma[(\alpha + 2)/\theta]}{[(\alpha + 1)/\theta]^{2/\theta} \Gamma(\alpha/\theta)}, \quad (2.4)$$

where $\alpha = 2r_1/\sigma_e^2(1 - K^{-\theta}) - 1$, and Γ denotes the gamma function (Diserud & Engen 2000). The variance σ_N^2 is strongly influenced by σ_e^2 and θ (figure 3c). Furthermore, for small values of θ variation in r_1 strongly affects the stationary distribution of population sizes (figure 4), whereas smaller effects on σ_N^2 of variation in r_1 occur for larger θ .

When demographic stochasticity is present, there is no stationary distribution. For $\sigma_d^2 > 0$, we may compute approximately the quasi-stationary distribution, again using the diffusion approximation (Lande *et al.* 2003). A

Figure 3. Ten trajectories of the population fluctuations during a period of 200 years in the theta-logistic model for (a) $\theta = 0.1$ and (b) $\theta = 1.5$, assuming $\sigma_e^2 = 0.01$. (c) The variance in the stationary distribution of population size (σ_N^2) in relation to θ for $\sigma_e^2 = 0.01$ and $\sigma_e^2 = 0.1$.

larger proportion of the distribution lies closer to zero in the quasi-stationary than in the stationary distribution obtained assuming $\sigma_d^2 = 0$ (figure 5). Ignoring demographic stochasticity may thus cause serious underestimation of the time to extinction.

Although variation in population growth rates strongly affects the characteristics of the population dynamics, surprisingly little is known about how, for example, r_1 varies among or within species. This may be related to difficulties in estimating r_1 due to the fact that reliable estimates of population growth rates require precise estimates of population size. Uncertain population estimates will lead to over-estimates of r_1 (Solow 1998) as well as the environmental variance. Furthermore, unbiased estimates of population growth rates are also difficult to obtain because many populations fluctuate around K so the population is

Figure 4. The stationary distribution of population sizes in the theta-logistic model—see equation (2.2a,b)—for the Gompertz ($\theta = 0$) and logistic ($\theta = 1$) type of density regulation for $r_1 = 0.025$ (solid lines) and $r_1 = 0.1$ (broken lines). Other parameters are $K = 100$ and $\sigma_e^2 = 0.01$.

Figure 5. The estimated quasi-stationary (broken line) and stationary (solid line) ($\sigma_d^2 = 0$) distributions of the theta-logistic model. The population parameters are $\theta = 0.5$, $r_1 = 0.1$, $K = 100$, $\sigma_e^2 = 0.01$ and $\sigma_d^2 = 1$ (for the quasi-stationary distribution).

rarely found at such small population sizes that the growth is close to r_1 (Aanes *et al.* 2002). In addition, large uncertainties will be present in the estimates of K in many time-series that in a statistical sense are short (Myers *et al.* 2001). This makes it even more difficult to obtain reliable unbiased estimates of r_1 because r_1 and K act together on $E(\Delta N/N|N)$ in (2.2b).

3. DENSITY-INDEPENDENT POPULATION GROWTH

First, we consider some populations that have strictly declined or increased in size over a period of at least 10 years and where the population counts are assumed to be relatively precise (table 1). We estimate the stochastic population growth rate s and σ_r^2 according to Engen & Sæther (2000), following Dennis *et al.* (1991).

When comparing only declining or increasing species, we still find large interspecific variation in s (table 1). The

Table 1. Characteristics of strictly declining or increasing species included in the present study. (s is the stochastic growth rate and $\sigma_r^2 = \text{Var}[\ln \lambda(t)]$, where $\lambda(t)$ is the population growth rate in year t .)

species	locality	period	s	σ_r^2	source
<i>Anas platyrhynchos</i>	Engure Lake, Latvia	1958–1993	0.094	0.152	Blums <i>et al.</i> (1993)
<i>Aptenodytes forsteri</i>	Terre Adélie, Antarctica	1952–1999	–0.014	0.026	H. Weimerskirch (personal communication)
<i>Branta leucopsis</i>	Gotland, Sweden	1976–2001	0.285	0.065	K. Larsson (personal communication)
<i>Bubulcus ibis</i>	Camargue, France	1967–1998	0.267	0.375	H. Hafner (personal communication)
<i>Ciconia ciconia</i>	Böhmen and Mähren, Czech Republic	1930–1984	0.071	0.034	Hladik (1986)
<i>Ciconia ciconia</i>	Estonia	1939–1981	0.034	0.015	Veromann (1986)
<i>Ciconia ciconia</i>	Denmark	1952–1971	–0.074	0.012	Skov (1986)
<i>Ciconia ciconia</i>	Netherlands	1929–1981	–0.068	0.090	Jonkers (1986)
<i>Ciconia ciconia</i>	Baden-Württemberg, Germany	1950–1965	–0.054	0.017	Engen & Sæther (2000) (from Bairlein & Zink 1979)
<i>Circus aeruginosus</i>	Britain	1927–1982	0.057	0.294	Underhill-Day (1984)
<i>Diomedea exulans</i>	Bird Island, South Georgia	1962–1996	–0.006	0.010	Croxall <i>et al.</i> (1997)
<i>Gymnogyps californianus</i>	California, USA	1965–1980	–0.077	0.120	Dennis <i>et al.</i> (1991)
<i>Haliaeetus albicilla</i>	Germany	1976–1997	0.044	0.003	Hauff (1998)
<i>Hirundo rustica</i>	Jutland, Denmark	1984–1999	–0.076	0.024	Engen <i>et al.</i> (2001)
<i>Milvus milvus</i>	central Wales	1951–1980	0.040	0.008	Davis & Newton (1981)
<i>Otis tarda</i>	Brandenburg, Germany	1975–1995	–0.076	0.012	Litzbarski & Litzbarski (1996)
<i>Pandion haliaetus</i>	Scotland	1958–1994	0.126	0.027	Dennis (1995)
<i>Perdix perdix</i>	Sussex, England	1970–2000	–0.058	0.069	Aebischer (personal communication)
<i>Phalacrocorax aristotelis</i>	Isle of May, Scotland	1946–1992	0.146	0.118	Harris <i>et al.</i> (1994)
<i>Phalacrocorax carbo</i>	Vorsø, Denmark	1978–1993	0.116	0.011	Van Eerden & Gregersen (1995)
<i>Phalacrocorax carbo</i>	Ormsø, Denmark	1978–1993	0.206	0.055	Van Eerden & Gregersen (1995)
<i>Pluvialis apricaria</i>	northeast Scotland	1973–1989	–0.176	0.134	Parr (1992)
<i>Recurvirostra avosetta</i>	North Sea coast, Germany	1951–1994	0.091	0.068	Hälterlein & Südbeck (1996)
<i>Sula bassanus</i>	Alisa Craig, Ayrshire, Scotland	1936–1976	0.0269	0.004	Nelson (1978)

Figure 6. The logarithm of the environmental variance σ_e^2 in relation to the specific growth rate r , assuming no density regulation. Solid lines and circles represent the initial analysis, broken line and open circles the meta-analysis that takes into account uncertainties in the parameter estimates (see text). For sources, see table 1.

most dramatic decline (table 1) was recorded in a population of *Pluvialis apricaria* in Scotland (Parr 1992). By contrast, *Branta leucopsis* at the Island of Gotland in the Baltic Sea was the most rapidly increasing population in the dataset, with $\hat{s} = 0.285$ (table 1).

There was a positive relationship between the specific growth rate r and $\ln\sigma_e^2$ among the species in the dataset (figure 6, correlation coefficient = 0.48, $p = 0.029$, $n = 21$). However, this relationship may be strongly influenced by sampling errors in the parameter estimates. To account for this we performed a meta-analysis (Hunter & Schmidt 1990), a technique that is currently becoming increasingly popular among comparative biologists (e.g. Arnqvist & Wooster 1995). We assume that r and $\ln\sigma_e^2$ are binnormally distributed among species. For populations that are not density regulated, it follows from standard normal theory (Kendall & Stuart 1977) that the sampling errors in these two parameters are independent. The uncertainty in the estimate of r must be estimated from the data, whereas the variance in the estimate of $\ln\sigma_e^2$ only depends on the sample size and can be calculated theoretically using well-known properties of the χ^2 -distribution. Finally, assuming that the sampling errors are approximately normally distributed, we calculated the conditional expectation of the values for each single species, conditioning on the raw estimates. The results of these adjustments of the estimates are shown in figure 6. The estimated correlation in the bivariate between-species model was 0.49, with significance level $p = 0.0580$ calculated by parametric bootstrapping. This therefore suggests the presence of an interaction between the expected dynamics and the stochastic component of the population fluctuations.

Overall, a large proportion of the variation in the stochastic population growth rate s was explained by differences in r (correlation coefficient = 0.95, $p < 0.001$, $n = 21$). However, the stochastic contribution to s differed between declining and increasing populations. In declining populations, σ_e^2 contributed significantly to the variation in s (correlation coefficient = -0.66, $p = 0.039$, $n = 10$), whereas no such significant effect was present in increas-

ing species (correlation coefficient = 0.40, $p > 0.2$, $n = 11$). This shows that not only the expected dynamics, but also quantifying the stochastic effects are important for predicting the rate of decline in such decreasing populations.

Variation in s among populations was not significantly ($p > 0.2$) related to differences in life history (clutch size or adult survival rate), either in declining or in increasing species.

4. DENSITY-DEPENDENT POPULATION GROWTH

Traditionally, population ecologists have analysed population dynamics by fitting autoregressive models to time series of fluctuations in population size (Bjørnstad & Grenfell 2001). Linearity at a logarithmic scale is often assumed (Royama 1992). Here, we take an alternative approach by estimating the parameters in the theta-logistic model (equation (2.2a,b)) by maximum-likelihood methods (see Sæther *et al.* (2000) and Sæther & Engen (2002) for a description of the methods). This enables us to estimate the form of the density regulation (see figure 3c).

In 11 populations where $\theta > 0$, the estimates of θ ranged from 0.15 to 11.17 (table 2). This implies that the assumption of log-linearity ($\theta = 0$) is not necessarily fulfilled in time-series of fluctuations of bird populations (e.g. Sæther *et al.* 2002). Large uncertainty was found in most estimates of r_1 with wide confidence intervals of $\lambda_1 = \exp(r_1)$ in several species (figure 7). This shows that r_1 (or λ_1) is often difficult to estimate even in comparatively long time-series of population fluctuations.

Even though we find large uncertainties in the estimates, a pattern of covariation appeared among several parameters of the theta-logistic model. As in the density-independent cases (figure 6), the environmental variance increased with r_1 (figure 8a, correlation coefficient = 0.75, $n = 11$, $p = 0.008$). Furthermore, the logarithm of θ decreased with r_1 (figure 8b, correlation coefficient = -0.69, $n = 11$, $p = 0.018$), showing that maximum density regulation occurs at lower relative (to K) population sizes in species with higher population growth rates. The estimates of γ , the strength of density regulation at K (equation (2.3)) also increased with σ_e^2 (figure 8c, correlation coefficient = 0.61, $n = 11$, $p = 0.048$).

We then examined how variation in the parameters affected interspecific variation in the variance of the stationary distribution (see equation (2.3)). Differences in σ_N^2 were only significantly correlated with σ_e^2 (correlation coefficient = 0.62, $p = 0.043$, $n = 11$).

The interspecific variation in r_1 was also correlated with life-history differences. Lower growth rates were found in species with high survival rates (figure 9a, correlation coefficient = -0.71, $n = 9$, $p = 0.031$) and small clutch sizes (figure 9b, correlation coefficient = 0.68, $n = 11$, $p = 0.021$) than in species at the other end of this 'slow-fast continuum' (Sæther & Bakke 2000).

5. PREDICTING POPULATION FLUCTUATIONS

Population viability analysis has during the last decades become an important tool in the management of threat-

Table 2. Estimates of parameters in density regulated bird populations.

(r , specific growth rate; θ , the format density regulation; σ_e^2 , environmental stochasticity; γ , strength of density dependence at the carrying capacity, K).

species	locality	period	r_1	θ	σ_e^2	γ	source
<i>Anser caerulescens</i>	Perouse Bay, Canada	1970–1987	0.09	2.05	0.041	0.58	Cooch & Cooke (1991)
<i>Aythya farina</i>	Engure Lake, Latvia	1970–1987	0.82	0.15	0.276	0.82	Blums <i>et al.</i> (1993)
<i>Ciconia ciconia</i>	Böhmen and Mähren, Czech Republic	1962–1984	0.09	3.74	0.014	0.37	Hladik (1986)
<i>Haematopus ostralegus</i>	Mellum, Germany	1946–1968	0.74	0.65	0.065	0.56	Schnakenwinkel (1970)
<i>Lagopus lagopus</i>	Kerloch, Scotland	1963–1977	1.50	0.47	0.411	1.94	Moss & Watson (1991)
<i>Melospiza melodia</i>	Mandarte Island, Canada	1975–1998	0.99	1.09	0.437	2.25	Sæther <i>et al.</i> (2000)
<i>Parus caeruleus</i>	Braunschweig, Germany	1964–1993	1.16	0.54	0.114	1.50	Winkel (1996)
<i>Phalacrocorax aristotelis</i>	Isle of May, Scotland	1946–1992	0.55	0.33	0.072	0.36	Harris <i>et al.</i> (1994)
<i>Phalacrocorax carbo</i>	Vorsø, Denmark	1978–1993	0.17	11.17	0.005	2.10	Van Eerden & Gregersen (1995)
<i>Recurvirostra avosetta</i>	Havergate, England	1947–1986	1.04	0.25	0.104	0.39	Hill (1988)
<i>Rissa tridactyla</i>	North Shields, England	1949–1984	0.17	2.05	0.014	0.37	Porter & Coulson (1987)

ened or vulnerable species (see reviews in Beissinger & Westphal 1998; Groom & Pascual 1998) because it provides a quantitative assessment of the probability for a population to decline to (quasi-)extinction. Our analyses show that large uncertainties are often found in the estimates of important parameters for population viability analysis—analyses such as the form of the density regulation (Sæther *et al.* 2000) and r_1 (figure 7), even in time-series of a length that are rarely available in populations of endangered and threatened species. Predictions from population viability analyses must therefore take into account these uncertainties. Elsewhere, we have suggested (Sæther *et al.* 2000; Engen & Sæther 2000; Engen *et al.* 2001; Sæther & Engen 2002) that the concept of population prediction interval can be useful in such analyses, embracing the effects of the expected dynamics and stochastic factors as well as uncertainties in parameter estimates on future population trajectories. The population prediction interval is defined as a stochastic interval that includes the unknown population size with a given probability $(1 - \alpha)$. We define extinction to occur when $N = 1$. We then predict extinction in a sexual population to occur after the smallest time at which this interval includes the extinction barrier. The width of the population prediction interval increases with the process variance (Heyde & Cohen 1985) and the estimation error. It is important to notice that the uncertainty in the parameters does not change the extinction risk of the population, but it will affect the confidence we have in the population predictions, including the probability of extinction.

We will illustrate our approach by an analysis of factors affecting the width of the population prediction interval in two populations of passerine birds. Many species of birds breeding in areas of Europe with a highly intensified agriculture have declined in numbers (Pain & Pienkowski 1997; May 2000; Møller 2001). In a study of *Hirundo rustica* on Jutland, Engen *et al.* (2001) predicted the time to extinction of such a population that declined from 184

in 1984 to 59 pairs in 1999. The estimates of the population parameters were $\hat{s} = -0.078$, $\hat{\sigma}_d^2 = 0.18$ and $\hat{\sigma}_e^2 = 0.024$, respectively. Ignoring uncertainties in the estimates, the width of the 90% population prediction interval included the extinction barrier after 28 years (figure 10a). Including uncertainties in the parameter estimates, this time was decreased by 25% to 21 years (figure 10b). Furthermore, in studies of time to extinction the demographic variance is assumed to be zero. Ignoring the demographic variance, the upper 90% population prediction interval included extinction first after 33 years (figure 10c). This occurs because the lack of demographic variance fails to account for the acceleration of the final decline to extinction produced by demographic stochasticity (Lande *et al.* 2003).

Similarly, in a widely fluctuating small population of *Melospiza melodia* in Mandarte Island accounting for uncertainty produced a more precautionary assessment of extinction than under the assumption of exactly known parameters (Sæther *et al.* 2000). Again, using the upper 90% population prediction interval the shortest time in which the population prediction interval included the extinction boundary $n = 1$ was 17 years whereas with no uncertainty in parameter estimates this interval was increased to 30 years.

6. DISCUSSION

This study demonstrates a strong covariation among the specific growth rate r_1 and other parameters characterizing fluctuations of bird populations. Both in density-independent and in density-dependent models the population growth rate increased with the environmental variance σ_e^2 (figures 6 and 8a). Large uncertainties were found in most estimates of r_1 in the density-dependent populations (figure 7). However, a relationship still appeared between r_1 and the form of the density regulation, expressed by θ in the theta-logistic model (figure 8b). Thus, maximum

Figure 7. The bootstrap replicates of the estimates of population growth rate $\lambda_1 = \exp(r_1)$ for the populations listed in table 2. (a) *Anser caeruleus*; (b) *Aythya ferina*; (c) *Ciconia ciconia*; (d) *Haematopus ostralegus*; (e) *Lagopus lagopus*; (f) *Melospiza melodia*; (g) *Parus caeruleus*; (h) *Phalacrocorax aristotelis*; (i) *Phalacrocorax carbo*; (j) *Recurvirostra avosetta*; (k) *Rissa tridactyla*.

Figure 8. (a) Environmental variance σ_e^2 , (b) the logarithm of θ in relation to the specific population growth rate r_1 , and (c) strength of density regulation at the carrying capacity γ in relation to σ_e^2 . For sources, see table 2.

density regulation occurred at larger densities (relative to K) in populations with a small r_1 than in populations with larger values of r_1 . A similar pattern has previously been noted by Fowler (1981, 1988). Furthermore, populations most rapidly growing at smaller densities were more subject to random fluctuations in the environment than populations with smaller values of r_1 (figure 8a).

A strong pattern of covariation occurs in avian life-history traits (Sæther 1988; Sæther & Bakke 2000; Bennett & Owens 2002), which can be considered as representing a 'slow-fast continuum' of life-history adaptations. At one end of this dimension we find species that are reproducing at a high rate, but with a short life expectancy at birth. At the other end, species that produce a small number of offspring, mature late in life but have a high adult survival rate, are found. This study shows that in density regulated populations a large proportion of the variance in the specific growth rate r_1 can be explained by the position of the

Figure 9. The specific population growth rate r_1 in relation to (a) adult survival rate and (b) clutch size in density regulated bird populations. For sources, see table 2.

species along this 'slow-fast continuum' (figure 9). The specific growth rate was higher in populations with large clutch sizes and low adult survival rates than in less fecund species with long life expectancy at maturity. This is in contrast to fishes, where Myers *et al.* (1999) failed to identify any relationship between r_1 and any life-history characteristics. The difference among these two studies may be related to larger uncertainties in the estimates of r_1 in fishes than in birds. Furthermore, relative smaller interspecific variation in r_1 may also be present in fishes than in birds.

The covariation among the specific growth rate r_1 , environmental variance σ_e^2 and life-history variation (figures 8a and 9) suggests the presence of some common underlying demographic process affecting the expected as well as the stochastic effects on the population dynamics of birds. In solitary birds, we have suggested that spatial limitation of access to breeding size may provide such a general mechanism (Sæther *et al.* 2002). In territorial long-lived species recruitment will be limited by the access to vacant territories. A negative relationship between annual variation in the number of recruits and adult recapture rate is expected in species with such a survival-restricted demography. By contrast, in short-lived species, a positive relationship is expected because high survival is also likely to give a high number of recruits because of

Figure 10. The upper bounds of population prediction intervals for a declining population of *Hirundo rustica* in Jutland, Denmark, when (a) assuming no uncertainty in the parameters, (b) including demographic and environmental stochasticity as well as uncertainties in the parameters, and (c) assuming no demographic stochasticity, $\sigma_d^2 = 0$.

common effects of the environment and small age-specific variation in density-dependent effects. Such fluxes of new recruits are likely to affect the population growth rate even at small densities, giving small values of θ . By contrast, in long-lived territorial species, variation in the number of recruits at small densities will only add to the pool of surplus individuals or to occupation of new territories, which probably has a small effect on the population growth. Around K adding extra birds probably increases mortality and rapidly leads to population decline, thus giving a large θ . As a consequence, θ was negatively related to the correlation coefficient between annual variation in the number of recruits and adult recapture rate.

Even though interspecific variation in r_1 was related to other population dynamical parameters (figure 8), differences in variability of the density regulated populations were not correlated to r_1 . The interspecific differences in

the variance of the stationary distribution (standardized in relation to K) of the populations included in this dataset were only significantly related to the environmental variance σ_e^2 . Thus, environmental stochasticity rather than variation in the expected dynamics was the major contribution to the interspecific differences in population variability recorded in the present study. This emphasizes the need for estimating and modelling stochastic effects for the understanding of avian population dynamics. Whether this relationship can explain variation in population dynamics in other taxa as well remains to be seen.

An important future challenge when conducting different environmental impact analyses will be to predict the consequences of different management actions on the future dynamics of the population in concern. Such an ability to correctly predict future population fluctuations is a prerequisite for conducting a population viability analysis of threatened and endangered populations. The results presented here (figure 10) suggest that development of population projections beyond a short time-span will be difficult for many species because of strong stochastic effects on the population dynamics as well as large uncertainties in the estimates of population parameters such as r_1 (figure 7). We strongly recommend that uncertainties in the population projections are evaluated, for instance by using the concept of the population prediction interval, when reporting the results of such analyses.

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