

Stochastic population dynamics and time to extinction of a declining population of barn swallows

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Summary

1. Time to extinction was predicted for a declining population of barn swallow *Hirundo rustica* in Denmark, using a model that includes demographic as well as environmental stochasticity and that takes the uncertainties in the parameter estimates into account.
2. We apply the concept of population prediction interval (PPI), which is a stochastic interval that includes the unknown variable that may be the extinction time or the population size at some future point of time, with a given probability $(1 - \alpha)$.
3. The lower bound of the upper one-sided prediction interval for the extinction time for $\alpha = 0.10$ was 22 years.
4. Ignoring uncertainties in the parameter estimates led to a 41% increase in this statistic.
5. Although the estimate of the demographic variance was small compared to other passerines ($\sigma_d^2 = 0.180$), a sensitivity analysis showed that it strongly influenced the predicted time to extinction compared to the model ignoring demographic stochasticity. A similar effect on the prediction of the time to extinction was found for the environmental variance σ_e^2 . In addition, choosing $\sigma_e^2 = 0$ strongly reduced the width of the prediction interval.
6. This demonstrates that reliable population projections require modelling of the environmental as well as the demographic stochasticity, and that the uncertainty in the estimates of the model parameters must be taken into account.

Key-words: barn swallow, environmental and demographic stochasticity, population prediction interval, stochastic population model, time to extinction.

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Introduction

Theoretical analyses have identified several factors that affect time to extinction of a population. In a deterministic model with no age-structure extinction will always occur when the specific growth rate r is negative, the time to extinction from initial population size N_0 being $-\frac{1}{r} \ln N_0$ (Richter-Dyn & Goel 1972). Population fluctuations are, however, also influenced by stochastic effects. The environmental variance σ_e^2 is generated by random variations affecting all individuals in the population similarly, whereas the demographic variance σ_d^2 is created by random independent individual variations

in births and deaths. These stochastic effects increase the risk of extinction because the population size may become small from random effects, but also because it reduces the population growth rate (Leigh 1981). The stochastic population growth rate, defined as the expected change in the logarithm of the population size between seasons, is $s = r - \sigma_e^2/2 - \sigma_d^2/2N$, where N is the population size and r is the per capita growth rate at an absolute scale (Lande 1998). The variance in the change in population size from one year to the next is $\sigma_e^2 N^2 + \sigma_d^2 N$. In large populations the environmental variance may create large stochastic fluctuations and it reduces the growth rate to $r_0 = r - \sigma_e^2/2$. Hence, environmental stochasticity may increase substantially the probability of extinction, even for large populations. When the population size is reduced, the impact of the demographic variance on the population growth rate increases, and may actually create a stochastically

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determined Allee-effect (Lande 1998). All these different effects of stochasticity imply that extinction may occur even when r is positive.

Reliable population projections require correct description of population growth and density dependence, as well as a realistic modelling of the stochasticity. In addition, uncertainties in the parameter estimates must be considered when predicting future population sizes or the time to extinction in a population viability analysis. Sæther *et al.* (2000a) suggested, following Dennis, Munholland & Scott (1991), that the population prediction interval (PPI) may be a useful concept in such analyses that embraces the expected dynamics, the stochasticity in the model, and the accuracy of the parameter estimates. A PPI is a stochastic interval that includes the unknown variable to be predicted with probability $(1 - \alpha)$. In population viability analysis, adopting the precautionary principle (IUCN 1994), one should use the upper one-sided intervals ranging from t_α to infinity, which means that the extinction time is predicted to be smaller than t_α with probability α . The interpretation of a prediction interval is the same as for a confidence interval, except that we draw inference about a stochastic quantity rather than a parameter. Uncertainty in the parameters does not change the risk of extinction of the population, but affects the confidence we have in the population predictions. In a small island population of song sparrow *Melospiza melodia* (Wilson), neglecting uncertainties in the parameter estimates led to an 33% overestimation of t_α (Sæther *et al.* 2000a). The lack of consideration of uncertainties and biases in population parameters has often made it difficult to verify predictions from population viability models (Beissinger & Westphal 1998). As a consequence, such difficulties have been used to question population viability as a useful management tool (Ludwig 1999). However, according to the 'precautionary principle' (IUCN 1994), the preciseness in the predictions should be considered and included in recommendations about the management of endangered or threatened species. Large uncertainties should result in a more cautious approach than in those cases where available information permits accurate population projections.

Many bird populations in the European agricultural landscape are now declining rapidly (Pain & Pienkowski 1997; May 2000, Donald, Green & Heath 2001). Although the population sizes in several of those cases are already probably far below the carrying capacity, the population size is often still large. Extinction of such abundant species does not seem to be of immediate concern. However, Lande & Orzack (1988) suggested that time to extinction even of large populations could be quite short. Thus, application of quantitative criteria for risk assessment as suggested by Mace & Lande (1991) seems necessary even for such species.

Assuming no density regulation, and using first-order Taylor expansion for the mean and variance, the

above modelling of stochasticity is approximately equivalent to: $E(\Delta X/X) = r - \sigma_e^2/2 - \sigma_d^2/2 \exp(-X)$ and $\text{var}(\Delta X/X) = \sigma_e^2 + \sigma_d^2 \exp(-X)$, where $X = \ln N$. Furthermore, the change in the logarithm of population size between years can often be approximated by a normal distribution. If there is no demographic stochasticity, the mean and variance are constant and the process is equivalent to a Brownian motion recorded only at discrete time steps. Dennis *et al.* (1991) have previously used Brownian motions to estimate the risk of extinction of several populations of endangered or threatened species. They introduced the concept of population prediction interval and developed it for population size N . They also presented estimators of various quantities (mean, median, percentiles, cumulative distribution function) associated with the distribution of time to extinction, T . Engen & Sæther (2000) extended these results by deriving prediction intervals also for the time to extinction. Both Dennis *et al.* (1991) and Engen & Sæther (2000) considered only the case with no demographic stochasticity.

Here we use a similar approach, including demographic stochasticity in a model of the dynamics of a declining population of barn swallow *Hirundo rustica* L. to derive prediction intervals for the time to extinction. In this way, we can examine quantitatively how various factors affect the uncertainties and the risk of extinction of this population.

Methods

STUDY AREA

The study was conducted at Kraghede (57°12' N, 10°00' E), Denmark, May–September 1970–99. The study site consists of open farmland with scattered plantations, ponds and hedgerows. The main crops are grass, barley, wheat and potatoes. Barn swallows breed preferentially on dairy farms. The total study area was originally *c.* 15 km², but was increased three times: in 1982 to 30 km², in 1987 to 45 km² and in 1998 to 55 km², to increase the population size as the population was declining. Population estimates are given for the total area, assuming no temporal variation in the proportion of the total population breeding in the extended parts of the study area. A detailed description of the study site and its breeding population of barn swallows is given in Møller (1994).

FIELD METHODS

A.P.M. has censused breeding barn swallows in the study area since 1970. Adult barn swallows have been ringed annually by mist netting with annual capture efficiency of more than 97% (A.P. Møller & T. Szép, unpublished manuscript) according to estimates of capture efficiency using capture–recapture estimates (Lebreton *et al.* 1992). Intensive searches for nest sites in all buildings, in culverts and under bridges have been

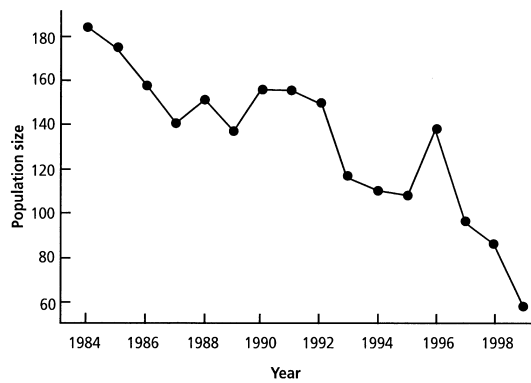


Fig. 1. Annual variation in the number of breeding pairs of the barn swallow in the Kraghede study area.

made weekly and all nestlings have been ringed when 12–14 days old. The number of breeding pairs has been estimated as the number of pairs building nests. The population has shown an almost continuous decrease from 184 pairs in the first study year in 1984 to 58 pairs in 1999 (Fig. 1).

Reproduction of barn swallows was recorded during regular visits (usually at least twice per week) to nests throughout the breeding season, often daily around the time of laying, hatching and fledging. Brood size at fledging was simply recorded as the number of nestlings present in the nest at the last visit. The frequency of second clutches was the proportion of pairs initiating a second clutch. Annual reproductive success was the number of fledglings produced in the first and the second brood for a pair.

POPULATION MODEL AND PARAMETER ESTIMATION

Following Engen, Bakke & Islam (1998) and Sæther *et al.* (1998, 2000a), an estimate of the demographic variance was obtained from data on individual variation in the contribution of breeding females to the next generation. This contribution is the number of female offspring recorded to the next or following generations plus 1 if the female herself survives to the next year (Sæther *et al.* 1998, 2000a, 2000b). The estimate of σ_d^2 was then obtained as the weighted mean across years of:

$$\frac{1}{k-1} \sum (R_i - \bar{R})^2,$$

where R_i is the contribution of an individual i to the next generation, \bar{R} is the mean contribution of the individuals and k is the number of recorded contributions in year t (Sæther *et al.* 1998).

The basic assumptions of the model is that the stochasticity in the population size can be described by a Markov process, the between-year change in log population size being normally distributed, with expectation:

$$E(\Delta X | X = x) = r - \frac{1}{2} \sigma_e^2 - \frac{1}{2} e^{-x} \sigma_d^2$$

and variance $\text{var}(\Delta X | X = x) = \sigma_e^2 + \sigma_d^2 e^{-x}$.

As usually performed for sexually reproducing species (Burgman, Ferson & Akçakaya 1993), the extinction barrier was chosen at $N = 1$.

Assuming that the population size can be fully censused each year, the available data are the observed log of population sizes X_1, X_2, X_n at times 1, 2, ... n , respectively. From this the likelihood function may be written (see Appendix I) and maximized numerically. Because we have good data for individual reproduction and survival over many years from a large number of individuals, we consider σ_d^2 to be known.

A joint confidence region for the stochastic growth rate:

$$r_0 = r - \frac{1}{2} \sigma_e^2$$

(Lande 1998) and σ_e^2 is derived using the approach of finding two stochastic variables which have distributions that can be determined completely, and that actually contains most of the information available about the unknown parameters. Then, a region where these variables take values with probability $(1 - \alpha)$ can be converted numerically into a confidence region for r_0 and σ_e^2 . This approach is described in greater detail in Appendix I.

POPULATION PREDICTION INTERVAL (PPI)

Prediction intervals are stochastic intervals covering the variable to be predicted with some coverage probability known approximately. In population viability analysis it is most appropriate to use upper one sided intervals $[t_\alpha, \infty]$ for the time to extinction with the property that $P(T > t_\alpha) \approx 1 - \alpha$, where T is the time to extinction (Dennis & Otten 2000; Engen & Sæther 2000; Sæther *et al.* 2000a). We make a similar definition for the prediction of the logarithm of the population size at a given time, that is $P(X > x_\alpha) \approx 1 - \alpha$. Hence X is the log population size at some given future point of time. The quantities t_α and x_α are some constructed function of the data and the known parameters, and they are therefore actually stochastic. In Appendix I we show how such intervals can be constructed using the same stochastic variables that we used to construct the confidence region in the previous section. The population process is simulated a large number of times with different parameter values reflecting the uncertainty in the parameters. Other approaches, such as using parametric or non-parametric bootstrap replicates of the parameter estimates (Dennis & Otten 2000; Sæther *et al.* 2000a), or using the Bayesian approach choosing the parameter from some posterior distribution (Ludwig 1996; Taylor *et al.* 1996; Tufto *et al.* 2000), could alternatively have been applied. The main point is not really which approach one applies at this step in the construction, but actually that the coverage of the interval, from a purely frequentistic point of view (see for example Dennis 1996), is checked by a large number

of stochastic simulations. This implies that we simulate new independent data sets with the same value of the population size at time zero (the last observation) as for the data (58, see Fig. 1) using the maximum likelihood estimates of the parameters, together with one simulation of the 'real' process from time 0 to extinction. For each such data set one also has to simulate a number of processes (for example 100) with different parameter values using one of the indicated methods. If the method used for constructing the prediction interval was exact, the rank of the extinction time for the 'real' process among the simulated processes should be uniformly distributed. To check this, we have repeated the whole process 10 000 times. In the end, because our method is only approximately correct, the results of these simulations may be used to adjust the chosen value of α to give a more correct coverage probability. We have done this by fitting a beta-distribution to the distribution of the relative rank values (ranging from 0 to 1). This class of distributions contains the rectangular distribution that would have been found for an exact PPI, but in addition it covers distributions that are seen to the left or right. The distribution of ranks and the fitted beta-distribution is shown in Fig. 2. From this, we may calculate a number α' so that $P(T_{\text{real}} > t_{\alpha'}) = 1 - \alpha$. The corrected prediction interval with coverage approximately equal to α is then $[t_{\alpha'}, \infty]$. More precisely, if $f(x)$ is the fitted beta-distribution, the relation defining α' is:

$$\int_0^{\alpha'} f(x) dx = \alpha.$$

One should be aware of this method still not being quite exact. This is because we have constructed the correction using the maximum likelihood estimates rather than the true parameter values. However, we have checked that this application of the 'plug in principle' (Efron & Tibshirani 1993) gives corrections that are fairly robust against variations in the parameters within the confidence region.

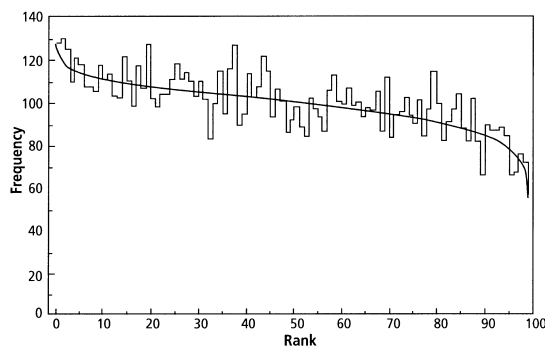


Fig. 2. The distribution of 10 000 relative ranks of the 'real' time to extinction among 99 simulated ranks with different parameter values reflecting the uncertainty in the parameter estimation. If the method were exact, the distribution would be uniform. The solid line is the beta-distribution $f(x)$ fitted to the simulations and used to calculate α' so that $P(T > t_{\alpha'}) \approx 1 - \alpha$ for the different values of α used in the analyses (e.g. Figs 4 and 5)

Results

The number of fledglings produced in the first clutch has decreased significantly during the period 1984–99 (linear regression: b (SE) = -0.091 (0.011), $F = 69.97$, d.f. = 1, 1706, $r^2 = 0.040$, $P < 0.0001$) which equals a predicted reduction by 1.46 offspring per brood during the period of 16 years. A decrease was also observed for the number of fledglings in the second brood (linear regression: b (SE) = -0.032 (0.009), $F = 11.55$, d.f. = 1, 966, $r^2 = 0.012$, $P = 0.0007$), resulting in a predicted reduction by 0.51 per brood throughout the study period. However, the total number of offspring produced per pair and season did not decrease significantly (linear regression: $F = 1.62$, d.f. = 1, 1706, $r^2 = 0.001$, $P = 0.20$). The reason for this absence of decrease in total success is a significant increase in the number of pairs having two broods per year (Spearman rank order correlation: $r_s = 0.22$, $N = 1708$, $P < 0.0001$).

Very few females were able to contribute to the next generation in this population. No females contributed more than two female offspring, whereas 79% of the females were either not recorded themselves or had any offspring a later year recruited to the population. A R_i value of 1 was found in 20.9% of the females. The estimate of the demographic variance σ_d^2 was 0.180.

The maximum likelihood estimates of the stochastic population growth rate for large population sizes was $r_0^* = -0.076$ and for the environmental variance $\sigma_e^{2*} = 0.024$. The confidence region was quite large (Fig. 3, environmental standard deviation ranging from 0.12 to 0.26 and r_0 from -0.18 – 0.04).

In Fig. 4 we plot the lower bound x_α for the prediction intervals for the log population size at time t as a function of t . The lower bounds t_α for the prediction intervals for the time to extinction are where the curves for x_α cross the axis. We predict with 10% confidence that extinction of this barn swallow population will

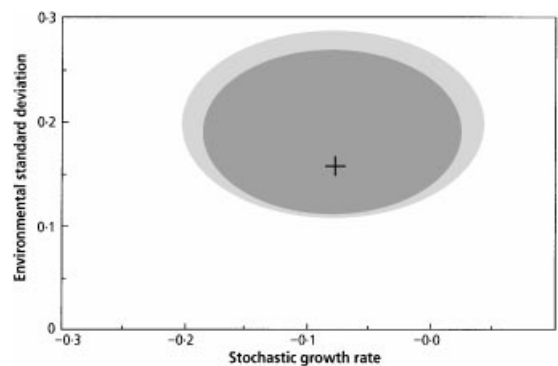


Fig. 3. Joint confidence regions for the stochastic growth rate r_0 and the environmental standard deviation σ_e with confidence coefficient 0.95 (light grey region) and 0.90 (dark grey region). The maximum likelihood estimate is shown at $r_0 = -0.076$ and $\sigma_e = 0.15$. The skewness of the region relative to the estimate of σ_e is due to the skewness of the χ^2 -distribution, as for the standard confidence interval for the variance in the normal model.

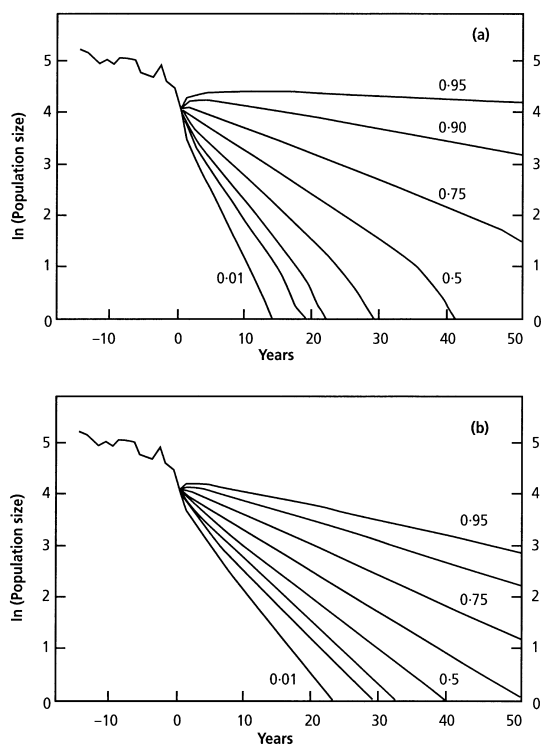


Fig. 4. The lower bound of different prediction intervals (x_α) for different values of α for the future size of the barn swallow population when (a) all available information is included and (b) when no uncertainty is assumed in the parameter estimates. The lower bound of the prediction interval for the time to extinction (t_α) is where the curves for x_α against time crosses the horizontal axis. $\alpha = 0.01, 0.05, 0.10, 0.25, 0.75, 0.90$ and 0.95 .

occur before 22 years (Fig. 5a). With 50% confidence extinction occurs before 53 years.

Correspondingly, Fig. 4 may also be read as prediction intervals for population sizes at different times and not only as prediction intervals for the time to extinction. For instance, the 90% two-sided prediction interval at a given time is $(x_{0.05}, x_{0.95})$. After 50 years this interval ranged from 0 to 64 individuals (Fig. 4a).

Ignoring uncertainties in the estimates, assuming that the parameters actually were known and equal to the maximum likelihood estimates, increased the predicted time to extinction (Fig. 4b). For instance, the lower bound of the interval for the extinction time for $\alpha = 0.10$ increased with 41%, from 22 years when including uncertainty (Fig. 4a) to 31 years. Accordingly, using the 'precautionary principle' (IUCN 1994), we should be more conservative when the estimates are uncertain, being aware of the fact that the situation actually may be much more critical than what we can conclude directly from the maximum likelihood estimates.

Assuming that the demographic variance was zero, the estimate of the environmental variance became approximately 10% larger (0.026), because the demographic stochasticity is then absorbed in the environmental noise term. Actually, the demographic term σ_d^2 is then replaced by a constant that is confounded with the constant from σ_e^2 . Ignoring the demographic

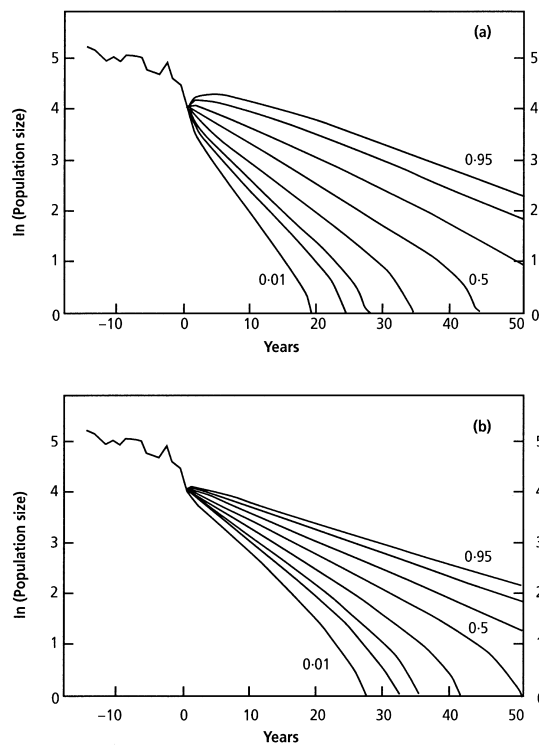


Fig. 5. The lower bound of different prediction intervals (x_α) for different values of α for the future size of the barn swallow population when (a) $\sigma_d^2 = 0$ and (b) $\sigma_e^2 = 0$. The lower bound of the prediction interval for the time to extinction (t_α) is where the curves for x_α against time crosses the horizontal axis. $\alpha = 0.01, 0.05, 0.10, 0.25, 0.75, 0.90$ and 0.95 .

variance strongly increased the predicted life expectancy of the population. For instance, $t_{0.10}$ increased from 22 (Fig. 4a) to 28 years (Fig. 5a), an increase of 27%. This probably occurred because inclusion of the demographic variance shortened the length of the final stage of the process to extinction (Figs 4 and 5a) by an increase in the variance as well as a decrease in the expected growth rate by the term $\sigma_d^2/2N$.

Ignoring environmental stochasticity strongly reduced the range of variation of the prediction interval. For instance, after 50 years $x_{0.95}$ was reduced from 64 individuals with both demographic and environmental stochasticity present (Fig. 4a) to 8.5 individuals when choosing $\sigma_e^2 = 0$ (Fig. 5b). As in the case for excluding demographic variance, the predicted time to extinction again increased.

Discussion

This Danish population of barn swallow had a mean decline of 7.6% per year (Fig. 4), resulting in that a prediction of extinction before 22 years (Fig. 4a) can be performed with 10% confidence. Accordingly, after IUCN's (1994) criteria, based on Mace & Lande (1991), this population should be classified as vulnerable. This occurs even though the population size at the last year of study was 58 pairs, illustrating that population size may be a poor predictor of extinction risk

and that even relatively abundant species may go rapidly extinct.

However, these analyses assume a closed population with small emigration or immigration. If a considerable fraction of the recruits settled outside the study area, this is likely to result in an underestimate of σ_d^2 because of a reduction in the proportion of females producing no recruits. The large size of the study area and the high recapture probability (Møller 1994) make it unlikely that this bias is substantial. Furthermore, immigration from outside will reduce the risk of extinction. However, the decline of the barn swallow has been known to occur over large areas (e.g. Gregory *et al.* 1999) so immigration from source areas may not be sufficient to prevent the decline.

Many bird species in the agricultural landscape in Europe now face severe declines in population sizes (Pain & Pienkowski 1997; May 2000; Donald *et al.* 2001) and may be related to recent changes in agricultural practice (Møller 2001). These results are based mainly on an analysis of population indices collected over large areas. The rate of decline in our study population was larger than recorded previously from one less comprehensive data source collected in the same region as our study situation. There is indeed a weak but statistically significant positive correlation between the population size in the study area and the bird census indices from the Danish national survey ($r = 0.65$, $N = 16$ years, $P = 0.006$, Møller 1994). The relative weak association between local intensive and regional, extensive surveys may be related to the problem that national bird census programmes rely on amateurs who do not visit randomly selected plots, and who do not cover the same study areas each year. As amateurs study birds because they like birds, it is possible that census plots with few birds have a higher probability of being discontinued than study plots with many birds. This could generate an apparent population trend that shows a smaller degree of decline than the actual decline in randomly selected plots. Accordingly, analysis based on population indices may underestimate the rate of decline so that the situation for many populations may be more severe than previously believed.

The reproductive success of barn swallows decreased during the period 1984–99 in both first and second broods, although there was no significant decrease in total annual reproductive success per pair. This latter observation was due to a significant increase in the proportion of pairs raising two broods per season. Analyses of local recruitment in the present barn swallow population have shown that significantly more individuals recruit from first than from second broods, partly because fledglings from first broods are in better body condition than nestlings from second broods (Møller 1994). Hence, this suggests that the decrease in the mean number of fledglings per pair for the first brood affected the population growth rate negatively.

The estimate of the demographic variance in this population of barn swallow was far lower than recorded

previously in the passerines song sparrow ($\sigma_d^2 = 0.66$), great tit *Parus major* L. ($\sigma_d^2 = 0.57$) and dipper *Cinclus cinclus* L. ($\sigma_d^2 = 0.27$) (Tufto *et al.* 2000). This low estimate is mainly because only a small proportion of the females is able to produce offspring that are later recruited into the population. Although we do not yet know the mechanism generating the decline of this population, degradation of quality of the breeding habitats, due probably to altered agricultural practices (Møller 2001), is a likely explanation. Whether a low demographic variance is a general feature of declining populations still remains to be determined.

Although the demographic variance was low, it especially affected the final stage of the process to extinction (Figs 4 and 5a), and strongly influenced the prediction of the time to extinction. In fact, the effect of the demographic stochasticity on the time to extinction was comparable to the effects of the environmental stochasticity (Fig. 5). In populations with larger demographic variance the demographic stochasticity will have an even stronger effect. This is in contrast to the results of a previous analysis of the viability of a great tit population, where the environmental variance affected the time to extinction more strongly than the demographic variance (Sæther *et al.* 1998). This is probably because our barn swallow population was smaller and much closer to extinction than the great tit population, which fluctuated around a carrying capacity of 216 pairs. In such a large population the effects of the demographic stochasticity on the variance in the population growth rate will be small (Lande 1998). To illustrate, we predicted the time to extinction of the barn swallow population, choosing the demographic variance previously estimated (Sæther *et al.* 1998) in the great tit population ($\sigma_e^2 = 0.569$, assuming no density dependence). This strongly shortened the predicted time to extinction, $t_{0.10}$ decreasing with 27% from 22 (Fig. 4a) to 16 years. Thus, reliable estimates of the demographic variance are crucial for a correct prediction of the time to extinction of small, declining populations. Accordingly, estimates of time to extinction (e.g. Dennis *et al.* 1991; Gaston & Nicholls 1995), ignoring demographic stochasticity, are likely to underestimate the risk of extinction of small populations. The lower 10% quantile of the estimated inverse Gaussian distribution of the time to extinction (Dennis *et al.* 1991), ignoring uncertainties in the estimates, was 34 years. However, when estimating the time to quasi-extinction (Ginzburg *et al.* 1982) at a population size considerably above zero, this effect is likely to be small.

The environmental stochasticity strongly influences the dynamics (Sæther *et al.* 2000b) and the time to extinction of small passerine populations (Sæther *et al.* 1998). Although our estimate of the environmental variance was lower than in three other passerine species (Tufto *et al.* 2000), assuming no environmental variance still increased the time to extinction (Fig. 5b). The value of $t_{0.10}$ was 35 years, an increase of 59% from the case where both demographic and environmental

stochasticity were present (Fig. 4a). Furthermore, the width of the prediction interval strongly decreased when no environmental stochasticity was assumed to be present (Fig. 5b). This illustrates the necessity of correctly estimating and modelling the stochasticity in the population dynamics when predicting population trajectories.

Several approaches can be chosen to include uncertainty in parameter estimates in the construction of the prediction interval. One approach is the Bayesian, in which a prior distribution, for example a non-informative one, is converted into a posterior distribution when conditioned on the observations (Berger 1985). This is a conceptually simple way to get rid of the nuisance parameters by integrating over their posterior distribution, finally claiming that one actually knows the probabilities of any event of interest. Several computer programs (e.g. Spiegelhalter *et al.* 1996) are now available to perform the analysis that will also make a Bayesian approach feasible for complicated models. The major problem with the Bayesian methods in population viability analysis is that they are not based on the frequency interpretation of probability (Dennis 1996). Accordingly, one will calculate the t_α and use the Bayesian interpretation directly, claiming that the probability that the population goes extinct after the observed t_α conditioned on the data is actually $1 - \alpha$. The actual frequentistic probability, however, interpreting t_α as a stochastic variable, may be somewhat different. The process of correcting the coverage probability so that the coverage is approximately correct with respect to the frequentistic definition of probability would usually be outside the range of what a Bayesian statistician would accept. When using Bayesian methods in population viability analysis, one should be aware of this problem and make it a general rule that coverage probabilities, regardless of the chosen method, should be checked carefully by intensive stochastic simulations to reveal the frequentistic properties of the method.

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Appendix

MAXIMUM LIKELIHOOD ESTIMATION

The population process is defined as a Markov process in discrete time with normally distributed changes in the log of population size between successive years; that is, for a given population size ΔX is normal with

$$E(\Delta X | X = x) = r_0 - \frac{1}{2} \sigma_d^2 e^{-x}$$

where $r_0 = r - \sigma_e^2/2$ is the stochastic growth rate in the absence of demographic stochasticity, and

$$\text{var}(\Delta X | X = x) = \sigma_e^2 + \sigma_d^2 e^{-x}.$$

The demographic variance σ_d^2 is estimated from a large number of recordings of females' individual contributions to the next generation within and between years (Engen *et al.* 1998; Sæther *et al.* 1998) and can therefore be considered known. If the process is recorded as x_1, x_2, \dots, x_n at n consecutive years, the log likelihood is

$$\ln L(r_0, \sigma_e^2) = -\frac{1}{2} \sum_{i=1}^{n-1} [\ln v_i + (x_{i+1} - m_i)^2 / v_i],$$

Where $m_i = x_i + r_0 - 1/2 \sigma_d^2 e^{-x_i}$ and $v_i = \sigma_e^2 + \sigma_d^2 e^{-x_i}$. This can easily be maximized by some numerical routine to give the maximum likelihood estimates r_0^* and σ_e^{*2} .

CONFIDENCE REGION

Writing $\beta_i(\sigma_e^2) = 1/\sqrt{\sigma_e^2 + \sigma_d^2}$ the variable $Y_i = (X_{i+1} - X_i + 1/2 \sigma_d^2 e^{-X_i}) \beta_i(\sigma_e^2)$, $i = 1, 2, \dots, n-1$, conditioned on $X_i = x_i$ is normal with unit variance and mean $r_0 \beta_i(\sigma_e^2)$. Actually, if the demographic variance is zero, the variables Y_i are independent normal variates also unconditionally. We base our confidence region on this being approximately correct also in the case of demographic stochasticity. Then

$$\hat{r}_0(\sigma_e^2) = \frac{\sum_{i=1}^{n-1} Y_i(\sigma_e^2)}{\sum_{i=1}^{n-1} \beta_i(\sigma_e^2)}$$

is an estimator of r_0 in the case that σ_e^2 is known, and

$$Z = \sum_{i=1}^{n-1} [Y_i(\sigma_e^2) - \hat{r}_0(\sigma_e^2) \beta_i(\sigma_e^2)]^2$$

is approximately χ^2 -distributed with $n-2$ degrees of freedom. Further,

$$U = \frac{\hat{r}_0(\sigma_e^2) - r_0}{\hat{\beta}(\sigma_e^2)} \sqrt{n-1},$$

where $\hat{\beta}_i(\sigma_e^2)$ is the mean of the $\beta_i(\sigma_e^2)$, is approximately standard normally distributed and independent of Z .

We can now choose a region ω in the plane so that $P[(U, Z) \in \Omega] = 1 - \alpha$. We have chosen Ω to be as small as possible; that is, choosing the region defined by the joint density being larger than some value which has to be determined numerically to give the coverage $1 - \alpha$. Finally, the mathematical expression $[U(r_0, \sigma_e^2), Z(r_0, \sigma_e^2)] \in \Omega$ is numerically transformed to the equivalent expression $(r_0, \sigma_e^2) \in \tau$ which is our confidence region shown in Fig. 3 with coverage $1 - \alpha$. In practice, this transformation is performed by computing $U(r_0, \sigma_e^2)$ and $Z(r_0, \sigma_e^2)$ for a huge grid of points (r_0, σ_e^2) and checking whether the corresponding (U, Z) take values in Ω or not.

PRELIMINARY PREDICTION INTERVAL

A preliminary prediction interval may be defined from the approach given in the previous section. Each value of (U, Z) defines a set of parameter values $r_0(U, Z)$ and $\sigma_e(U, Z)$. Let $X_t(U, Z)$ be the state of the process at time t starting at the x_n at time zero with these parameters, and let $T(U, Z)$ be the extinction time. If the process has gone extinct before time t then $X_t(U, Z) = 0$.

If we just want to predict the time to extinction we may choose quantiles of the distribution of $T(U, Z)$ for this purpose. Let t_α be the lower α -quantile; that is, $P[T(U, Z) > t_\alpha] = 1 - \alpha$. Then the interval $[t_\alpha, \infty]$ is an upper one-sided prediction interval for the time to extinction. We want the coverage of this interval with respect to the real process to be $1 - \alpha$; that is, $P[T_{\text{real}} > t_\alpha]$ should be approximately equal to $1 - \alpha$. We emphasize that T_{real} as well as t_α are stochastic variables, t_α actually being a function of the data. In the next section we show how to check this coverage and eventually how to correct the coverage probabilities obtaining better approximations.

In practice, one may be interested in predicting the fate of the population within some finite time span, say t . Then, there are two possibilities. Either the population goes extinct before time t , or the population size is positive at t . The upper one-sided prediction interval for the time to extinction then only apply if its lower limit is smaller than t . If this is not the case we will rather report the prediction interval for the population

size at time t . This latter prediction interval can be constructed in the same way using the lower α -quantile of the distribution of $X_t(U, Z)$ rather than that of $T(U, Z)$.

PREDICTION INTERVAL WITH APPROXIMATELY CORRECT COVERAGE

The coverage of the prediction intervals defined in the previous section can easily be checked by stochastic simulations. We first simulate one real process and generate the data using the maximum likelihood estimates for r_0 and σ_e^2 . This process is further simulated to the upper time limit t giving T_{real} if this is less than t or otherwise a positive X_{real} at time t . Then we simulate (U, Z) a large number of times, compute $r_0(U, Z)$ and $\sigma_e^2(U, Z)$ using the simulated data, and simulate these processes up to time t . Finally, the rank of the 'real' process among those simulated using the (simulated) data is recorded. If T_{real} is smaller than t we just count the number of processes with extinction time smaller than T_{real} , otherwise we count the number of paths with $X_t(U, Z)$ smaller than X_{real} , which is then positive.

The method will have exact coverage probability for any α if the rank is uniformly distributed among its possible values. Fig. 2 shows the distribution of these ranks using 99 simulated processes for each simulated data set, and 10 000 recordings of the rank. Here we have used $t = 1000$ so that extinction is almost certain to occur before t . The distribution is significantly different from the uniform although the deviation is not large. We have fitted a beta-distribution, which is a family of distributions including the uniform, to the relative ranks (ranging from 0 to 1). From the fitted distribution we can calculate $P(T_{\text{real}} > t_{\alpha})$. The prediction interval with coverage approximately equal to $1 - \alpha$ is finally found as indicated in the main text using a new α -value, say α' so that $P(T_{\text{real}} > t_{\alpha'}) = 1 - \alpha$.

One should be aware of that this method is still not quite exact. This is due to the fact that the correction has been carried out using a specific set of parameter values, actually the maximum likelihood estimators, and not the real values of the parameters. However, it turns out that the correction procedure itself is rather robust against changes in these values within the confidence region.