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Time to extinction in relation to mating system and type of density regulation in populations with two sexes

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Summary

1. Population viability models usually consider only the female segment of the population. However, random variation in sex ratio as well as the mating system may also affect variation in fitness among females. Here we develop population models incorporating demographic stochasticity in both sexes. Furthermore, we consider the effects on the estimated time to extinction and whether density regulation acts only on females or on total population size.
2. We applied these models to two populations of polygynous great reed warblers *Acrocephalus arundinaceus* L. with differences in population trends to investigate the importance of considering sex in population viability models.
3. Demographic stochasticity was larger in a polygynous than in a monogamous mating system.
4. The estimated time to extinction was considerably shorter for a monogamous than for a polygynous mating system, particularly if density regulation acted only on females than rather on the total population.
5. This study demonstrates that structure of mating system must be included when making population viability analysis based on counts of total population sizes. It is especially important to model the specific effects of density regulation on the two sexes.

Key-words: demographic stochasticity, density regulation, mating system, sex-specific population dynamics, great reed warbler.

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Introduction

Analyses of population dynamics or demography usually consider only the female segment of the population (Caswell 2001). It is assumed implicitly that there are a sufficient number of males available for the females to find an appropriate mate, and that the numbers of males do not affect the dynamics or the demographic characteristics of the females. However, several lines of evidence do indicate that this assumption may not always be valid. One of the most extreme examples of how processes affecting the numbers of each sex may be strongly interrelated is provided by infanticide that occurs when the death of the male defending or controlling the females in an area leads to severe reduction in the reproductive success, because the new incoming male will kill as many offspring fathered by the previous male as possible (Hausfater & Hrdy 1984; Swenson *et al*. 1997). More indirect effects of variation in the proportion of males also may be present. In the moose *Alces alces* L. differences in the adult sex ratio explained a large proportion of both temporal and spatial variation in several reproductive traits (Solberg

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et al. 1999; Sæther, Solberg & Heim 2003; Sæther *et al.* 2004). Similar effects have also been recorded in red deer *Cervus elaphus* L. (Clutton-Brock *et al.* 2002). These examples suggest that in many cases it is important to consider the effects of both sexes on demographic processes in a population (Mysterud, Coulson & Stenseth 2002).

In some populations many individuals fail to obtain a mate (Newton 1998). Dale (2001) showed that in many small isolated bird populations a high proportion of males was unmated, probably because of low return rates of females due to female-biased dispersal in birds (Clarke, Sæther & Røskaft 1997). Similarly, in several bird species a proportion of female floaters may also be present (Sæther & Fonstad 1981; Smith & Arcese 1989; Newton 1998). The effects of a surplus of one sex in the population will depend on the mating system. In a strictly monogamous system the lack of males will immediately reduce the reproductive output of females. In contrast, in a polygynous mating system these effects are likely to be greatly reduced because a single male can fertilize multiple females (Emlen & Oring 1977). However, the intensity of sexual selection measured by the adult sex ratio in the population may also have other less evident consequences including effects on the reproductive rate of females (see reviews in Møller & Legendre 2001; Kokko & Brooks 2003; Møller 2003).

Demographic stochasticity is random variation among individuals in fitness (Lande, Engen & Sæther 2003). Theoretical analyses have demonstrated that demographic stochasticity has a major impact on the dynamics of small populations on the order of 100 individuals or less (Lande 1998; Brook, Burgman & Frankham 2000; Lande *et al.* 2003). However, some evidence suggests that once sex and mating system are incorporated into the models, significant effects of sex ratios on extinction risk may occur even at much larger populations (Legendre *et al.* 1999). Demographic stochasticity will therefore strongly affect the mean time to extinction (Lande 1993; Sæther & Engen 2003). Engen, Lande & Sæther (2003) showed in a population model with two sexes that the demographic variance σ_d^2 governing fluctuations in population size in a constant environment could be partitioned into three components. The first component arises from variation among individual females in survival and reproduction of both sexes (σ_{df}^2). We have shown previously that in small passerine birds this component ranges from 0·20 to 0·65 (Sæther *et al.* 1998, 2000a,b; 2002a, in press; Tufto *et al.* 2000) when only female offspring are considered. The second component is generated by the binomial distribution of the number of surviving males (σ_{dm}^2). Finally, the third component σ_{sex}^2 is due to stochastic fluctuations in the adult sex ratio. Thus, in a population with two sexes the demographic variance can be decomposed as:

$$\sigma_d^2 = q\sigma_{df}^2 + (1 - q)\sigma_{dm}^2 + \sigma_{sex}^2, \qquad \text{eqn 1}$$

where q is the expected sex ratio in the breeding population, s the adult survival rate and $\sigma_{dm}^2 = s(1 - s)$. Engen *et al.* (2003) showed that the sex ratio component is especially large at small population sizes due to large sex ratio fluctuations. Temporal autocorrelations in the sex ratio, which may be substantial with long generation times, also will have a large effect on σ_{sex}^2.

Allee effects that reduce population growth rates at small population sizes (Allee *et al.* 1949) can strongly affect population dynamics and may cause rapid extinction of small populations (Dennis 1989, 2002). Lande (1998) demonstrated that demographic stochasticity by itself could induce a stochastic Allee effect that will cause most sample paths in small populations to decrease. Furthermore, stochastic fluctuations in the sex ratio, resulting in a lack of mates, may also lead to reduced reproductive rate at low population sizes and have direct negative effects on the mean population growth rate. Because demographic stochasticity operates differently in monogamous and polygynous mating systems (Engen *et al.* 2003), this may indicate that the risk of extinction at small population sizes may be related to the mating system.

In addition to changing the influence of the stochastic factors, using the total population size may also affect the deterministic component of the population dynamics (e.g. the strength and form of density dependence). In most demographic or population dynamical analyses density dependence is considered only within the female segment of the population. For instance, in many polygynous mammals the males visit the females only during a short period during the rut (Dubois *et al.* 1996). However, in many cases the number of males will also affect the demographic characteristics of the females. For instance, in many temperate ungulates, changes in age and sex-composition affect the demography and the population dynamics in complicated ways (Coulson *et al.* 2001; Clutton-Brock & Coulson 2002; Clutton-Brock *et al.* 2002; Mysterud *et al.* 2002).

The purpose of the present study is to partition the demographic variance into the three components in two populations of the great reed warbler *Acrocephalus arundinaceus* L. with different dynamical characteristics. We will then examine how assumptions regarding the structure of the mating system affect the stochastic components of the population dynamics, dependent on whether the density regulation operates on total population size or only within the female segment of the population. To obtain a proper understanding of magnitude of the effects of mating system our major comparison involves the two extremes of a strictly monogamous and a polygynous mating system. We explore how this affects the estimated time to extinction of the two populations. This will enable us to examine how mating system and form of density regulation interact to influence the viability of small bird populations.

Population model

DENSITY-DEPENDENCE ACTING ON TOTAL POPULATION SIZE

Let N and X be the total population size and the number of females, respectively. Then, assuming that the density regulation depends on the total population size and acts only on the fecundity so that mean fecundity for a given environment $\mathbf{Z}$ is a function of the population size, $f(N, \mathbf{Z})$. Writing $\bar{f}(N)$ for the mean of $f(N, \mathbf{Z})$ over temporal environmental fluctuations in $\mathbf{Z}$, the carrying capacity is determined by $\bar{f}(K) = 0$. For this type of density regulation Engen *et al.* (2003) showed, approximating the coloured noise process by a process with white noise, that in a polygynous mating system

$$\sigma^2_{sex} = q(1-q)\bar{f}^2(1+s)/(1-s). \qquad \text{eqn 2}$$

In a monogamous mating system the effects of sex ratio fluctuations become more complicated because fluctuations in the sex ratio may also create an Allee effect, that is, an unstable equilibrium at some small population size (Dennis 1989, 2002; Lande 1998). Engen *et al.* (2003) showed in a monogamous mating system that:

$$\sigma^2_{sex} = \frac{1}{4}\bar{f}^2\left(1 - \frac{2}{\pi}\right)G_\varepsilon \approx 0.0908\,\bar{f}^2 G_\varepsilon. \qquad \text{eqn 3}$$

Here $G_\varepsilon = 1 + 2\sum_{h=1}^{\infty}\rho_\varepsilon(h)$, where $\rho_\varepsilon(h)$ is the correlation function for the noise, required for correction of the white noise approximation.

DENSITY REGULATION ACTING WITHIN THE FEMALE SEGMENT OF THE POPULATION

To analyse the effects of density regulation operating only in the female segment of the population we consider the model obtained by substituting $f(X/q, \mathbf{Z})$ for $f(N, \mathbf{Z})$ where q denotes the mean proportion of females in the population. The carrying capacity K_f for the females is then defined by $\bar{f}(K_f/q) = 0$, so that $K_f = qK$, making the two models of density regulation directly comparable because they will actually generate population fluctuations around the same total population size. We will now consider how fluctuations in the sex ratio will generate additional variance in the change in population size from one year to another, ΔN, for two types of mating systems. We show in Appendix I (eqns A4 and A6) that when the density regulation operates within the female segment of the populations,

$$\sigma^2_{sex} = q(1-q)\left(\bar{f} + N\frac{d\bar{f}}{dN}\right)^2(1+s)/(1-s) \qquad \text{eqn 4}$$

for a polygynous mating system, and

$$\sigma^2_{sex} = \frac{1}{4}\bar{f}^2\left(1 - \frac{2}{\pi}\right)G(s)$$
$$+ \frac{1}{4}\left(N\frac{d\bar{f}}{dN}\right)^2\left(1 - \sqrt{\frac{2}{\pi N}}\right)^2(1+s)/(1-s) \qquad \text{eqn 5}$$

for a monogamous mating system. These expressions for σ^2_{sex} differ from those derived by Engen *et al.* (2003) due to $f(N, \mathbf{Z})$ being replaced by the stochastic term $f(X/q, \mathbf{Z})$. In eqn 4 this gives the term $N\,df/f(N)$, whereas in eqn 5 it generates the last term that is proportional to $(N\,df/dN)^2$. For further details, see Appendix I.

SPECIES

The great reed warbler is a medium-sized passerine bird that winters in sub-Saharan tropical Africa and breeds in Europe and Asia. The males return to the Swedish breeding grounds in early May, and the females about 2 weeks later. The great reed warbler has a facultative polygynous mating system (Dyrcz 1986, 1988); at Lake Kvismaren, about 40% of the territorial males form pair bonds with two to five females, whereas about 20% of the territorial males remain unpaired (Bensch & Hasselquist 1991; Hasselquist, Bensch & von Schantz 1995; Hasselquist 1998). In the German population, about 11% of the males form pair bonds with two females and 14% of the territorial males remain unpaired (Leisler *et al.* 1995). In general, the proportion of polygynous males as well as the frequency of extra-pair mating was smaller in the German than in the Swedish population (Hasselquist *et al.* 1995; Leisler *et al.* 1995, 2000; Hasselquist, Bensch & von Schantz 1996; Leisler & Wink 2000).

STUDY AREAS

Swedish population

A population of great reed warblers was studied at Lake Kvismaren (59°10′N, 15°25′E) in southern Central Sweden in 1986–2002. Each year, fieldwork was carried out daily from late April to early May when the first great reed warblers arrive, to the beginning of August when the last young become fledged. All territorial males and breeding females were mist-netted the first year they settled in our study area, in most cases very soon after arrival (Bensch & Hasselquist 1991; Bensch *et al.* 1998; Hasselquist 1998). A high degree of philopatry was found in the Swedish population (Hansson *et al.* 2002).

German population

The German study site is located 290 m above sea level in a fishpond area north-west of Erlangen (49°40′N, 10°51′E) in northern Bavaria (see Leisler *et al.* 1995 for a closer description). The study area was monitored by

regular visits during the whole breeding period from the end of April to the middle of July. Adults were colour-ringed individually, whereas nestlings were ringed with metal rings.

Methods

POPULATION CENSUSES

An examination of the time-series of the population fluctuations (Fig. 1) shows different patterns in the two study areas. The Swedish population has fluctuated during the last years around a mean value. In contrast, the German population has declined over a period of several years.

ESTIMATION OF PARAMETERS

The demographic variance in the female segment of the population was estimated as the weighted mean across years of the fitness contributions of the females (number of female offspring born during the year that survive for at least 1 year plus 1 if the female herself survives) to next generations (Engen, Bakke & Islam 1998; Sæther *et al.* 1998, 2000a,b; Sæther & Engen 2002a).

In order to estimate σ_{dm}^2, including male offspring as well as females (Engen *et al.* 2003), we assume an equal number of adult males and females in the two breeding populations (i.e. $q = 0.5$) and write $R_{TOT} = M + F +$

Fig. 1. Fluctuations in total ($\bigcirc$) and female ($\bullet$) population size of the Swedish population of great reed warblers at Lake Kvismare and of the German population in the Fränkischer Weiher region.

$J = O + J$ for the total contribution of the female to the next generation. Here M and F are the numbers of male and female offspring that survive to the next generation ($O = M + F$), and J is an indicator variable for the mother's survival to the next generation. We can then estimate according to Appendix C in Engen *et al.* (2003) the contribution σ_{dm}^2 to σ_d^2 from the females when only data on female offspring are available. Based on the recapture rate of adults, we assume an adult survival rate $s = 0.51$ ($n = 12$ years) and $s = 0.43$ ($n = 25$ years) in the Swedish and German population, respectively. Furthermore, assuming no sexual difference in adult survival, the component of the demographic variance generated by binomial distribution of male survival then becomes $\sigma_{dm}^2 = s(1 - s)(1 - q)$.

The final component in the demographic variance of the total population (eqn 1) is the contribution due to stochastic temporal variation in the sex ratio σ_{sex}^2. This contribution will depend on the mating system (see eqns 2, 3, A4, A6).

Based on the differences in the pattern of population fluctuations in the two different study areas (Fig. 1), we fitted different population models to the two populations. In the declining German population, we assumed a population model without density regulation. We assume that the change in the logarithm of population size among years ($\Delta \ln N$) is normally distributed. If r is the deterministic growth rate, i.e. $\exp(r) = E(N_{t+1}/N_t \,|\, N_t)$ and σ_e^2 is the environmental stochasticity (Engen, Sæther & Møller 2001), the stochastic growth rate

$$s = E(\Delta \ln N \,|\, N = n) \approx r - \sigma_e^2/2 - \sigma_d^2/2N \qquad \text{eqn 5a}$$

and

$$\mathrm{var}(\Delta \ln N \,|\, N = n) \approx \sigma_e^2 + \sigma_d^2/N. \qquad \text{eqn 5b}$$

If $X_t = N_t$, the likelihood function (omitting the constant factors) then becomes:

$$L(r, \sigma_e^2) = \prod_{i=2}^{k} \frac{1}{\sqrt{(\sigma_e^2 + \sigma_d^2 \exp(-X_{i-1}))}}$$

$$\exp\left\{ -\frac{[X_i - X_{i-1} - r + \sigma_e^2/2 + (\sigma_d^2 \exp(-X_{i-1}))/2]^2}{2(\sigma_e^2 + \sigma_d^2 \exp(-X_{i-1}))} \right\}$$

$$\text{eqn 6}$$

that is maximized numerically with respect to the two unknown parameters r and σ_e^2.

For the Swedish population we assumed a logistic type of density regulation (Lande *et al.* 2003), where

$$E(\Delta \ln N \,|\, N) = r_1 \left[1 - \frac{N - 1}{K - 1} \right]. \qquad \text{eqn 7}$$

Here r_1 is the specific growth rate at the smallest possible population size (excluding extinction) at $N = 1$. In many passerine species a logistic model describes
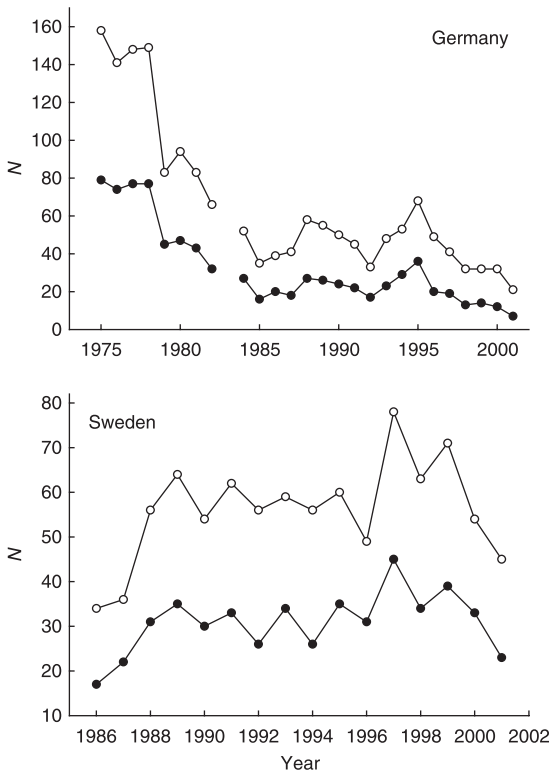
the pattern of density regulation quite well (Sæther *et al.* 2000a; Sæther & Engen 2002b). Following Engen *et al.* (1998) and Sæther *et al.* (2000a), the population parameters r_1, K and σ_e^2 were then estimated by maximum likelihood. Parametric bootstrapping (Efron & Tibshirani 1993) was used to estimate the bias in the estimate of r_1 (see procedures in Sæther *et al.* 2002a).

TIME TO EXTINCTION

We examined the effect of mating system on the extinction process by simulating the process approximating ΔN using a normally distributed variable with mean and variance defined by eqns A1 and A5. Under logistic density regulation we have $\bar{f}(N) = f_0 (1 - \beta N)$ so that $\beta = [1 - (1 - s)/f_0]/K$. The Swedish population showed stationary fluctuations around K (Fig. 1), making it difficult to obtain estimates of the reproductive rate f_0 at low densities (see Aanes *et al.* 2002). Thus, we assumed f_0 to be the maximum number of female fledglings produced during a year, assuming an even sex ratio at fledging (Bensch *et al.* 1999), multiplied by the maximum annual survival rate, giving $\hat{f}_0 = 2{\cdot}13 * 0{\cdot}82 = 1{\cdot}75$ (see also Sæther, Engen & Matthysen 2002b for a similar approach). In the declining German population (Fig. 1), we assumed that the reproductive rate currently recorded was representative of f_0, giving $\hat{f}_0 = 0{\cdot}52$. In this population we assumed K to be large ($K = 1000$) to produce a small value of β and hence very weak density dependence in $\bar{f}(N)$.

Although these approximations may be rather rough at very small population sizes, Engen *et al.* (2003) found the model to be a fair approximation down to population sizes of five to 10 individuals. Because the populations are likely to spend only short periods at very small population sizes, we chose to use the approximations all the way down to extinction at $N = 1$ individual.

Results

All components of the demographic variance were larger in the stationary Swedish population than in the declining German population (Table 1). The demographic variance in the female segment of the population constituted 65% and 73% of the contribution from females to the demographic variance in the total Swedish and German populations, respectively. A large influence of mating system was found on the contribution to demographic stochasticity due to sex ratio fluctuations. In both populations σ_{sex}^2 was about five times higher for the polygynous mating system than for the monogamous mating system (Table 1). As a consequence, the total demographic variance assuming a monogamous mating system was about half the value of the demographic variance for the polygynous mating system (Table 1). The environmental stochasticity in the total population size was, however, smaller for a polygynous ($\hat{\sigma}_e^2 = 0{\cdot}0056$ in the Swedish and

Table 1. Components of demographic stochasticity for monogamous and polygynous mating systems in the Swedish and German populations of the great reed warbler. σ_f^2 is the demographic variance in the female segment of the population, σ_d^2 the demographic variance for the total population, and σ_{df}^2, σ_{dm}^2 and σ_{sex}^2 the contribution to σ_d^2 from females, males and sex ratio fluctuations, respectively

| | | | | Mating system | | | |
| | | | | Polygyny | | Monogamy | |
Population	σ_f^2	σ_{df}^2	σ_{dm}^2	σ_{sex}^2	σ_d^2	σ_{sex}^2	σ_d^2
Germany	0·360	0·491	0·122	0·816	1·184	0·166	0·533
Sweden	0·520	0·798	0·125	0·744	1·268	0·143	0·667

$\hat{\sigma}_e^2 = 0{\cdot}0323$ in the German population) mating system than when assuming monogamous mating $\hat{\sigma}_e^2 = 0{\cdot}0192$ in the Swedish and $\hat{\sigma}_e^2 = 0{\cdot}0423$ in the German population).

The great reed warbler has a facultative polygynous mating system (Dyrcz 1986, 1988). In the study population in Kvismare, on average 38% of the males were polygynous (Hasselquist 1998), whereas in Germany the proportion of males with more than one mate varied from 8 to 35% during a 5-year period (Leisler & Wink 2000). For such a polygynous mating system the risk of extinction of the total population was dependent on the type of density regulation. If density regulation acted on the whole population, the risk of extinction in a polygynous mating system was orders of magnitude larger for the Swedish population than when density regulation operated within only the female segment of the population (Fig. 2). For instance, in the latter case the cumulative probability of extinction after 5000 years was 0·0059, compared to 0·2239 if the density regulation acted on the whole population. A similar pattern was also present in the rapidly declining German population (Fig. 1), although the effect of differences in the pattern of density regulation was less pronounced (Fig. 3) than for the Swedish population (Fig. 2).

So far, we have assumed that all females obtain a mate in such a polygynous mating system. However, a surplus of non-breeding females has been recorded in many bird species (Newton 1998). In the Swedish population, the expected time to extinction decreased with a decrease in the proportion of females being mated (Fig. 4). This decline was smaller for density regulation acting on total population size than when it acted within the female segment of the population.

The risk of extinction of the total population is larger if we assume a monogamous mating system than under a polygynous mating system (Figs 2, 3). The magnitude of the difference in extinction risk between the mating system in the stationary Swedish population was much higher for density regulation acting only on the females than when it acted on total population size.
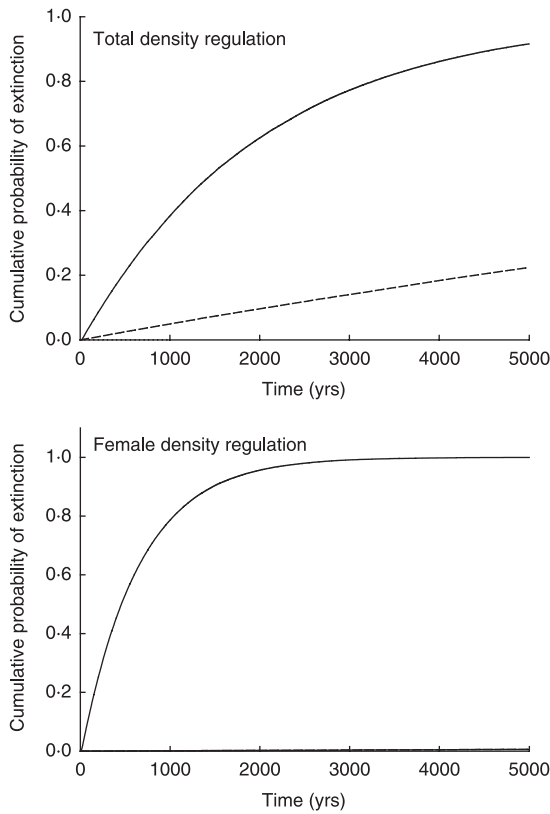
Fig. 2. The cumulative probability of extinction of the Swedish population of great reed warblers in relation to mating system (solid line: monogamy, dotted line: polygyny) and type of density regulation.
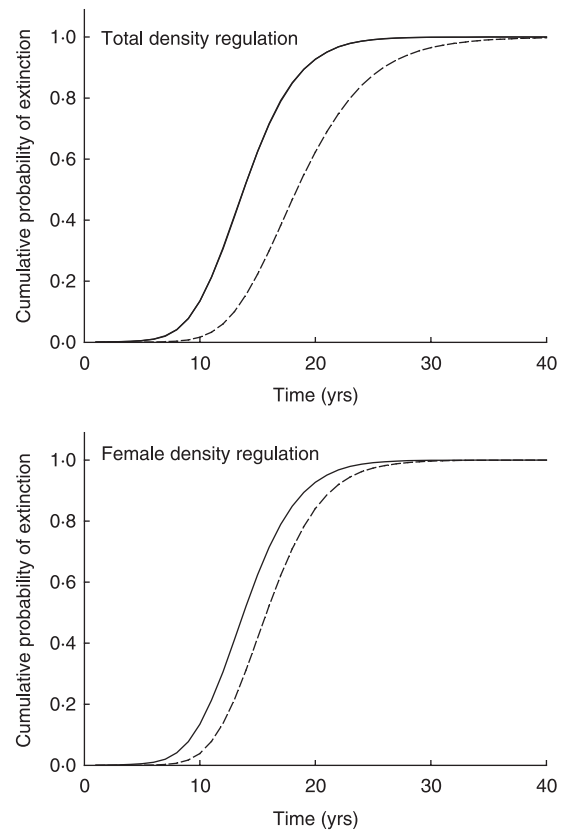

Fig. 3. The cumulative probability of extinction of the German population of great reed warblers in relation to mating system (solid line: monogamy, dotted line: polygyny) and type of density regulation.

Discussion

Our analyses have shown that sex ratio fluctuations may strongly affect the estimated time to extinction. These effects are influenced strongly by the mating system. In general, the time to extinction becomes shorter in a monogamous than in polygynous mating system (Figs 2, 3). This difference was larger in the Swedish population when density regulation acts only within the female segment than when it operates on the total population size. This demonstrates that sex effects must be included when making population predictions based on counts of total population sizes, and supports previous results obtained by simulation studies (Brook *et al.* 1999; Brook, Burgman & Frankham 2000).

The mathematical results are based on the same simplifying assumptions as in Engen *et al.* (2003), implying several first-order approximations. These are valid for large populations but were shown to give sufficient accuracy even down to quite small population sizes. Furthermore, we also used a first-order approximation (a linearization) for comparing the two models of density regulation. The accuracy of this approximation also depends on the population size, but as the new term involved is always relatively small, the errors involved at small population sizes will also be small. Thus, we believe that our model gives a relatively accurate representation of the fluctuations even for small populations.
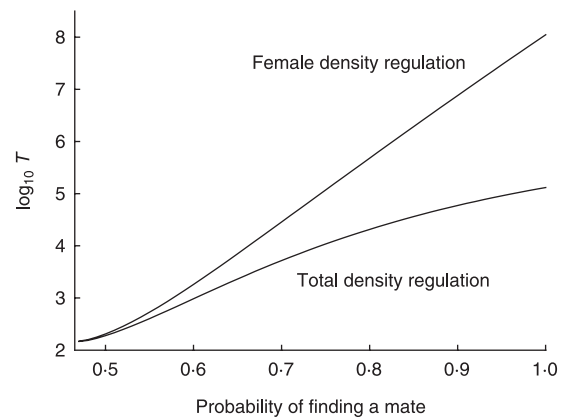

Fig. 4. The expected time to extinction ($\log_{10} T$) of the Swedish population of great reed warblers in relation to the probability of a female being mated for different types of density regulation. A polygynous mating system is assumed.

Our analyses are based on several simplifying assumptions that may not always be valid (see Møller & Legendre 2001; Kokko & Brooks 2003; Møller 2003). First, we assume an age-independent adult survival rate that also is independent of sex. Especially in polygynous species sex-specific differences in survival have been recorded (Promislow, Montgomerie & Martin 1992; 1994). A second assumption is that the reproductive

success of the females in the polygynous mating system is independent of the proportion of males in the population. Such effects arise if low availability of males results in more females forming pair bonds with polygynous males and thus obtaining less help with parental care, causing reduction in their reproductive success (see Møller & Legendre 2001 for further discussion). For instance, great reed warbler females with secondary status when feeding nestlings have poorer reproductive success than females with primary status (Bensch & Hasselquist 1994; Bensch 1996; Sejberg, Bensch & Hasselquist 2000). Thirdly, we assume that the sex ratio in the population fluctuates only stochastically. Some evidence now suggests that offspring sex ratio may be affected by population structure through largely unknown feedback mechanisms (Sæther *et al.* 2003; 2004); however, no such evidence has been found in the Swedish great reed warbler population (Bensch *et al.* 1999). Finally, the density dependence is assumed to affect only the fecundity rate, which is not necessarily true for sedentary small passerines (Arcese *et al.* 1992). Only further analyses with the use of an explicit simulation model will reveal how these effects will influence the present results.

Nevertheless, even with the simplifying assumptions, our modelling effort was able to demonstrate the influence of variation in mating system on the expected time to extinction of the great reed warbler population (Figs 2, 3). In general, time to extinction for the total population size was shorter for a monogamous than for a polygynous mating system. This is in accordance with the results of Legendre *et al.* (1999), modelling the effects of stochastic variation in sex ratio for establishment success. They showed that when the mating system changed from polygyny to mongamy a large increase in the initial population size was necessary for keeping the extinction risk constant. The large proportion of unmated females present in many monogamous breeding populations (Newton 1998) also suggests that such an extreme monogamous mating system may be a valid description of the mating system in many bird species. Thus, predictions of extinction risk for total population size must include explicit assumptions about the mating system.

These effects of mating system were strongly dependent on how density regulation acted on the total population (Figs 2–4). In polygynous passerine birds such as the pied flycatcher *Ficedula hypoleuca* (Pallas) there is some evidence of intrasexual agression among females (Slagsvold & Lifjeld 1994), which may indicate the potential for density-dependence within the female segment of the population (Arcese 1989). Also, in the great reed warbler female behaviour seems to be influenced by the presence of other females (Bensch & Hasselquist 1992). Accordingly, removal experiments in passerine bird species have shown the presence of a surplus of non-breeding females during the breeding season (Sæther & Fonstad 1981). Even in species with weaker territorial defence than in many passerines

there is some evidence that density regulation may operate mainly among females. For instance, in some ungulates males and females use different areas during most of the year (e.g. Mouflon *Ovis ammon* L. (Dubois *et al.* 1996). Furthermore, even in species where the sexes are less spatially segregated (e.g. red deer (Conradt, Clutton-Brock & Thomson 1999) and white-tailed deer *Odocoileus virginianus* (Boddaert) (McCullough 1979) density regulation acts mainly within the female segment of the population. In contrast, in some other ungulate populations density dependence seems to operate through total population size (Mysterud *et al.* 2002), due probably to greater sexual overlap in resource use.

To summarize, our analyses of two populations of great reed warbler demonstrate that predictions of future population sizes based on total population counts must include explicit assumptions on how density regulation acts and the structure of the mating system (Brook *et al.* 1999, 2000). In particular, analyses of the time to extinction for the total population, which is central for the field of population viability analyses (see Beissinger & McCullough 2002), is likely to be strongly biased if such information is unavailable.

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Appendix I

Here we assume that density regulation operates only within the female segment of the population so that mean fecundity for a given environment **Z** is a function of the female population size, $f(X/q, \mathbf{Z})$. Here N is the total population size, X the number of females in the population and q is the mean proportion of females.

POLYGYNOUS MATING SYSTEM

For a polygynous mating system and density regulation depending on total population size, Engen *et al.* (2003) showed that the yearly change in population size could be written approximately as:

$$\Delta N = N[\bar{f}(N)q - (1 - s)] + \sqrt{N}\sigma_d\delta_d + N\sigma_e\delta_e, \quad \text{eqn A1}$$

where $\sigma_e^2 = \text{var}[f(N, \mathbf{Z})q + s(\mathbf{Z})|N]$. Here $s(\mathbf{Z})$ is the annual survival rate in environment **Z** and s is the mean of $s(\mathbf{Z})$ over the temporal environmental fluctuations in **Z**. The variables δ_d and δ_e are inde-

pendent standard normally distributed so that $\text{var}(\Delta N | N) = \sigma_d^2 N + \sigma_e^2 N^2$.

The demographic variance component σ_d^2 is given by eqn 1. The stochastic fluctuation in the sex ratio generates a variance-component given by:

$$\sigma_{sex}^2 = q(1 - q)\bar{f}^2(1 + s)/(1 - s),$$

which increases with the adult survival due to autocorrelations in the sex ratio generated by this survival. This temporal autocorrelation has been corrected for in eqn A1 that is a model with white noise (Engen *et al.* 2003).

The demographic term in eqn A1 may alternatively be written in the form:

$$\sigma_d\delta_d = \sigma_{dm}\sqrt{1 - q}\,\delta_{dm} + \sigma_{df}\sqrt{q}\,\delta_{df} + \sigma_{sex}\delta_{sex} \quad \text{eqn A2}$$

where δ_{dm}, δ_{df} and δ_{sex} are independent variables with zero mean and unit variance.

Conditioned on N the number of females is approximately binomially distributed (see Engen *et al.* 2003)

and the standardized variable in eqn 3 describing the sex ratio fluctuations then becomes:

$$\delta_{sex} = (X/N - q)/\sqrt{q(1 - q)/N}.$$

We then have:

$$X/q = N + \delta_{sex}\sqrt{N(1 - q)/q}.$$

When the density regulation depends on the number of females only, we find the first order approximation

$$\bar{f}(X/q) \approx \bar{f}(N) + \frac{d\bar{f}}{dN}\delta_{sex}\sqrt{N(1 - q)/q}. \qquad \text{eqn A3}$$

Replacing $\bar{f}(N)$ by this expression in eqn A1, ignoring higher-order terms, we find the only difference is that the factor $\bar{f}$ in the coefficient of δ_{sex} is replaced by $\bar{f} + (d\bar{f}/dN)N$. Hence, the demographic variance component due to sex ratio fluctuations turns out to be:

$$\sigma^2_{sex} = q(1 - q)\left(\bar{f} + N\frac{d\bar{f}}{dN}\right)^2 (1 + s)/(1 - s). \qquad \text{eqn A4}$$

Because density regulation implies that the derivative of $\bar{f}(N)$ is negative, we see that σ^2_{sex} is likely to be somewhat smaller for density regulation operating only within the female segment of the population than when it acts on total population size.

MONOGAMOUS MATING SYSTEM

Following Engen *et al.* (2003) we assume that newborn individuals are females with probability $q = 0.5$ and a strictly monogamous mating system where the number of females mated is the minimum of the number of males and females in the population. Then, when density regulation acts through N, the reproductive rate has

mean $\bar{f}(N)X$ if $X < N - X$ and otherwise $\bar{f}(N)(N - X)$, which may be rewritten as $\bar{f}(N)(N/2)(1 - |\delta_{sex}|/\sqrt{N})$. As was the case for the polygynous mating system, our aim is to examine the effects of density regulating operating only within the female segment of the population. This is obtained by replacing $\bar{f}(N)$ with $\bar{f}(X/q)$. Using the same approach as for the polygynous mating system, and observing that δ_{sex} and $|\delta_{sex}|$ are independent, we find that the mean of ΔN is unaffected, with an Allee effect as described by Engen *et al.* (2003), that is:

$$E(\Delta N | N) = N\left[\frac{1}{2}\bar{f}(N)\left(1 - \sqrt{\frac{2}{\pi N}}\right)\right] - (1 - s). \qquad \text{eqn A5}$$

However, the demographic variance component σ^2_{sex} now includes an additional term

$$\frac{1}{4}\left(N\frac{d\bar{f}}{dN}\right)^2\left(1 - \sqrt{\frac{2}{\pi N}}\right)^2 (1 + s)(1 - s), \text{ giving:}$$

$$\sigma^2_{sex} = \frac{1}{4}\bar{f}^2\left(1 - \frac{2}{\pi}\right)G(s)$$
$$+ \frac{1}{4}\left(N\frac{d\bar{f}}{dN}\right)^2\left(1 - \sqrt{\frac{2}{\pi N}}\right)^2 (1 + s)/(1 - s). \text{ eqn A6}$$

The factor $G(s)$ corrects for the temporal autocorrelations in the sex ratio. More precisely, $G(s) = 1 + \sum_{h=1}^{\infty} \rho(h, s)$, where

$$\rho(h, s) \approx \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\left|\left(xs^h + y\sqrt{1 - s^{2h}}\right)\right|\frac{1}{2\pi}e^{-(x^2+y^2)/2}dxdy.$$

By inspection of eqn A6 we see that the value of σ^2_{sex} will now be larger when the density regulation operates only within the female segment of the population. This is in contrast to the patterns found for the polygynous mating system.