

EFFECTIVE SIZE OF FLUCTUATING POPULATIONS WITH TWO SEXES AND OVERLAPPING GENERATIONS

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We derive formulas that can be applied to estimate the effective population size N_e for organisms with two sexes reproducing once a year and having constant adult mean vital rates independent of age. Temporal fluctuations in population size are generated by demographic and environmental stochasticity. For populations with even sex ratio at birth, no deterministic population growth and identical mean vital rates for both sexes, the key parameter determining N_e is simply the mean value of the demographic variance for males and females considered separately. In this case Crow and Kimura's generalization of Wright's formula for N_e with two sexes, in terms of the effective population sizes for each sex, is applicable even for fluctuating populations with different stochasticity in vital rates for males and females. If the mean vital rates are different for the sexes then a simple linear combination of the demographic variances determines N_e , further extending Wright's formula. For long-lived species an expression is derived for N_e involving the generation times for both sexes. In the general case with nonzero population growth and uneven sex ratio of newborns, we use the model to investigate numerically the effects of different population parameters on N_e . We also estimate the ratio of effective to actual population size in six populations of house sparrows on islands off the coast of northern Norway. This ratio showed large interisland variation because of demographic differences among the populations. Finally, we calculate how N_e in a growing house sparrow population will change over time.

KEY WORDS: Demographic variance, fluctuating populations, genetic drift, house sparrow, overlapping generations.

The concept of effective population size N_e was introduced by Wright (1931) by setting the variance of allele frequency during one generation of random genetic drift equal to that of an ideal population of constant size with discrete, nonoverlapping generations reproducing by random sampling of gametes. The effective size of a population determines the expected rates of random genetic drift and loss of selectively neutral heterozygosity, which are proportional to $1/(2N_e)$ for a diploid population. The effective population size, in combination with natural selection, also determines the fixation probabilities of mutations. Thus, identifying factors influencing the effective population size is fundamental

for understanding evolution in finite populations (Wright 1931, 1969; Lande 1979, 1980, 1985; Kimura 1983) and for developing management strategies for threatened or vulnerable species (Frankham et al. 2002).

In an ideal diploid population half of the random genetic drift is caused by Mendelian segregation and half is due to variance in family size (Crow and Kimura 1970). In real populations N_e is often considerably smaller than the actual population size N because of uneven sex ratio, deviation from a Poisson distribution of family sizes and temporal variation in population size (Grant and Grant 1992; Caballero 1994; Nunney and Elam 1994; Frankham 1995;

Vucetich et al. 1997; Creel 1998; Frankham et al. 2002; Waples 2002, 2006; Hedrick 2005). For populations that change in size, Crow and Denniston (1988) distinguished the variance effective size (governing the sampling variance of allele frequency per generation) from the inbreeding effective size (governing the expected rate of increase in identity by descent). The variance effective size depends mainly on the number of offspring produced, whereas the inbreeding effective size is mainly dependent on the number of parents. In stable populations with nonoverlapping generations and no inbreeding these two effective population sizes are equal.

During recent years great advances have been made in studies of the structure of vertebrate mating systems by applying modern molecular biological techniques (Hughes 1998). A general pattern that appears is that even in putatively monogamous species the variance in reproductive success may differ greatly between the sexes (Clutton-Brock 1998; Newton 1989), especially due to extra-pair copulations (Møller and Ninni 1998; Westneat and Stewart 2003; Whittingham and Dunn 2005). Simulations have shown that such deviations from an ideal population strongly affect N_e (Nunney 1993). In addition, the mean and variance in age-specific vital rates may also differ between the sexes. For instance, in birds (Promislow et al. 1992) as well as in mammals (Promislow 1992) intersexual differences in survival are associated with traits subject to sexual selection. Understanding the consequences of such observations requires methods for calculating effective population sizes that account for different mating systems as well as different life histories in males and females.

Most of the theory developed for effective population sizes assumes nonoverlapping generations. However, natural populations generally have overlapping generations, which greatly complicates calculation of effective population sizes. Formulas for effective population size in iteroparous species with overlapping generations (Felsenstein 1971; Hill 1972, 1979; Emigh and Pollak 1979; Nunney 1991, 1993; Orive 1993; Caballero 1994; Pollak 2000) assume a constant environment and age structure, and usually, constant population sizes. These assumptions ignore that in most natural populations demographic stochasticity (random variation in individual fitness) and environmental stochasticity (correlated variation in fitness among individuals in a population Lande et al. 2003) produce fluctuations in age structure and total population size that are essential when calculating the effective size of natural populations.

Engen et al. (2005a) used diffusion theory for an age structured population in a fluctuating environment to describe demographic stochasticity in total population size. This was applied by Engen et al. (2005b) to calculate the effective size of populations, following Pollak (2000), by using the dynamic properties of a subpopulation of individuals bearing a rare selectively neutral allele. Individuals with this allele are then all heterozygotes that mate with individuals not bearing the allele. Engen et al. (2005b)

argued theoretically and showed by stochastic simulations that the effective population size found by this approach also predicts the correct magnitude of genetic drift for intermediate gene frequencies. If the demographic variance for the subpopulation of individuals bearing the rare allele is σ_{dg}^2 , the effective population size is

$$N_e \approx N / (\sigma_{dg}^2 T), \quad (1)$$

where N is the total actual population size and T is the mean deterministic generation time for males and females. Although the actual generation time will fluctuate stochastically around the deterministic value due to demographic and environmental stochasticity, Engen et al. (2005b) verified the accuracy of the approximations in this formula.

Numerical computation of effective population sizes can be performed using formulas of Engen et al. (2005b), but the general results for two sexes are too complicated to permit analytical comparisons with other models. Here we consider the important special life history in which individuals become reproductive after one year and thereafter have constant mean vital rates that may be different for males and females. This will apply to life histories that are typical for many animal species, particularly small birds. We assume that individuals enter the adult population one year after they are born and that census of the population occurs immediately before reproduction so that the size of the population (with overlapping generations) is enumerated by the number of adults. In this way we avoid the problem of age structure, but we still need to apply the theory of Engen et al. (2005a) for demographic stochasticity with a two-dimensional square matrix to describe the joint dynamics of two sexes. This generalizes previous work by Nunney (1991, 1993); Nunney and Elam (1994), and Charlesworth (2001) based on Hill's (1972, 1979) model for the effective size of a population of constant size. Our method facilitates an analysis of the influence of several simultaneously varying parameters and the covariance among them on the effective size of a population with such a simplified life history (Caswell 1978; Crow and Denniston 1988). We will also examine how changes in N_e over longer time periods are influenced by fluctuations in population size. Our method extends previous approaches (Lande and Barrowclough 1987; Nunney and Elam 1994; Vucetich et al. 1997; Waples 2002, 2006) by allowing for differences between sexes as well as changes in population size and stochastic fluctuations in sex ratio.

Wright's (1931) formula $N_e = 4N_f N_m / (N_f + N_m)$ expresses the effective size of a randomly mating population with separate sexes and Poisson distributed family size in terms of numbers of females N_f and males N_m in the population. Crow and Kimura (1970, p. 359) derived a more general version of this formula expressing the variance effective population size N_e for a population with

discrete nonoverlapping generations as a function of the effective population sizes of females and males, N_{ef} and N_{em} , considered separately,

$$N_e = \frac{4N_{ef}N_{em}}{N_{ef} + N_{em}}. \quad (2)$$

However, as they only considered nonoverlapping generations their definition of N_{ef} and N_{em} were simply the variances of family sizes. To deal with overlapping generations, we need to generalize these definitions using the distribution of their vital rates.

We have two major aims. First, we show how the effective population size of each sex, N_{ef} and N_{em} , depends on the distribution of vital rates and relate this to the concept of demographic variance of each sex considering females producing females and males producing males only. This enables us to compare our results to Crow and Kimura's (1970) generalization of Wright's (1931) formula (eq. 2). We show that Wright's formula remains valid for overlapping generations and fluctuating population size if males and females have the same mean dynamics, the sex ratio at birth is 1:1 and the expected population growth rate is zero. Under these simplifying assumptions the variance σ_{dg}^2 , which determines the effective population size, is simply the mean value of the demographic variance for the pure male and pure female populations, a relationship that enables easy estimation of N_e if full information about mothers and fathers of offspring is available. If the mean survival and fecundity are different for the two sexes, a simple extension of Wright's formula is derived when the sex ratio at birth is 1:1. In this case σ_{dg}^2 is a linear combination of the demographic variances for males and females considered separately, with coefficients determined by their vital rates. Second, we illustrate the application of this approach by calculating N_e/N in six populations of the house sparrow *Passer domesticus* in northern Norway. This allows us to examine the relative contribution of males and females to differences in N_e among populations and to analyze the sensitivity of N_e to variation in different demographic traits. By combining these theoretical and empirical approaches we develop practical recommendations for obtaining reliable estimates of N_e/N for species with this relatively common type of life history.

Each Sex Considered Separately

The demographic variance is usually only defined for the female segment of the population (Sæther et al. 1998), but here we will see that the effective size of a population with two sexes relates to the demographic variance of each sex considered as separate populations. To generalize Wright's formula (eq. 2) to the case of overlapping generations, we need to find the effective population size of monoecious populations with the same vital rates as the male and female segments of the two-sex population.

Consider a monoecious population with the same vital rates as the females in which a small fraction of individuals is heterozygotes bearing a rare selectively neutral allele. Write N_f for the total population size and X_f for the number of individuals with the rare allele. Let b_f and σ_f^2 be the mean and variance of the number of offspring (all of which are females) produced by one individual in a given year, and let s_f be the adult annual survival probability. As only one of two alleles of each of a mother's offspring is inherited from her due to Mendelian segregation, the birth rate is $b_f/2$ and the expected population size the next year is $N_f + E\Delta N_f = \lambda N_f = (b_f/2 + s_f)N_f$. The expected number of individuals with the rare allele in the next generation is $X_f + E\Delta X_f = (b_f/2 + s_f)X_f = \lambda X_f$ because the rare allele is transmitted to the offspring with probability 1/2 whereas the other allele of the offspring must come from the major part of the population homozygous for the common allele. Appendix 1 shows that under these assumptions the variance of the annual change in allele frequency $p = X_f/(2N_f)$ is

$$\text{var}(\Delta p) \approx \frac{[b_f/4 + \sigma_f^2/4 + s_f(1 - s_f) + c_f]p}{2N_f}. \quad (3)$$

The parameter c_f is the covariance between an individual's number of offspring and the indicator variable (0 or 1) for its survival. The deterministic generation time for this population is $T_f = \lambda/(\lambda - s_f)$ (Lande et al. 2003) and the variance of the allele frequency across one generation is $T_f \text{var}(\Delta p)$. From the definition of variance effective population size (Crow and Denniston 1988) this equals $p/(2N_{ef})$ for small values of p . Hence, we find in accordance with equation (1) that

$$N_{ef} = \frac{N_f}{\sigma_{dgf}^2 T_f} = \frac{N_f}{[b_f/4 + \sigma_f^2/4 + s_f(1 - s_f) + c_f]T_f}. \quad (4)$$

We further define N_{em} by the same model replacing subscripts f by m .

It is interesting to observe that the parameter σ_{dgf}^2 , defined by equation (4), which is affected by demographic stochasticity as well as the genetic stochasticity caused by Mendelian segregation, is identical to the demographic stochasticity of the pure female segment of a dioecious population σ_{df}^2 , according to the definition in Sæther et al. (1998) and discussed in more detail by Engen et al. (2003), if the sex ratio of newborns is 1:1. The demographic variance of the female segment of a population is defined as the variance of a single female's contribution to the next year's female population that is (see Appendix 1)

$$\sigma_{df}^2 = b_f q(1 - q) + \sigma_f^2 q^2 + s_f(1 - s_f) + 2qc_f,$$

where q is the probability of a newborn being a female. Hence, for 1:1 sex ratio at birth, that is, $q = 1/2$, we see that $\sigma_{dgf}^2 = \sigma_{df}^2$, an equality leading to some simple relations between effective population size and demographic variance.

Two Sexes

Using the same parameters as in the previous section with subscripts *f* and *m* for females and males and following a matrix procedure similar to that of Engen et al. (2005b) we show, in Appendix 1, the derivation of the effective size of a population with two sexes. The deterministic growth rate is $\lambda = qb_f + s_f = (1 - q)b_m + s_m$, where *q* is the probability that a newborn individual is a female. To simplify the expressions we further write (with subscripts) $\tau = \sigma^2/b$ for the overdispersion relative to the Poisson distribution for the number of offspring, and $\gamma = c/b$ and $r = q(1 - q)$. The mean generation time of the population is $T = (T_f + T_m)/2 = [\lambda/(\lambda - s_f) + \lambda/(\lambda - s_m)]/2$. In Appendix 1 we further show that the variance parameter σ_{dg}^2 in equation (1) determining the effective population size is

$$\sigma_{dg}^2 = \frac{(a_1 + a_2)(b_f + b_m)}{\lambda^2(2\lambda - s_f - s_m)^2}, \quad (5)$$

where

$$a_1 = b_f b_m r [1 + r(\tau_f + \tau_m - 2) + 2\gamma_f(1 - q) + 2\gamma_m q], \quad (6)$$

$$a_2 = b_m s_f (1 - s_f)(1 - q)^2 + b_f s_m (1 - s_m)q^2. \quad (7)$$

Figure 1A shows examples of how the ratio of effective to actual population size N_e/N depends on the sex ratio at birth *q* and the generation time *T*. These results are in agreement with the effect of bias in sex ratio previously noted by Nunney (1993) who, with Hill (1979), assumed a constant population size.

If the sex ratio is close to 1:1, we find by inserting $q = 1/2$ in equations (5–7), that

$$\sigma_{dg}^2 = \frac{1}{2\lambda^2 b} (b_m \sigma_{df}^2 + b_f \sigma_{dm}^2), \quad (8)$$

where $b = (b_m + b_f)/2$. If we for simplicity assume that the major intersexual difference in demographic stochasticity is due to stronger selection in males than in females, we see that the effects of sexual selection on N_e/N , that is, increasing σ_{dm}^2 relative to σ_{df}^2 , are dependent on survival (Fig. 1B). Furthermore, the decrease in N_e/N for a given σ_{dm}^2 decreases with increasing generation time *T*.

The special case of nonoverlapping generations corresponds to $s_f = s_m = 0$, which implies that $\gamma_f = \gamma_m = 0$ giving

$$\sigma_{dg}^2 = [1 + q(1 - q)(\tau_f + \tau_m - 2)](b_f + b_m)/(4\lambda^2).$$

Using the relations $\lambda = qb_f = (1 - q)b_m$, this may alternatively be written as

$$\frac{N_e}{N} = \frac{4q(1 - q)\lambda}{1 + q(1 - q)(\tau_f + \tau_m - 2)}. \quad (9)$$

For a Poisson distributed of offspring number, a 1:1 sex ratio and $\lambda = 1$, this gives $\sigma_{dg}^2 = 1$ and $N_e = N$ in accordance with Wright

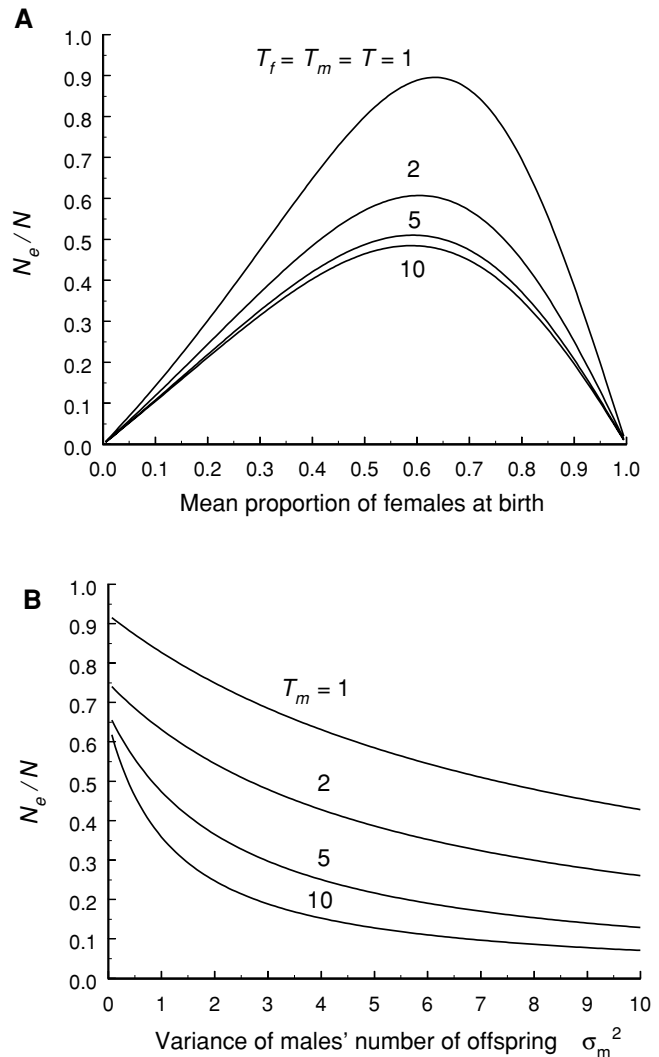


Figure 1. The upper panel (A) shows the relative effective population size N_e/N as a function of the proportion of females at birth *q* for different values of the generation time *T* that is the same for males and females. The other parameters are $\lambda = 1$, $\sigma_f^2 = b_f$, $\sigma_m^2 = 2\sigma_f^2$, and $c_f = c_m = 0$. The lower panel (B) shows the ratio of effective to actual population size N_e/N as a function of the variance of the males' number of offspring σ_m^2 for different values of the male generation time T_m . The other parameters are $q = 0.5$, $\lambda = 1$, $T_f = 3$, $\sigma_f^2 = b_f$, and $c_m = c_f = 0$.

(1931). We further arrive at Wright's formula for random mating populations with two sexes and nonoverlapping generations, $N_e = N/\sigma_{dg}^2 = 4N_f N_m / (N_f + N_m)$ by inserting $q = N_f / (N_f + N_m)$ and $\tau_f = \tau_m = 1$ in equation (9). The sex ratio in the population is q as $s_m = s_f = 0$ for nonoverlapping generations.

We can now also compare the more general version of Wright's (1931) formula (eq. 2) for nonoverlapping generations with our results for overlapping generations. For a 1:1 sex ratio at birth we derived equation (8), expressing σ_{dg}^2 as a linear combination of the demographic variance of each sex. Because there

are equal numbers of males and females at birth, the number N_f of females in the population is $NT_f/(T_f + T_m) = NT_f/(2T)$ giving $N_{ef} = N_f/(\sigma_{df}^2 T_f) = N/(2\sigma_{df}^2 T)$. Hence expressing all three variances in equation (8) in terms of effective population sizes and solving for N_e we obtain a simple generalization of Wright's formula, also valid for nonoverlapping generations,

$$N_e = \frac{4\lambda^2 b N_{ef} N_{em}}{b_f N_{ef} + b_m N_{em}}. \quad (10)$$

Note that b_m , the mean number of offspring produced by males, is not a free parameter but is determined by b_f , s_f , and s_m through the relation $\lambda = b_m/2 + s_m = b_f/2 + s_f$. Hence, if $\lambda = 1$ then $b_m = 2(1 - s_m) = 2d_m$ where d_m is the death rate for males. With a similar notation for females and the mean death rate we then see that the birth rates in equation (10) can be replaced by the death rates at equilibrium.

We now see that Wright's formula is also valid for overlapping generations if $\lambda = 1$ and $b_f = b_m$, which occurs if $s_f = s_m = 1 - b_m/2$. Hence, the application of equation (2) to fluctuating populations with overlapping generations requires identical expected dynamics of males and females and constant expected population size ($\lambda = 1$). However, the demographic stochasticity in number of offspring defined by σ_{df}^2 and σ_{dm}^2 and the covariances c_f and c_m may still differ between sexes.

Influence of Population Fluctuations on N_e

INSTANTANEOUS EFFECT

Demographic stochasticity in the process for the number of individuals heterozygous for the rare allele has been calculated using the results of Engen et al. (2005a) for the demographic variance of an age structured population subject to environmental fluctuations. Writing \mathbf{Z} for the vector of environmental variables determining the vital rates, the parameters s , σ^2 , and c with subscripts f or m are all in general functions of \mathbf{Z} . Stochastic fluctuations in the environment \mathbf{Z} between years then generate fluctuations in the parameters. According to Engen et al. (2005a) the parameters in equations (3–7) should in general be replaced by their expected values through time, that is, for example σ_f^2 should in general be interpreted as $E(\sigma_f^2|\mathbf{Z})$. As a consequence σ_f^2 should be estimated by the mean value through years of the within year sum of square estimates based on the number of offspring produced by females (for details, see Engen et al. 2005a). The same reinterpretation and estimation technique apply to the covariance terms c_f and c_m .

Similarly, terms of the type $s(1 - s)$ generated by the binomial distribution of surviving individuals also should be replaced by $E\{s(\mathbf{Z})[1 - s(\mathbf{Z})]\}$ which can be written as $Es(1 - Es) - \text{var}(s)$. However, we can easily see that the influence of environmen-

tal fluctuations on this term usually can be neglected. For example, if the mean survival through years is $Es = 0.5$ so that $Es(1 - Es) = 0.25$, and the standard deviation in s generated by fluctuations in the environment is 0.1, the correct value should be 0.24. Nevertheless, it is interesting to observe that the environmental variance in s actually leads to a decrease in the binomial term and hence an increase in the effective population size. In extreme cases the environmental variance in s cannot be neglected. If, for example, s takes values 0.01 and 0.99 with probabilities 0.5 so that $Es = 0.5$, then the binomial term is only 0.01, which is far from 0.25. (These comments also apply to the corresponding variance and covariance terms in appendix C in Engen et al. [2005a], used to calculate the effective population size for a more general age structured model.)

LONG-TERM EFFECT

In the general model of Engen et al. (2005b) it is shown that the environmental variance will also influence N_e through its effect on fluctuations in population size. Because the variance of change in allele frequency is proportional to $1/N_e$ (and $1/N$), genetic drift over longer time periods is determined by the mean value of $1/N$, that is, the harmonic mean population size over the period considered, Δt , assuming this is sufficiently short that allele frequencies do not change much (Wright 1931, 1938; Vucetich et al. 1997; Kalinowski and Waples 2002; Waples 2002, 2006). Engen et al. (2005b) showed that the effective population size defined by considering genetic drift over a time period Δt , assuming no density regulation, is given by

$$N_e(\Delta t) \approx \frac{N_0}{\sigma_{dg}^2 T} \frac{(\sigma_e^2 - r)\Delta t}{e^{(\sigma_e^2 - r)\Delta t} - 1}, \quad (11)$$

where $r = \ln \lambda$ is the deterministic growth rate and σ_e^2 is the environmental variance. From this we find that $dN_e/d\sigma_e^2 < 0$ for all values of r and σ_e^2 so that increasing environmental variance increases genetic drift if the demographic stochasticity is kept constant. These results are valid also for the model considered here. It is, however, important to be aware, as mentioned above that large environmental stochasticity will also affect the parameter σ_{dg}^2 .

Effective Population Size of House Sparrows

We now show how to estimate the ratio N_e/N from data from local populations using for illustration a house sparrow *P. domesticus* metapopulation off the coast of northern Norway. From data on variance in individual fitness, that is, the number of recruits produced to the following breeding season and individual adult

survival (Lande et al. 2003), we estimate all parameters in equations (5–7) for six local populations during the breeding seasons 1994–2001, giving estimates of N_e/N as well as the demographic variance for each sex.

Since spring 1993, a large proportion of the house sparrows on the islands has been captured by mist-netting and individually marked with a metal ring and plastic color rings either during the summer (May–August), or in the autumn (from end of September until mid-November). During the breeding season (May–August) fledglings in all accessible nests were also individually marked with a metal and plastic color rings (for further details, see Ringsby et al. 1998). Moreover, all birds marked outside the breeding season could be classified as either juveniles or adults. However, after the molt in autumn, the age of unmarked individuals was difficult to estimate. Because of the high proportion of marked adult birds in the populations (Ringsby et al. 1999), we felt confident that assuming all unmarked individuals caught late autumn and onwards to be juveniles only introduced an insignificant error in the determination of parent–offspring relationships.

An individual was defined as a recruit if it was recaptured or observed on the natal study island during a breeding season subsequent to the year it hatched. The high recapture rate in this metapopulation (Ringsby et al. 1999) makes us confident that birds that hatched in a given year, but were not recaptured or observed during the subsequent study years, were correctly classified as nonrecruits. We also assumed that all unmarked adult birds caught on one of the study islands during the breeding seasons 1995–2002 were one-year-old recruits that hatched on the same island the previous year.

The first time a bird was marked, either as a fledgling, juvenile, or adult, a small blood sample was taken from its brachial vein. The number of recruits produced by each adult, within each season was determined by genetic analyses of DNA extracted from the collected blood, using up to nine polymorphic microsatellite loci (for further details on the genotyping procedures see Jensen et al. 2003, 2004). Several methods are now available for estimating parent–offspring relationship in natural populations based on molecular marker data (see review in Jones and Ardren 2003). We used the parenthood analysis software Cervus 2.0 (Marshall et al. 1998) to determine the parents of recruits that hatched on the islands during the breeding seasons from 1994 to 2001 (see Appendix 2 for further description of the procedures). Each island was analyzed separately, and maternity was determined before we ran analyses to determine paternity (for further description of the parenthood-assignment procedures see Jensen et al. 2003, 2004). This procedure resulted in an assigned maternity or paternity that was correct in at least 90% of cases. A single mother or father was determined for 566 and 562 of the 724 recruits, respectively. In addition 109 recruits had more than one probable mother whereas 123 had more than one probable father. All together, we

thus determined the mother for 93% and the father for 95% of the recruits.

The number of recruits produced by each adult male and female in the populations in a given year was based on the parenthood analyses. Recruits with more than one probable parent were assigned to adult males and females according to the probabilities of being the true parent (see Appendix 2), and parameters in equations (5–7) were then estimated for each choice. This procedure was repeated 1000 times with recruits reassigned to the adult population each time. The mean values of the parameters in equations (5–7) were used in the analysis.

If an adult individual produces B recruits and the indicator of its survival is J , which equals 1 for survival and otherwise 0, then b and s were estimated as the mean values of B and J for each sex giving estimates of λ and T assuming $q = 1/2$. Following Engen et al. (2005a) the parameter γ is the mean through time of $\text{cov}(B, J)$ divided by b . The variances σ^2 for each sex were estimated by the sum of squares

$$\hat{\sigma}^2 = \frac{1}{n-t} \sum_{j=1}^t \sum_{i=1}^{n_j} (B_{ij} - \bar{B}_j)^2,$$

where B_{ij} is the number of offspring produced by individual i in year j , $j = 1, 2, \dots, t$, $i = 1, 2, \dots, n_j$, $\sum_{j=1}^t n_j = n$, and \bar{B}_j is the mean number of offspring registered year j . A similar sum of squares replacing B with J was used to estimate $E[s(1-s)]$, whereas the covariance term $\text{cov}(B, J)$ was estimated by the sum of cross-products

$$\hat{c} = \frac{1}{n-t} \sum_{j=1}^t \sum_{i=1}^{n_j} (B_{ij} - \bar{B}_j)(J_{ij} - \bar{J}_j).$$

For each recruit with uncertain parenthood one of its probable parents was chosen as the true one, and added the number of recruits that were assigned to individual males and females with 90% confidence. This sampling procedure was repeated 1000 times with replacement. The mean values of the estimates of B as well as the estimates of $\text{cov}(b, J)$ were obtained from each sample. If parents were chosen from the list of possibilities only once (rather than 1000 times), uncertainty in the estimates could be determined by standard bootstrapping, that is, choosing parents and resampling the variables ($b, \text{cov}(B, J)$) with replacement within each year. However, it was required that we corrected for the fact that we use the mean value over a large number of estimates obtained by assigning recruits with uncertain genetic parenthood. This can be done by simply subtracting from the above bootstrap estimates the variance component due to sampling of parents only, which was found through the process of choosing parents and performing the estimation for each choice. For the data analyzed below this subtracted variance component was small compared to the total sampling variance.

Uncertainty in the estimates were determined by bootstrapping, resampling the variables (B, J) with replacement within each year.

The mean value of the σ_{dg}^2 across the six island populations was $\bar{\sigma}_{dg}^2 = 0.90$. The range of variation was however large (Table 1). Statistically significant variation in N_e/N around the mean value (0.37) was found among the islands ($\chi^2 = 34.89$, $df = 5$, $P < 0.001$). This variation remained even after accounting for the interisland differences in population dynamics by adjusting the adult survival rate to give $\lambda = 1$ at all islands (Table 1). This indicates that interisland variation in demography was large enough to strongly influence differences in N_e/N .

The effective population size is influenced by demographic variation in both sexes (eq. 1–3). In our study area there was a close association between the sex-specific components of the demographic variance among the six island populations (Fig. 2, $r = 0.96$, $P < 0.003$, $n = 6$). This was related to a high intersexual correlation in the generation time T ($r = 0.90$, $P = 0.049$, $n = 6$) and the fecundity rate b ($r = 0.94$, $P = 0.015$, $n = 6$), whereas the overdispersion of the fecundity and the covariance between fecundity and survival was less correlated between the two sexes ($r = 0.47$, $P = 0.357$, and $r = -0.27$, $P = 0.605$).

To evaluate the consequences for $N_e(\Delta t)$ of fluctuations in population size we estimated deterministic population growth rate and environmental variance r and σ_e^2 for the population on the island of Aldra. This population was colonized by four individuals (i.e., one female and three males) in 1998 growing to 42 individuals in 2004. We assumed that the subsequent growth could be modeled as a diffusion process (Lande et al. 2003) with stochastic population growth rate

$$s = E(\ln N_{t+1} | \ln N_t) = r - \frac{1}{2}\sigma_e^2 - \frac{1}{2}\sigma_d^2/N_t,$$

Table 1. Variation among island populations of house sparrows in the population growth rate λ estimated from the individual based demographic data, the total demographic variance σ_{dg}^2 , and the ratio (\pm standard error of the estimate) of effective population size N_e to actual population size N . The estimates for $\lambda = 1$ are calculated by adjusting the recruitment rate. For locations of the study islands, see map in Ringsby et al. (2002).

Island	λ	σ_{dg}^2	N_e/N	$\lambda=1$	
				σ_{dg}^2	N_e/N
Aldra	0.98	0.92	0.48 \pm 0.10	0.80	0.50
Gjerøy	0.86	0.84	0.39 \pm 0.03	0.70	0.60
Hestmannøy	0.87	0.99	0.45 \pm 0.02	0.82	0.63
Indre Kvarøy	0.80	0.86	0.37 \pm 0.03	0.65	0.71
Nesøy	0.85	0.72	0.32 \pm 0.05	0.60	0.58
Ytre Kvarøy	0.66	1.05	0.20 \pm 0.03	0.63	0.77

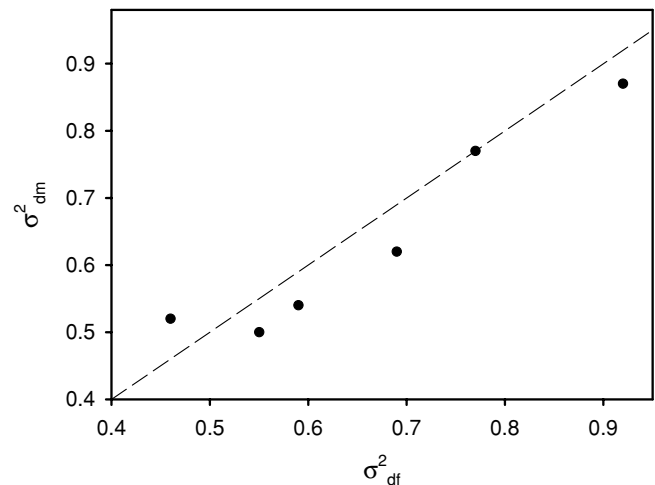


Figure 2. The relationship between the demographic variance for the male σ_{dm}^2 and the female segment σ_{df}^2 of the island house sparrow populations. The dotted line indicates the line through the origin with unit slope.

and variance

$$\text{var}(\ln N_{t+1} | \ln N_t) = \sigma_e^2 + \sigma_d^2/N_t,$$

where N_t is the population size at time t . The parameters r and σ_e^2 were estimated by following the procedure of Engen et al. (2001), assuming σ_d^2 known.

Fluctuations in population size will also influence genetic drift over longer time intervals (Engen et al. 2005b). For a given initial population size N_0 the value of $N_e(\Delta t)$ in the rapidly growing population at Aldra will be influenced by $r - \sigma_e^2$ as in equation (11). The estimate of the deterministic growth rate and environmental variance from the time series of population fluctuation (including the immigrants) was $\hat{r} = 0.295$ and $\hat{\sigma}_e^2 = 0.07$. For a time interval Δt of 10 years, we expect from equation (11) that $N_e(10) = 128$ (Fig. 3), which is considerably larger than the $N_e(1) = 57$ based on instantaneous drift. This increase was mainly affected by r , but was also influenced by σ_e^2 . For instance, $\sigma_e^2 = 0.01$ would result in a 34.2% increase in the difference between $N_e(10)$ and $N_e(1)$. Similarly, assuming $\sigma_{dm}^2 = 2\sigma_{df}^2$, results in a 35.3% decrease in the increase between $N_e(10)$ and $N_e(1)$ (Fig. 3).

Discussion

Engen et al. (2005b) derived the effective population size of a fluctuating age structured population in terms of the means, variances, and covariances of the vital rates. Estimating the effective size of an age structured population in a fluctuating environment is difficult because it requires detailed age-specific demographic data on both sexes Engen et al. (2005b). This approach may be used for numerical calculations of effective sizes, but it becomes

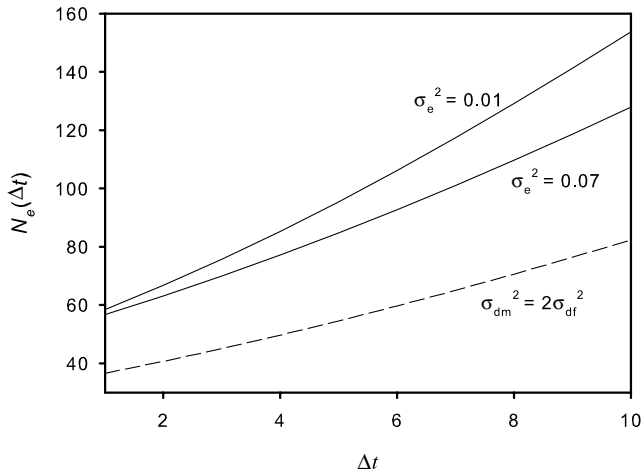


Figure 3. Effective population size $N_e(\Delta t)$ defined by the expected genetic drift over a time interval Δt in a rapidly growing house sparrow population on the island of Aldra for the estimated environmental variance $\hat{\sigma}_e^2 = 0.07$. The prediction for smaller environmental variance ($\sigma_e^2 = 0.01$) is also indicated. Other parameters were $N_0 = 42$, $r = 0.32$, and $\sigma_{dg}^2 = 0.32$. The number of offspring is assumed to be Poisson distributed. The dotted line shows the same relationship for $\sigma_{dm}^2 = 2\sigma_{df}^2$.

too complicated for analytical comparisons. Here we simplify this general approach by assuming age-independent vital rates (effectively eliminating age structure among adults) but we still allow for two sexes with different vital rates, unequal sex ratio at birth, overlapping generations, and stochastic fluctuations in population size. This simple life history is typical of many animal species, particularly small passerine birds (Charnov 1993; Sæther and Bakke 2000), and leads to a relatively simple expression for the ratio between the effective population size N_e and the actual size N at a particular time. In general this ratio can be expressed as $N_e/N = 1/(\sigma_{dg}^2 T)$ where σ_{dg}^2 is given by equations (5–7).

The sex ratio at birth strongly influences N_e (Fig. 1A). In this life history the variance σ_{dg}^2 determining the rate of genetic drift is a linear combination of the demographic variances for males and females (eq. 8). If the adult survival rates for males and female are identical, which implies $b_m = b_f$ and if the expected population size remains constant, $\lambda = 1$, then σ_{dg}^2 is simply the mean of the demographic variances for the sexes. If data are available for within-year variation in offspring of males as well as females the demographic variance for each sex can be estimated by a sum of squares (Engen et al. 1998; Sæther et al. 1998). The variance σ_{dg}^2 and the effective population size can then be estimated by inserting these demographic variances into equation (8). If the sex ratio at birth deviates from 1:1 then each parameter in equations (5–7) must be estimated from demographic data on reproduction and survival (Engen et al. 2005a).

The generation time T is another key variable determining effective population sizes with N_e/N decreasing with T

(Fig. 1B). Several results indicate that effective population sizes for long-lived species with overlapping generations should be approximately half the actual population size (Hill 1979; Nunney 1991; Engen et al. 2005b) when there are no sex differences in the dynamics. Using equation (8) we can also analyze the effective population size when there are sex differences in the vital rates, provided that the sex ratio at birth is 1:1 and the deterministic growth rate λ equals one. Writing B for the number of offspring and J for the indicator of survival of an individual, the demographic variance for one sex is $\sigma_d^2 = \text{var}(B + J) = b/4 + \sigma^2/4 + c + s(1 - s)$. Using $T = 1/(1 - s)$ and $b/2 + s = 1$ gives

$$\sigma_d^2 = \frac{(3/2 + \tau/2 + 2\gamma - 1/T)}{T} = \frac{\delta}{T},$$

where δ is defined by the equation. Inserting this in equation (8) for both sexes yields

$$\frac{N_e}{N} = \frac{1}{\sigma_{dg}^2 T} = \frac{2}{\delta_m + \delta_f}. \tag{12}$$

For long-lived species $b_f = 2(1 - s_f)$ is small (Sæther and Bakke 2000), so it is often realistic that at most one offspring is produced in a given year. Then, $\text{var}(B_f) = EB_f$ so that $\tau_f = 1$. If there is no correlation between survival and reproduction, we further have that $\gamma_f = 0$, giving $\delta_f = 2 - 1/T_f$. If these assumptions hold for both sexes, we obtain the reduced formula

$$\frac{N_e}{N} = \frac{2T_f T_m}{4T_f T_m - T_f - T_m}. \tag{13}$$

For long generation times this becomes approximately 1/2 in accordance with Nunney (1993). Furthermore, with nonoverlapping generations for both sexes, that is, $T_f = T_m = 1$, equation (13) produces $N_e = N$ in accordance with Wright (1931).

The ratio of variance of male to the variance of female reproductive success is closely related to the opportunity for sexual selection if there is no sexual difference in life history (Shuster and Wade 2003). By our approach sexual differences in reproductive success will affect σ_{dm}^2 and σ_{df}^2 that allows us to quantitatively assess (e.g., Sæther et al. 2004a) how changes in social organization affect N_e/N . However, many estimates of N_e obtained using demographic data (Grant and Grant 1992; Nunney and Elam 1994; Frankham 1995; Creel 1998) have only included the female segment of the population or neglected variation in male reproductive success. Our analyses show that demographic variation in males has a strong influence on N_e/N (Fig. 1B). This has important implications for the conservation of small populations because management actions or human activities that influence the social structure of the population (Caro 1998), and have altered the variance in mating success of the sexes, can have major impacts on its genetic composition (Fig. 1).

The demographic variance for females has previously been estimated using the approach of Sæther et al. (1998) for a number of bird populations (Sæther et al. 2004b). These analyses showed large interspecific differences in the demographic variance, ranging from 0.007 to 0.854. To estimate N_e/N the same kind of analysis must be performed also for males, considering only fathers and their production of sons. In most cases this will require application of modern molecular genetic methods (e.g., Coltman et al. 2003; Jones and Ardren 2003; Jensen et al. 2004; Coltman 2005; Garant and Kruuk 2005). Even in the general case of uneven expected sex ratio at birth, N_e/N can be estimated from data on the mean fecundity and survival for both sexes, as well as the variance in survival and the covariance between individual fecundity and survival, using equations (5–7).

Our house sparrow example illustrates that differences in N_e/N among six populations within a restricted geographic area were large and statistically significant, ranging from 0.20 to 0.48 (Table 1). The contribution of each sex to this interpopulation variation was quite similar because there was a close correlation between the demographic stochasticity of males and females among populations (Fig. 2). Nunney (2000) suggested that N_e/N based on demographic data will typically be in the range 0.25–0.75. The estimates from the present study include a large proportion of this range. This demonstrates that N_e/N is not a species-specific characteristic, but may show large differences over short geographical distances, dependent on the magnitude of intraspecific variation in local demography.

A comparison of the estimates of λ based on demographic data (Table 1) and the growth rates based on the trajectories of the populations (Sæther et al. 1999) revealed large differences. In most populations, the estimates of λ from demographic data gave too small growth rates. This was due to our restriction of the analysis to local populations, ignoring the interchange of individuals among localities within this metapopulation (Altwegg et al. 2000; Tufto et al. 2005). This resulted in an overestimate of the mortality because emigrating individuals were treated as dead. If we adjusted the adult survival rate to give $\lambda = 1$, this caused a substantial increase in N_e/N for all populations (Table 1). However, the range of variation in N_e/N still was large.

Over longer time intervals genetic drift will be strongly influenced by deterministic population growth rate as well as demographic and environmental stochasticity affecting the harmonic mean population size over the period considered (Wright 1931, 1938; Vucetich et al. 1997; Kalinowski and Waples 2002; Waples 2002, 2006). Assuming no density dependence, environmental stochasticity will strongly affect the rate of genetic drift in a rapidly growing house sparrow population (Fig. 3), that is, the rate of drift increases with larger environmental stochasticity and hence the increase in $N_e(\Delta t)$ of the growing population with Δt will decrease with increasing environmental stochasticity. This

occurs because the rate of drift given by equation (11) is influenced by $r - \sigma_e^2$. From this we also see that a reduction in r will have a similar impact on the rate of drift as an increase in σ_e^2 . Likewise, the intensity of sexual selection will also strongly affect changes in $N_e(\Delta t)$ (Fig. 3). Thus, understanding the long-term fluctuations in frequency of neutral alleles in natural populations requires estimating not only genetic parameters but also demographic parameters of deterministic population growth rate and environmental stochasticity.

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LITERATURE CITED

- Altwegg, R., T. H. Ringsby, and B.-E. Sæther. 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows. *J. Anim. Ecol.* 69:762–770.
- Caballero, A. 1994. Developments in prediction of effective population size. *Heredity* 73:657–673.
- Caro, T. 1998. The significance of behavioral ecology for conservation biology. Pp. 3–26 in T. Caro, ed. *Behavioral ecology and conservation biology*. Oxford Univ. Press, New York.
- Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theor. Pop. Biol.* 14:215–230.
- . 2001. *Matrix population models*. 2nd ed. Sinauer, Sunderland, MA.
- Charlesworth, B. 2001. The effect of life-history and mode of inheritance on neutral genetic variability. *Genet. Res.* 77:153–166.
- Charnov, E. L. 1993. *Life history invariants*. Oxford Univ. Press, Oxford.
- Clutton-Brock, T. H. 1998. *Reproductive success. Studies of individual variation in contrasting breeding systems*. Univ. of Chicago Press, Chicago.
- Coltman, D. W. 2005. Testing marker-based estimates of heritability in the field. *Mol. Ecol.* 14:2593–2599.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck C., and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Creel, S. 1998. Social organization and effective population sizes in carnivores. Pp. 246–265 in T. Caro, ed. *Behavioral ecology and conservation*. Oxford Univ. Press, Oxford.
- Crow, J. F., and C. Denniston. 1988. Inbreeding and variance effective population numbers. *Evolution* 42:482–495.
- Crow, J. F., and M. Kimura. 1970. *An introduction to population genetics theory*. Burgess Publishing Company/ALPHA EDITIONS, Minneapolis, MN.
- Emigh, T., and E. Pollak. 1979. Fixation probabilities and effective population numbers in diploid populations with overlapping generations. *Theor. Popul. Biol.* 15:86–107.
- Engen, S., Ø. Bakke, and A. Islam. 1998. Demographic and environmental stochasticity—concepts and definitions. *Biometrics* 54:39–45.

- Engen, S., B.-E. Sæther, and A. P. Møller. 2001. Stochastic population dynamics and time to extinction of a declining population of barn swallow. *J. Anim. Ecol.* 70:789–797.
- Engen, S., R. Lande, and B.-E. Sæther. 2003. Demographic stochasticity and Allee effects in populations with two sexes. *Ecology* 84:2378–2386.
- Engen, S., R. Lande, B.-E. Sæther, and H. Weimerskirch. 2005a. Extinction in relation to demographic and environmental stochasticity in age structured models. *Math. Biosc.* 195:210–227.
- Engen, S., R. Lande, and B.-E. Sæther. 2005b. Effective size of a fluctuating age structured population. *Genetics* 170:941–954.
- Felsenstein, J. 1971. Inbreeding and variance effective numbers in populations with overlapping generations. *Genetics* 68:581–597.
- Frankham, R. 1995. Effective population-size adult population-size ratio in wildlife—a review. *Genet. Res.* 66:95–107.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. Introduction to conservation genetics. Cambridge Univ. Press, Cambridge.
- Garant, D., and L. B. Kruuk. 2005. How to use molecular marker data to measure evolutionary parameters in wild populations. *Mol. Ecol.* 14:1843–1859.
- Grant, P. R. and B. R. Grant. 1992. Demography and the genetically effective sizes of two populations of Darwin finches. *Ecology* 73:766–784.
- Hedrick, P. W. 2005. Large variance in reproductive success and the N_e/N ratio. *Evolution* 59:1596–1599.
- Hill, W. G. 1972. Effective size of populations with overlapping generations. *Theor. Popul. Biol.* 3:278–289.
- . 1979. A note on effective population size with overlapping generations. *Genetics* 92:317–322.
- Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology* 79:383–399.
- Jensen, H., B. E. Sæther, T. H. Ringsby, J. Tufto, S. C. Griffith, and H. Ellegren. 2003. Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (*Passer domesticus*). *J. Evol. Biol.* 16:1296–1307.
- . 2004. Lifetime reproductive success in relation to morphology in the house sparrows *Passer domesticus*. *J. Anim. Ecol.* 73:599–611.
- Jones, A. G., and W. R. Ardren. 2003. Methods of parentage analysis in natural populations. *Mol. Ecol.* 12:2511–2523.
- Kalinowski, S. T., and R. S. Waples. 2002. Relationship of effective to census size in fluctuating populations. *Conserv. Biol.* 16:129–136.
- Karlin, S., and H. M. Taylor. 1981. A second course in stochastic processes. Academic Press, New York.
- Kimura, M. 1983. The neutral theory of molecular evolution. Cambridge Univ. Press, Cambridge.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution applied to brain: body size allometry. *Evolution* 33:402–416.
- . 1980. Genetic variation and phenotypic evolution during allopatric speciation. *Am. Nat.* 116:463–479.
- . 1985. Expected time for random genetic drift of a population between stable phenotypic states. *Proc. Natl. Acad. Sci. USA* 82:7641–7645.
- Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pp. 87–123 in M. E. Soulé, ed. *Viable populations for conservation*. Cambridge Univ. Press, Cambridge.
- Lande, R., S. Engen, and B.-E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford Univ. Press, New York.
- Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* 7:639–655.
- Møller, A. P., and P. Ninni. 1998. Sperm competition and sexual selection: a meta-analysis of paternity studies of birds. *Behav. Ecol. Sociobiol.* 43:345–358.
- Newton, I. 1989. Lifetime reproductive success in birds. Academic Press, London.
- Nunney, L. 1991. The influence of age structure and fecundity on effective population size. *Proc. R. Soc. Lond. B* 246:71–76.
- . 1993. The influence of mating system and overlapping generations on effective population size. *Evolution* 47:1329–1341.
- . 2000. The limits to knowledge in conservation genetics. The value of effective population size. *Evol. Biol.* 32:179–194.
- Nunney, L., and D. R. Elam. 1994. Estimating the effective population size of conserved populations. *Conserv. Biol.* 8:175–184.
- Orive, M. E. 1993. Effective population size in organisms with complex life-histories. *Theor. Pop. Biol.* 44:316–340.
- Pollak, E. 2000. The effective population size of some age structured populations. *Math. Biosc.* 168:39–65.
- Promislow, D. E. L. 1992. Costs of sexual selection in natural populations of mammals. *Proc. R. Soc. Lond B* 247:203–210.
- Promislow, D. E. L., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. *Proc. R. Soc. Lond B* 250:143–150.
- Ringsby, T. H., B.-E. Sæther, and E. J. Solberg. 1998. Factors affecting juvenile survival in House Sparrow *Passer domesticus*. *J. Avian Biol.* 29:241–247.
- Ringsby, T. H., B.-E. Sæther, R. Altwegg, and E. J. Solberg. 1999. Temporal and spatial variation in survival rates of a sparrow, *Passer domesticus*, metapopulation. *Oikos* 85:419–425.
- Ringsby, T. H., B.-E. Sæther, J. Tufto, H. Jensen, and E. J. Solberg. 2002. Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology* 83:561–569.
- Shuster, S. M., and M. J. Wade. 2003. Mating systems and strategies. Princeton Univ. Press, Princeton, NJ.
- Slate, J., T. Marshall, and J. Pemberton. 2000. A retrospective assessment of the accuracy of the paternity inference program CERVUS. *Mol. Ecol.* 9:801–808.
- Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- Sæther, B.-E., S. Engen, A. Islam, R. McCleery, and C. Perrins. 1998. Environmental stochasticity and extinction risk in a population of small song bird, the great tit. *Am. Nat.* 151:441–50.
- Sæther, B.-E., T. H. Ringsby, Ø. Bakke, and E. J. Solberg. 1999. Spatial and temporal variation in demography of a house sparrow metapopulation. *J. Anim. Ecol.* 68:628–637.
- Sæther, B.-E., S. Engen, R. Lande, A. P. Møller, S. Bensch, D. Hasselquist, J. Beier, and B. Leisler. 2004a. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. *J. Anim. Ecol.* 73:925–934.
- Sæther, B. E., S. Engen, A. P. Møller, H. Weimerskirch, M. E. Visser, W. Fiedler, E. Matthysen, M. M. Lambrechts, A. Badyaev, P. H. Becker, J. E. Brommer, D. Bukacinski, M. Bukacinska, H. Christensen, J. Dickinson, C. du Feu, F. Gehlbach, D. Heg, H. Hötter, J. Merilä, J. T. Nielsen, W. Rendell, R. J. Robertson, D. L. Thomson, J. Török, and P. Van Hecke. 2004b. Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. *Am. Nat.* 164:793–802.
- Tufto, J., T. H. Ringsby, A. A. Dhondt, F. Adriaenssen, and E. Matthysen. 2005. A parametric model for estimation of dispersal patterns applied to five passerine spatially structured populations. *Am. Nat.* 165:E13–E26.
- Vucetich, J. A., T. A. Waite, and L. Nunney. 1997. Fluctuating population size and the ratio of effective to census population size. *Evolution* 51:2017–2021.
- Waples, R. S. 2002. The effective size of fluctuating salmon populations. *Genetics* 161:783–791.

- . 2006. Seed banks, salmon and sleeping genes: effective population size in semelparous, age structured species with fluctuating abundance. *Am. Nat.* 167:118–135.
- Westneat, D. F. and I. R. K. Stewart. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Syst.* 34:365–396.
- Whittingham, L. A. and P. O. Dunn. 2005. Extra-pair and within-pair copulation reproductive success on the opportunity for selection in birds. *Behav. Ecol.* 16:138–144.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:98–160.
- . 1938. Size of population and breeding structure in relation to evolution. *Science* 87:430–431.
- . 1969. Evolution and the genetics of populations. Vol. 2. The theory of gene frequencies. Univ. of Chicago Press, Chicago.

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Appendix 1

THE EFFECTIVE POPULATION SIZE FOR ONE SEX

To find the variance of $X_f + \Delta X_f$ for one sex consider a single female with the rare allele that produces B_f offspring and Y_f offspring with the rare allele. Let further J_f be the indicator variable for its survival ($J_f = 1$ or 0) so that the total contribution to the next generation of individuals with the rare gene is $Y_f + J_f$. The variable Y_f is then binomial with parameters (B_f , $1/2$) when conditioned on B_f . The contribution to the variance of ΔX_f is $\text{var}(Y_f + J_f) = \text{Evar}(Y_f + J_f | B_f, J_f) + \text{varE}(Y_f + J_f | B_f, J_f)$, which is $\text{E}(B_f/4) + \text{var}(B_f/2 + J_f) = b_f/4 + \sigma_f^2/4 + s_f(1 - s_f) + c_f$, where $c_f = \text{cov}(B_f, J_f)$. Summing the contributions from each individual this gives the drift $\text{var}(\Delta X_f) = \sigma_{d_{gf}}^2 X_f = [b_f/4 + \sigma_f^2/4 + s_f(1 - s_f) + c_f] X_f$. Then, we can either assume that the stochasticity in N_f can be ignored when calculating the variance of the change in the frequency of an allele $\text{var}(\Delta p)$, or apply the transformation formulas for diffusions (Karlin and Taylor 1981), to find

$$\text{var}(\Delta p) = \text{var}[(X_f + \Delta X_f)/(2N_f + 2\Delta N_f) - X_f/(2N_f)].$$

Both approaches leads to the approximation

$$\text{var}(\Delta p) \approx \frac{[b_f/4 + \sigma_f^2/4 + s_f(1 - s_f) + c_f] p}{2N_f}.$$

DEMOGRAPHIC VARIANCE FOR ONE SEX

Consider a single female producing B_f offspring and with survival indicator J_f being one if she survives and otherwise zero so that $P(J_f = 1) = s_f$. Conditioned on B_f , her number of female offspring, say U_f , is binomial with parameters (B_f , q). By definition (Engen et al. 1988) the demographic variance for the female segment of the population is then $\sigma_{d_{gf}}^2 = \text{var}(U_f + J_f)$. Arguing conditionally as in the previous section this gives

$$\sigma_{d_{gf}}^2 = q(1 - q)b_f + q^2\sigma_f^2 + s_f(1 - s_f) + 2qc_f.$$

Hence $\sigma_{d_{gf}}^2 = \sigma_{d_f}^2$ if $q = 1/2$.

EXPECTED DYNAMICS FOR TWO SEXES

Let $\mathbf{W}_t = (X_t, Y_t)^T$ be the number of adult females and males respectively in the subpopulation with the rare gene, where τ denotes matrix transposition. Then, if there is no density regulation the expected dynamics are given by

$$\mathbf{E}\mathbf{W}_{t+1} = \mathbf{L}\mathbf{W}_t,$$

where the projection matrix is

$$\mathbf{L} = \begin{bmatrix} \frac{1}{2}qb_f + s_f & \frac{1}{2}qb_m \\ \frac{1}{2}(1 - q)b_f & \frac{1}{2}(1 - q)b_m + s_m \end{bmatrix}.$$

The parameters b_f and b_m are the mean number of offspring of a single female and male that survive to enter the adult population, s_f and s_m are the adult female and male survival rate, and q is the probability that a newborn individual is a female. The factors $\frac{1}{2}$ occur because a mother or father with the rare allele transmits it to their offspring with probability $\frac{1}{2}$. Because the allele is rare, nearly all individuals bearing it are heterozygotes that mate with an individual not bearing the allele.

Let $\mathbf{u} = (u_1, u_2)^T$ and $\mathbf{v} = (v_1, v_2)$ denote the right and left eigenvectors of \mathbf{L} associated with the dominant eigenvalue λ defined by $\mathbf{L}\mathbf{u} = \lambda\mathbf{u}$ and $\mathbf{v}\mathbf{L} = \lambda\mathbf{v}$. If \mathbf{u} is scaled so that $u_1 + u_2 = 1$, it is the stable sex distribution corresponding to the deterministic model (Caswell 2001). We apply this scaling of \mathbf{u} in all subsequent formulas. Because males and females must have the same expected reproduction, we have $u_1 b_f = u_2 b_m$ giving $u_1 = b_m/(b_f + b_m)$ and $u_2 = b_f/(b_f + b_m)$. From the equation $\mathbf{L}\mathbf{u} = \lambda\mathbf{u}$ we find that the dominant eigenvalue λ is $qb_f + s_f$ as well as $(1 - q)b_m + s_m$. This relates the mean birth rates for males and females as $b_m = (qb_f + s_f - s_m)/(1 - q)$. The mean generation time of the population is $T = (T_f + T_m)/2 = [\lambda/(\lambda - s_f) + \lambda/(\lambda - s_m)]/2$ where the mean generation time for each sex is $T_f = \lambda/(qb_f)$ and $T_m = \lambda/[(1 - q)b_m]$. Using these relations we see that the sex distribution alternatively may be expressed as $u_1 = qT_f/[qT_f + (1 - q)T_m]$ and $u_2 = (1 - q)T_m/[qT_f + (1 - q)T_m]$. The scaled right eigenvector \mathbf{v} turns out to be $(1 - q, q)$. The sensitivities of this model are $\partial\lambda/\partial L_{ij} = v_i u_j / (\mathbf{v}\mathbf{u})$ (Caswell 1978, 2001, p. 209).

STOCHASTIC DYNAMICS

Engen et al. (2005b) showed that environmental stochasticity will not affect the instantaneous genetic drift, so we only consider the demographic component of the stochasticity (for details, see Engen et al. [2005a,b]). Writing \mathbf{G} for the stochastic matrix operating in a given year so that $\mathbf{W}_{t+1} = \mathbf{G}\mathbf{W}_t$, we show below that the expectation of \mathbf{G} is \mathbf{L} and that the non zero variances and covariances $\text{cov}(G_{ij}, G_{kl})$ of its elements can be expressed using constants $a_{ij,kl}$ defined by $a_{i1,j1} = X_t \text{cov}(G_{i1}, G_{j1})$

and $a_{i2,j2} = Y_i \text{cov}(G_{i2}, G_{j2})$. According to Engen et al. (2005a) the demographic variance of the process $W_t = X_t + Y_t$ is then approximately

$$\sigma_{dg}^2 = \lambda^{-2} \sum_{ijk} u_j^{-1} \frac{\partial \lambda}{\partial L_{ij}} \frac{\partial \lambda}{\partial L_{kj}} a_{ij,kj} = (\lambda \mathbf{v} \mathbf{u})^{-2} \sum_{ijk} u_j v_i v_k a_{ij,kj},$$

where all three indices ijk run over 1 and 2 so that the sum has eight terms.

We now use the notation σ^2 for the variance in the number of offspring produced, with appropriate subscript indicating the parent's sex, and c for the covariance between the number of offspring and the indicator of the parent's survival. To simplify the expressions we further write $\tau = \sigma^2/b$ for the overdispersion relative to the Poisson distribution for the number of offspring, and $\gamma = c/b$ and $r = q(1 - q)$. Using the expressions for the coefficients $a_{ij,kl}$ derived above, equation (4) can then be written as $\sigma_{dg}^2 = k(a_1 + a_2)$ where a_1 and a_2 are given in the main text.

COMPUTATION OF COEFFICIENTS $a_{ij,kl}$

Consider a single heterozygote female that produces B_f offspring and has indicator of survival J_f being one if she survives to the next census and otherwise zero. Let F and M be the number of her daughters and sons with the rare gene that survive to the next census so that $B_f - F - M$ is the number of offspring she produces that do not have the rare gene. As she mates with a male that does not have the rare gene, the variables $(B_f - F - M, F, M)$ possess a trinomial distribution with parameters $[B_f, \frac{1}{2}, \frac{1}{2}q, \frac{1}{2}(1 - q)]$ when conditioned on B_f . Hence, using well-known properties of the multinomial distribution the conditional mean and variances of her contribution to the next generation of individuals with the rare gene are

$$\begin{aligned} E(F + J_f | B_f, J_f) &= \frac{1}{2}qB_f + J_f \\ \text{var}(F + J_f | B_f, J_f) &= \frac{1}{4}q(2 - q)B_f \\ E(M | B_f, J_f) &= \frac{1}{2}(1 - q)B_f \\ \text{var}(M | B_f, J_f) &= \frac{1}{4}(1 - q)(1 + q)B_f \\ \text{cov}(F + J_f, M | B_f, J_f) &= -\frac{1}{4}q(1 - q)B_f. \end{aligned}$$

The unconditional variance of $F + J_f$ is found by using the general formula $\text{var}(F + J_f) = \text{Evar}(F + J_f | B_f, J_f) + \text{var}E(F + J_f | B_f, J_f)$. Using the notation $EB_f = b_f$, $\text{var}(B_f) = \sigma_f^2$, $\text{cov}(B_f, J_f) = c_f$ and $EJ_f = s_f$ so that $\text{var}(J_f) = s_f(1 - s_f)$ we find

$$\text{var}(F + J_f) = \frac{1}{4}q(2 - q)b_f + \frac{1}{4}q^2\sigma_f^2 + s_f(1 - s_f) + qc_f.$$

Because the element G_{11} of the projection matrix \mathbf{G} is the mean value of X_t such independent contributions $F + J_f$, the mean and variance of this element is

$$E(G_{11}) = EE(Z + J_f | B_f, J_f) = \frac{1}{2}qb_f + s_f$$

and

$$\text{var}(G_{11}) = X_t^{-1} \left[\frac{1}{4}q(2 - q)b_f + \frac{1}{4}q^2\sigma_f^2 + s_f(1 - s_f) + qc_f \right].$$

Similarly, we find

$$E(G_{21}) = EE(M | B_f, J_f) = \frac{1}{2}(1 - q)b_f$$

and

$$\text{var}(G_{21}) = X_t^{-1} \left[\frac{1}{4}(1 - q)(1 + q)b_f + \frac{1}{4}(1 - q)^2\sigma_f^2 \right].$$

To find the covariance term we use $\text{cov}(F + J_f, M) = \text{Ecov}(F + J_f, M | B_f, J_f) + \text{cov}[E(F + J_f | B_f, J_f), E(M | B_f, J_f)]$, giving

$$\begin{aligned} \text{cov}(G_{11}, G_{21}) &= X_t^{-1} \left[-\frac{1}{4}q(1 - q)b_f \right. \\ &\quad \left. + \frac{1}{4}q(1 - q)\sigma_f^2 + \frac{1}{2}(1 - q)c_f \right]. \end{aligned}$$

Considering in the same way the contributions from the males, we find similar expressions for $\text{var}(G_{22})$, $\text{var}(G_{12})$, and $\text{cov}(G_{22}, G_{12})$ by the same argument, replacing q by $1 - q$, indices f by m , and X_t by Y_t . Using the definitions of the coefficients $a_{ij,kl}$ above, we then have

$$\begin{aligned} a_{11,11} &= \frac{1}{4}b_fq(2 - q) + \frac{1}{4}q^2\sigma_f^2 + s_f(1 - s_f) + qc_f \\ a_{21,21} &= \frac{1}{4}b_f(1 - q)(1 + q) + \frac{1}{4}(1 - q)^2\sigma_f^2 \\ a_{11,21} &= a_{21,11} = -\frac{1}{4}b_fq(1 - q) + \frac{1}{4}q(1 - q)\sigma_f^2 + \frac{1}{2}(1 - q)c_f \\ a_{12,12} &= \frac{1}{4}b_mq(2 - q) + \frac{1}{4}q^2\sigma_m^2 \\ a_{22,22} &= \frac{1}{4}b_m(1 - q)(1 + q) + \frac{1}{4}(1 - q)^2\sigma_m^2 \\ &\quad + s_m(1 - s_m) + (1 - q)c_m \\ a_{12,22} &= a_{22,12} = -\frac{1}{4}b_mq(1 - q) + \frac{1}{4}q(1 - q)\sigma_m^2 + \frac{1}{2}qc_m. \end{aligned}$$

Appendix 2

The software Cervus 2.0 (Marshall et al. 1998) uses information on which marked adult birds were present on an island in a given year, combined with information on the estimated proportion of adult birds that was marked, information on allele frequencies at the microsatellite loci in each island population, and the genotypes of recruits and their potential parents. Then a LOD score (log-likelihood ratio) was calculated for the likelihood that a potential parent was the genetic parent of the recruit. A LOD score of zero means that the potential parent is equally as likely to be the true

mother or father of the recruit as a randomly selected female or male in the population, respectively. A positive LOD score does on the other hand mean that the potential mother or father is more likely to be the true mother or father of the recruit than a randomly selected female or male (Marshall et al. 1998). The difference in LOD scores (i.e., Δ LOD) of the two most likely potential parents were compared with a critical value generated in the simulation module of Cervus, above which the most likely potential parent is the true parent in at least 90% of the cases (Marshall et al. 1998; Slate et al. 2000).

In some cases there were a number of potential parents with positive LOD scores, but where none had a sufficiently large Δ LOD to satisfy the criterion generated by Cervus to provide

at least 90% confidence that the alleged parent was the true one. In these cases we assumed that the true parent was among the potential parents with a LOD score higher than 1.39, which means that the parent was about four times more likely to be the true parent than a randomly selected female or male in the population. For recruits who had one or more potential mothers or fathers with $\text{LOD} > 1.39$, these putative parents were given a probability of being the true parent equal to their individual LOD score divided by the sum of the LOD scores of all the putative parents. Recruits that had no likely mother or father (i.e., all potential parents have $\text{LOD} < 1.39$), were excluded from the analyses because they were likely to be immigrants or offspring of parents that were not sampled.