

# Effective Size of a Fluctuating Age-Structured Population

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## ABSTRACT

Previous theories on the effective size of age-structured populations assumed a constant environment and, usually, a constant population size and age structure. We derive formulas for the variance effective size of populations subject to fluctuations in age structure and total population size produced by a combination of demographic and environmental stochasticity. Haploid and monoecious or dioecious diploid populations are analyzed. Recent results from stochastic demography are employed to derive a two-dimensional diffusion approximation for the joint dynamics of the total population size,  $N$ , and the frequency of a selectively neutral allele,  $p$ . The infinitesimal variance for  $p$ , multiplied by the generation time, yields an expression for the effective population size per generation. This depends on the current value of  $N$ , the generation time, demographic stochasticity, and genetic stochasticity due to Mendelian segregation, but is independent of environmental stochasticity. A formula for the effective population size over longer time intervals incorporates deterministic growth and environmental stochasticity to account for changes in  $N$ .

CONCEPTS of effective population size are fundamental for understanding evolutionary dynamics at the molecular and phenotypic levels (EWENS 1979; LANDE 1979, 1985, 1986; KIMURA 1983) and for applications in conservation biology (LANDE and BARROW-CLOUGH 1987; NUNNEY and ELAM 1994; LANDE 1995; CREEL 1998; NUNNEY 2000). The effective size of a population,  $N_e$ , determines the expected rate of random genetic drift, increase in inbreeding coefficients, and loss of selectively neutral heterozygosity, each of which is proportional to  $1/(2N_e)$  per generation for a diploid autosomal locus. Effective population size also interacts with selection to influence the fixation probabilities of advantageous and deleterious mutations (WRIGHT 1931, 1969).

WRIGHT (1931) defined the effective size of a population as that which produces the same rate of random genetic drift as in an ideal population of constant size,  $N$ , composed of monoecious diploid individuals reproducing by random sampling of gametes with discrete, nonoverlapping generations (implying an approximately Poisson distribution of family sizes). In an ideal population half of the random genetic drift is caused by Mendelian segregation, and half is produced by variance in family size (CROW and KIMURA 1970). In real populations  $N_e$  generally is substantially smaller than  $N$ , often by an order of magnitude, because of uneven sex ratio, excess variance in family size (greater than the mean), and temporal fluctuations in population num-

bers (WRIGHT 1931, 1969; CROW and KIMURA 1970; CABALLERO 1994; FRANKHAM 1995). For populations that change in size, CROW (1954) and 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), noting that in any generation the former depends mainly on the number of offspring whereas the latter depends mainly on the number of parents (see also MALÉCOT 1969; CROW and KIMURA 1970; EWENS 1982).

Overlapping generations and age structure considerably complicate the calculation of effective population size. Nearly all real populations have overlapping generations; even annual plants typically have a soil seed bank with variable seed dormancy and delayed germination, and monocarpic plants and semelparous animals such as salmon have variable age at maturity, which causes generations to overlap (NUNNEY 2002; WAPLES 2002; VITALIS *et al.* 2004). Age structure can strongly influence effective population size because differences in individual life span often augment the variance in lifetime reproductive success (CLUTTON-BROCK 1988; NEWTON 1989). Formulas for effective population size with overlapping generations have been derived by several authors (FELSENSTEIN 1971; HILL 1972, 1979; EMIGH and POLLAK 1979; POLLAK 1980, 2000; NUNNEY 1991, 1993; ORIVE 1993; reviewed by CABALLERO 1994), all of whom assumed a constant environment and, usually, a constant population size and age structure.

For populations exposed to natural environments, fluctuating population size is often the most important fac-

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tor reducing  $N_e$  below the average actual size (WRIGHT 1931, 1940, 1969; CROW and KIMURA 1970; FRANKHAM 1995). All natural populations fluctuate due to a combination of demographic and environmental stochasticity. Demographic stochasticity occurs because of chance events of reproduction and mortality that are independent among individuals, which produces random fluctuations in population growth rate primarily in small populations. Environmental stochasticity exerts similar impacts on the survival and reproduction of all individuals (of a given age and sex), causing population growth rate to fluctuate substantially in populations of all sizes. For populations with synchronized annual reproduction these stochastic effects can be described by the demographic and environmental variances that can be estimated, respectively, from the variance of individual fitness within years and the variance in mean fitness among years (ENGEN *et al.* 1998; LANDE *et al.* 2003). Demographic and environmental stochasticity produces fluctuations in both the age structure and total size of a population (TULJAPURKAR 1990; LANDE *et al.* 2003). Accounting for these effects is essential for calculating the effective size of a population with overlapping generations.

Here we utilize recent theories from stochastic demography to derive general formulas for the variance effective size of an age-structured population. We first consider a haploid population, then a monoecious diploid population, and finally a diploid population with separate sexes. In each case we derive the effective population size per generation from the product of the generation time and the sampling variance per unit time in the frequency of a selectively neutral allele, obtained from the infinitesimal variance in a diffusion approximation. Consequently, these basic formulas for  $N_e$  describe the effective population size at a given time, rather than across a longer time span during which population size may fluctuate considerably. We conclude by showing how the basic formulas for effective population size can be extended to account for fluctuations in population size over longer time intervals.

### HAPLOID POPULATION

We briefly review recent results in stochastic demography using female-biased models counting only mothers and daughters. Such models are directly applicable to genotypic evolution in haploid or asexual (all female) populations or in haploid sex-linked loci in the heterogametic sex of dioecious populations. In all demographic models the discrete time unit is taken as one year, but  $N_e$  is always calculated in units of genetic generation time.

**Stochastic demography background:** For a density-independent age-structured population in a fluctuating environment, COHEN (1977, 1979) and TULJAPURKAR (1982, 1990) analyzed the stochastic dynamics of  $\ln N$ , the natural logarithm of total population size,  $N = \sum N_i$ ,

where  $N_i$  represents the number of individuals in the  $i$ th age class. Denote the population column vector as  $\mathbf{N} = (N_0, N_1, \dots, N_k)^T$ , where the superscript  $T$  indicates matrix transposition. With annual censuses just after reproduction and no density regulation, the population vector in the next year is projected by the matrix multiplication  $\mathbf{LN}$ , where

$$\mathbf{L} = \begin{bmatrix} B_0 & B_1 & \dots & B_{k-1} & B_k \\ S_0 & 0 & \dots & 0 & 0 \\ 0 & S_1 & \dots & 0 & 0 \\ \vdots & & \ddots & \vdots & \vdots \\ 0 & \dots & 0 & S_{k-1} & 0 \end{bmatrix}. \quad (1)$$

This has the form of a Leslie matrix but with age-specific “vital rates” of annual reproduction,  $B_i$ , and survival,  $S_i$ , that fluctuate through time because of demographic and environmental stochasticity (LESLIE 1945; CASWELL 1989, 2001).

Tuljapurkar derived approximate formulas for the expected growth rate of  $\ln N$ , also known as the long-run growth rate, and its environmental variance, assuming a large population size and neglecting demographic stochasticity. His approximation for the long-run growth rate is  $\ln \lambda - \sigma_e^2/2$ , which depends on two parameters, (i) the asymptotic multiplicative growth rate of the population in the average environment,  $\lambda$ , which is the dominant eigenvalue of the projection matrix in the average environment, containing the time-averaged vital rates, and (ii) the environmental variance,  $\sigma_e^2$ , which is the summation of the environmental variances and covariances of the vital rates weighted by the sensitivities of  $\lambda$  with respect to small changes in the vital rates,

$$\sigma_e^2 \approx \sum_i \sum_j \lambda^{-2} \frac{\partial \lambda}{\partial \pi_i} \frac{\partial \lambda}{\partial \pi_j} \text{Cov}_e(\pi_i, \pi_j) \quad (2)$$

(TULJAPURKAR 1982, 1990; CASWELL 1989, 2001). In this formula  $\pi_i$  denotes a nonzero element in the projection matrix and  $\text{Cov}_e$  represents the environmental component of the covariance.

LANDE and ORZACK (1988) showed that the long-run growth rate and the environmental variance can be employed, respectively, as the infinitesimal mean and infinitesimal variance in a diffusion approximation for  $\ln N$ . ENGEN *et al.* (2005) generalized this approach to include both demographic and environmental stochasticity in the density-independent growth of an age-structured population. Writing the demographic variance as  $\sigma_d^2$ , they showed that the expected rate of increase of  $\ln N$  is approximately  $\ln \lambda - \sigma_e^2/2 - \sigma_d^2/(2N)$ , which can be employed as the infinitesimal mean in a diffusion approximation for  $\ln N$ , with infinitesimal variance  $\sigma_e^2 + \sigma_d^2/N$ .

Components of the demographic variance can be spe-

cified as follows. Let the number of offspring produced by an individual in age class  $i$  have expected value  $b_i$  and variance  $\sigma_i^2$ . Write  $c_i$  for the covariance between the number of offspring and the indicator  $J_i$  of the mother's survival, that is,  $J_i = 1$  if the mother survives and otherwise zero. We let  $J_i$  have mean  $s_i$ , which necessarily implies the binomial variance of individual survival  $\text{Var}(J_i) = s_i(1 - s_i)$ . For simplicity, we assume no demographic covariance of vital rates between age classes. The demographic variance then becomes

$$\sigma_d^2 \approx \sum_{i=0}^k \frac{\lambda^{-2}}{u_i} \left[ \left( \frac{\partial \lambda}{\partial b_i} \right)^2 \sigma_i^2 + \left( \frac{\partial \lambda}{\partial s_i} \right)^2 s_i(1 - s_i) + 2 \frac{\partial \lambda}{\partial b_i} \frac{\partial \lambda}{\partial s_i} c_i \right] \quad (3)$$

(ENGEN *et al.* 2005), where  $(u_0, u_1, \dots, u_k)^T$  is the stable age distribution and  $s_k = c_k = 0$ . The demographic variance,  $\sigma_d^2$ , is the summation of the demographic variances and covariances of the vital rates weighted by the sensitivities of  $\lambda$  with respect to small changes in the vital rates and inversely weighted by the relative frequency of each age class. Expressions for the stable age distribution and the sensitivity coefficients appear in APPENDIX B.

Using the transformation formulas for the infinitesimal moments of a one-dimensional diffusion process (APPENDIX A), the diffusion for  $\ln N$  can be transformed to a diffusion for the total population size,  $N$ , which has infinitesimal mean  $rN$  and infinitesimal variance  $\sigma_d^2 N + \sigma_c^2 N^2$ , where  $r = \ln \lambda$ . Accuracy of the diffusion approximation requires that  $r$  is small in magnitude so that  $r \approx \lambda - 1$  (LANDE *et al.* 2003).

**Effective population size:** These results suggest a straightforward method of deriving the effective size of a haploid age-structured population in a fluctuating environment. Consider a particular allele at a selectively neutral locus in such a population with no density regulation. Let  $Z$  be the number of individuals carrying the allele, and let  $Y$  be the number of individuals without the allele, so that the total population size is  $N = Y + Z$  and the allele frequency is  $p = Z/(Y + Z)$ . Diffusion approximations for  $Z$  and  $Y$  have the same form with identical parameters as for the total population, but with infinitesimal means and variances having  $Z$  and  $Y$ , respectively, in place of  $N$ . These variables experience the same sequence of environments, so their infinitesimal covariance is  $\sigma_c^2 YZ$ . The bivariate diffusion process for  $Z$  and  $Y$  can be transformed to a bivariate diffusion for  $N$  and  $p$  (APPENDIX A). We find that the allele frequency  $p$  has infinitesimal mean 0, reflecting the selective neutrality of the allele, and infinitesimal variance  $V_p = p(1 - p)\sigma_d^2/N$ , with no infinitesimal covariance between  $p$  and  $N$ . Note that the environmental variance makes no contribution to the infinitesimal mean or variance of  $p$  because by definition at any given moment environmental stochasticity exerts identical effects on selectively neutral genotypes.

In a haploid population with discrete, nonoverlapping

generations, the variance effective size (CROW 1954) is defined by equating the sampling variance per generation in the frequency of a neutral allele to  $p(1 - p)/N_e$ , which is the sampling variance in an ideal haploid of size  $N_e$ . The infinitesimal variance  $V_p$  approximates the sampling variance per unit time in the frequency of a neutral allele. Multiplying this by the generation time,  $T$ , defined as the mean age of parents of newborn individuals (APPENDIX B), gives the sampling variance in allele frequency per generation. Equating  $V_p T$  to the sampling variance per generation in an ideal haploid population with nonoverlapping generations,

$$V_p T = p(1 - p)/N_e;$$

substituting the above formula for the infinitesimal variance produces the effective population size per generation,

$$N_e = \frac{N}{\sigma_d^2 T}. \quad (4a)$$

Although environmental stochasticity does not influence the effective population size at any given moment, it does produce fluctuations in the total population size that decrease  $N_e$  measured over longer time intervals, as shown in the last section.

This formula agrees with previous expressions derived by Felsenstein (1971) and Hill (1979) under some simplifying assumptions. Using the stable age distribution and sensitivity coefficients in APPENDIX B to rewrite the demographic variance (Equation 3), assuming no covariance between age-specific survival and reproduction within years,  $c_i = 0$ , the effective population size becomes

$$N_e = \frac{N \bar{b} T}{\sum_{i=0}^k l_i \lambda^{-i-1} [\sigma_i^2 + s_i(1 - s_i) v_{i+1}^2]}, \quad (4b)$$

where  $\bar{b}$  is the average per capita reproductive rate and  $v_{i+1}$  is the reproductive value of age class  $i + 1$ . In the numerator  $N \bar{b}$  is the number of newborns entering the population per year. Assuming reproduction by random sampling of gametes within each age class, the number of progeny from parents of each age has a Poisson distribution with  $\sigma_i^2 = b_i$ . In the denominator the summation of the first term in brackets then becomes 1 (by the Euler-Lotka equation, APPENDIX B). Further assuming a constant population size and age structure,  $\lambda = 1$ , produces Felsenstein's formula for the effective size of a haploid population in a constant environment. The numerator in Hill's formula is the same, but the denominator is then the variance in lifetime reproductive success. CHARLESWORTH (1980) showed that these apparently different expressions are equivalent. Felsenstein (1971) also derived a formula essentially similar to (4b) for a growing haploid population in a constant environment with a Poisson distribution of reproduction, or at most one offspring per individual, in each age class.

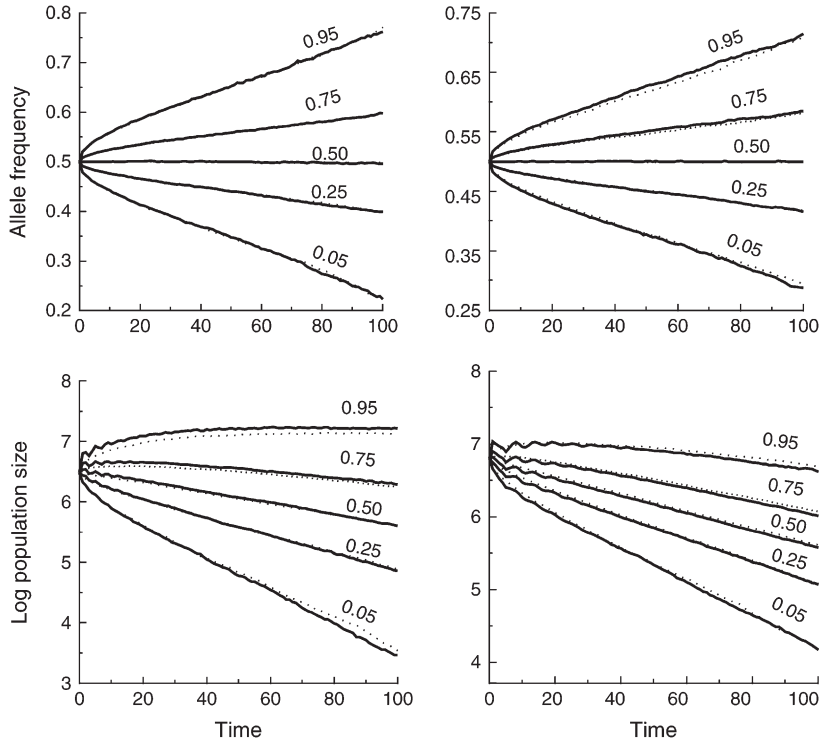


FIGURE 1.—Distributions of frequency of a neutral allele,  $p$ , and the natural log of total population size,  $\ln N$ , in a density-independent age-structured population, as functions of time. Solid lines show quantiles of the distributions based on 10,000 simulations of the full age-structured model. Dotted lines show corresponding quantiles of the distributions based on 10,000 simulations of the two-dimensional diffusion approximation (see text). In each time unit all offspring of a given female are fathered by the same male, the number of offspring for each female is Poisson distributed, and females mate at random within the general constraint of their preference for males of different ages (APPENDIX C). The expected proportion of females at birth is  $q = 0.5$ . Genotypes at a selectively neutral locus are initially in Hardy-Weinberg equilibrium for each age and sex class. Female fecundities are multiplied by a common stochastic environmental factor that is lognormally distributed with mean 1 and variance 0.1. Left (top and bottom), a life history with four age classes. Mean survival rates of females for age 0–3 are 0.6, 0.8, 0.7, and 0, and mean fecundities are 0, 0, 2, and 3. Males have identical survival rates, and female preferences for males of age 0–3 are proportional to 0, 1, 2, and 2. Initial total numbers of individuals in the four age classes are 200, 180, 150, and 120. These parameters give the constant coefficients  $\lambda = 0.9954$ ,  $T = 3.51$ ,  $\sigma_c^2 = 0.0070$ ,  $\sigma_d^2 = 0.4563$ ,  $\sigma_{d,g}^2 = 0.6292$ . Right (top and bottom), a life history with seven age classes. Mean survival rates of females for age 0–6 are 0.8, 0.95, 0.85, 0.65, 0.5, 0.5, and 0, and mean fecundities are 0, 0, 0, 0, 2, 3, and 4. Male survival rates for the seven age classes are 0.7, 0.9, 0.85, 0.5, 0.3, 0.2, and 0 and female preferences for males of age 0–6 are proportional to 0, 1, 2, 3, 4, 3, and 2. Initial total numbers of individuals in the seven age classes are 200, 180, 150, 120, 100, 80, and 60. These parameters give the constant coefficients  $\lambda = 0.9902$ ,  $T = 5.78$ ,  $\sigma_c^2 = 0.0033$ ,  $\sigma_d^2 = 0.3971$ , and  $\sigma_{d,g}^2 = 0.5187$ .

Several classical demographic parameters that appear in our formulas for effective population size, including the multiplicative growth rate,  $\lambda$ , and generation time,  $T$ , apply to a population in a constant environment with a stable age distribution. This is justified because the stochastic demographic theories reviewed above, in which these parameters naturally arise, and the diffusion theory to which they have been applied assume small or moderate fluctuations in the vital rates, so that stochastic deviations from the deterministic parameters usually are not very large (LANDE *et al.* 2003). Stochastic simulations of a full age-structured model demonstrate explicitly that under this assumption such formulas have good accuracy (ENGEN *et al.* 2005, and see Figure 1).

MONOECIOUS DIPLOID POPULATION

In contrast to standard population genetic models of monoecious or hermaphroditic populations, we assume that reproduction is controlled (or limited) by the female function of monoecious individuals and allow age-specific reproduction to differ through female and male functions. This is not only more realistic for most dioecious plants and hermaphroditic animals, but is also conveniently consistent with classical demographic models for populations with separate sexes, which are female biased (APPENDIX B). Using a projection matrix of the same

form as Equation 1, we define  $B_i$  as the mean number of offspring per parent produced through female function by the  $N_i$  monoecious individuals in the  $i$ th age class. The proportion surviving from age  $i$  to  $i + 1$  is  $S_i$ .

Initially we consider a rare allele at a selectively neutral locus in a large population (as in POLLAK 2000) so that all individuals carrying the allele are heterozygotes; later we demonstrate that the results also apply to intermediate allele frequencies. Let  $\mathbf{Z} = (Z_0, Z_1, \dots, Z_k)^T$  be the population vector for individuals with this allele, and write  $Z$  for the sum of these elements. The expected dynamics of  $\mathbf{Z}$  is then given by the expected projection matrix  $E\mathbf{L}$  and is the same as the expected dynamics of  $\mathbf{N}$ . The stochastic processes for  $\mathbf{N}$  and  $\mathbf{Z}$  also have identical environmental stochasticity, but differ in their demographic stochasticity because of additional components in  $\mathbf{Z}$  due to random sampling of alleles in Mendelian segregation.

For diploid populations we extend the application of stochastic demography to obtain an approximation for the sampling variance per unit time in the frequency of a rare allele. This involves deriving the demographic variance in  $Z$ , the subpopulation of heterozygotes containing the rare allele, which we denote as  $\sigma_{d,g}^2$  because it contains components from both demographic stochasticity and Mendelian segregation.

Before analyzing the influence of Mendelism, we show

that environmental stochasticity has no influence on the neutral allele frequency. Consider a large population, of sufficient size to neglect demographic stochasticity,  $N \gg \sigma_d^2/\sigma_c^2$  (LANDE *et al.* 2003). Define  $\mathbf{Y} = 2\mathbf{N} - \mathbf{Z}$  and denote the sum of elements in this vector as  $Y$ , so that the neutral allele frequency is  $p = Z/(Y + Z)$ . In each time unit the same environmental effects operate on  $\mathbf{Y}$  and  $\mathbf{Z}$  and through time they are influenced by the same sequence of environments. Thus, neglecting demographic stochasticity, the diffusion approximation for  $Y$  has infinitesimal mean and variance  $rY$  and  $\sigma_c^2 Y^2$ , and those for  $Z$  are  $rZ$  and  $\sigma_c^2 Z^2$ , with the infinitesimal covariance  $\sigma_c^2 YZ$ . Transforming this bivariate diffusion to the new variables  $N$  and  $p$  (APPENDIX A) reveals that, as in the haploid case, environmental stochasticity has no influence on  $p$ .

We now turn to the influence of Mendelian segregation. Suppose that a rare heterozygous individual in age class  $i$  produces  $y$  offspring as a mother in the next time unit and has survival  $J_i$ , with  $\Pr(J_i = 1) = s_i$  and  $\Pr(J_i = 0) = 1 - s_i$ . The number of rare alleles that this individual contributes as a mother in the next time unit to the 0th age class, say  $y_f$ , conditioned on  $y$ , is then binomially distributed with parameters  $(y, 1/2)$ . Applying the formulas for conditional mean and variance, this leads to

$$E y_f = E(y/2) = b_i/2$$

$$\begin{aligned} \text{Var}(y_f) &= E \text{Var}(y_f|y) + \text{Var} E(y_f|y) = E(y/4) + \text{Var}(y/2) \\ &= b_i/4 + \sigma_i^2/4 \end{aligned}$$

and the covariance between individual survival and reproduction in age class  $i$  is

$$\begin{aligned} \text{Cov}(y_f, J_i) &= E[E(y_f J_i | y, J_i)] - E[E(y_f | y)]E(J_i) \\ &= E(y J_i / 2) - E(y/2)E(J_i) = \text{Cov}(y/2, J_i) = c_i/2. \end{aligned}$$

In the population of heterozygotes bearing the rare allele the individuals also contribute to the next generation as fathers. Writing  $b_{mi}$ ,  $\sigma_{mi}^2$ , and  $c_{mi}$  for the mean, variance, and covariance with survival for the number of offspring  $y_m$  that an individual produces as a father we find that the total number of individuals  $y_f + y_m$  with the rare allele produced by a heterozygote has expected value  $(b_i + b_{mi})/2$  and variance  $(b_i + b_{mi} + \sigma_i^2 + \sigma_{mi}^2)/4$  provided that there is no covariance between the number of offspring an individual produces as mother and as father. The covariance between  $y_m + y_f$  and the survival  $J_i$  is  $c_i/2 + c_{mi}/2$ . The demographic variance for the subpopulation of heterozygotes has the same form as Equation 3 but with variances and covariances accounting for reproduction and Mendelian segregation through both male and female function,

$$\begin{aligned} \sigma_{dg}^2 \approx & \sum_{i=0}^k \lambda^{-2} \left[ \left( \frac{\partial \lambda}{\partial b_i} \right)^2 \frac{b_i + b_{mi} + \sigma_i^2 + \sigma_{mi}^2}{4} + \left( \frac{\partial \lambda}{\partial s_i} \right)^2 s_i (1 - s_i) \right. \\ & \left. + \frac{\partial \lambda}{\partial b_i} \frac{\partial \lambda}{\partial s_i} (c_i + c_{mi}) \right]. \end{aligned} \quad (5)$$

Note that the  $b_{mi}$  cannot be chosen arbitrarily but are constrained by the values of the  $b_i$  because the total number of offspring produced through paternal and maternal function must be the same. Hence their expectations also are the same, giving  $\sum b_i u_i = \sum b_{mi} u_i$ . Furthermore, because all individuals are monoecious, the Euler-Lotka equation for  $\lambda$  (APPENDIX B) must be the same for the reproductive schedules through male and female function. The genetic generation time, defined as the average age of parents of newborn offspring, is therefore given by the standard formula (APPENDIX B) but using the average reproductive rates through male and female function,

$$T = \sum_{i=0}^k (i + 1) l_i \frac{b_i + b_{mi}}{2} \lambda^{-i-1}. \quad (6)$$

Approximating the dynamics of the frequency of the rare allele  $p = Z/(2N)$  as a diffusion process, the infinitesimal mean is 0, reflecting that the allele is selectively neutral, and the infinitesimal variance is  $\approx \sigma_{dg}^2 p/(2N)$ . Multiplying the infinitesimal variance by the genetic generation time and equating this to the sampling variance in the frequency of a neutral allele in an ideal diploid population with nonoverlapping generations,  $p(1 - p)/(2N_c)$ , with  $p$  assumed to be small, produces the effective population size per generation,

$$N_c = \frac{N}{\sigma_{dg}^2 T}. \quad (7)$$

**Intermediate allele frequencies:** To check what happens when the neutral allele is not rare, imagine that all  $2N$  alleles at the locus are divided randomly into a large number of different neutral alleles with the same frequency, say  $p = 1/n$ . Then the variance of the change in the sum of these frequencies is 0 since their sum is 1, giving

$$np\sigma_{dg}^2/(2N) + n(n - 1)c = 0,$$

where  $c$  denotes the covariance between the change in frequencies of two alleles. For large  $n$  this gives  $c \approx -p\sigma_{dg}^2/(2Nn)$ . Then we can redefine an allele as a group of  $m$  of the original  $n$  alleles thus having frequency  $P = mp$ . The variance of the change in the frequency of this allele is

$$\text{Var}(P) \approx mp\sigma_{dg}^2/(2N) + m(m - 1)c \approx \sigma_{dg}^2 P(1 - P)/(2N).$$

This argument also applies with separate sexes, supporting the generality of results derived under the assumption of small allele frequencies.

#### SEPARATE SEXES

**Demographic model:** The mating system is assumed to be polygamous, with reproduction governed (or limited) by females. Let  $\mathbf{N}$  be the population column vector  $(F_0, F_1, \dots, F_k, M_0, M_1, \dots, M_k)^T$ , where  $F_i$  and  $M_i$  denote

the number of females and males in the  $i$ th age class. The projection matrix  $\mathbf{A}$  giving the population vector in the next time unit  $\mathbf{AN}$  can then be partitioned into four submatrices, each with  $k + 1$  rows and columns,

$$\mathbf{A} = \begin{bmatrix} \mathbf{A}_{ff} & \mathbf{A}_{mf} \\ \mathbf{A}_{fm} & \mathbf{A}_{mm} \end{bmatrix}, \tag{8a}$$

where  $\mathbf{A}_{ff}$  is the projection matrix for the female population (Equation 1) and  $\mathbf{A}_{mf}$  is a matrix with all elements 0. The contribution from females to sons is given by

$$\mathbf{A}_{fm} = \begin{bmatrix} B_{f,m,0} & B_{f,m,1} & \dots & B_{f,m,k} \\ 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix}, \tag{8b}$$

where  $B_{f,m,i}$  is the mean number of sons (second subscript) per female (first subscript), while the contribution from males to sons is determined only by the survival probabilities,

$$\mathbf{A}_{mm} = \begin{bmatrix} 0 & 0 & \dots & 0 & 0 \\ S_{m,0} & 0 & \dots & 0 & 0 \\ 0 & S_{m,1} & \dots & 0 & 0 \\ \vdots & \ddots & & \vdots & \\ 0 & 0 & \dots & S_{m,k-1} & 0 \end{bmatrix}. \tag{8c}$$

Here  $S_{m,i}$  denotes the mean number of males in age-class  $i$  surviving to the next time unit. The components of these matrices are all realized mean values in a finite population (not theoretical expectations) and therefore are stochastic variables. Using the same notation for the female projection matrix, we have

$$\mathbf{A}_{ff} = \begin{bmatrix} B_{f,f,0} & B_{f,f,1} & \dots & B_{f,f,k-1} & B_{f,f,k} \\ S_{f,0} & 0 & \dots & 0 & 0 \\ 0 & S_{f,1} & \dots & 0 & 0 \\ \vdots & \ddots & & \vdots & \\ 0 & 0 & \dots & S_{f,k-1} & 0 \end{bmatrix}. \tag{8d}$$

Note that  $B_{m,f,i} = B_{m,m,i} = 0$ . We write  $s_{m,i}$  for the expected value of  $S_{m,i}$  and similarly for females. These expectations are then the probabilities of survival. For the expectations of the realized birth rates  $B_{f,f,i}$  and  $B_{f,m,i}$ , we write  $qb_{f,i}$  and  $(1 - q)b_{f,i}$ , where  $q$  is the probability that an offspring is a daughter and the subscript  $f$  denotes contributions from females. The analogous contributions from males are 0.

The dominant eigenvalue of the expected projection matrix  $E\mathbf{A}$  is determined only by the elements of the expected female matrix  $E\mathbf{A}_{ff}$ , which therefore has the same dominant eigenvalue  $\lambda$ . Hence all sensitivities relating to vital rates for males are 0.

Elements of the two-sex projection matrix  $\mathbf{A}$  are influenced by demographic and environmental stochasticity. The demographic variances and covariances of the elements are inversely proportional to the total population size (ENGEN *et al.* 2005). The dynamics of the total population size can be approximated by a diffusion process. Because the population dynamics are female biased, fluctuations in male abundance do not affect the long-run growth rate or the demographic and environmental variances. If the population at a particular time has a large number of males, in the absence of density dependence this will have no impact on future population sizes after some time has passed.

Denoting the demographic variance for the total population and for females, respectively, as  $\sigma_a^2$  and  $\sigma_{af}^2$ , evaluated using the method of ENGEN *et al.* (2005), we find that  $\sigma_a^2 = \sigma_{af}^2/q$ . Hence, the total population can be approximated by a diffusion with infinitesimal mean  $rN$  and infinitesimal variance  $\sigma_a^2 N + \sigma_e^2 N^2$ , while the female population has infinitesimal mean  $rF$  and infinitesimal variance  $q\sigma_a^2 F + \sigma_e^2 F^2$ . Using the transformation formulas for a one-dimensional diffusion process (APPENDIX A), the diffusion for  $N' = F/q$  has the same infinitesimal mean and variance as that for the total population, indicating, as discussed in the preceding paragraph, that the total population behaves like the female population, magnified by a factor  $1/q$ .

**Expected dynamics of a rare allele:** To compute the effective size of the population we assume a large total population size  $N = \Sigma(F_i + M_i)$  and consider a neutral allele with a small frequency such that the total number of these alleles in the population is sufficiently large that a diffusion approximation for the dynamics of the allele frequency is accurate. Then we can assume as an approximation that individuals carrying this allele always are heterozygous and mate with individuals that lack this allele.

Let the column vectors  $\mathbf{X} = (X_0, X_1, \dots, X_k)^T$  and  $\mathbf{Y} = (Y_0, Y_1, \dots, Y_k)^T$  represent the numbers of females and males, respectively, that are in different age groups and carry the rare allele. Writing  $\mathbf{Z} = (Z_0, Z_1, \dots, Z_{2k+1})^T = (\mathbf{X}^T, \mathbf{Y}^T)^T$  for the full age-sex vector of allele numbers, the value of  $\mathbf{Z}$  in the next time unit can be expressed as  $\mathbf{GZ}$ , where  $\mathbf{G}$  is the two-sex genetic projection matrix, which has the same structure as  $\mathbf{A}$  but with somewhat different components. Partitioning  $\mathbf{G}$  into the same type of submatrices,  $\mathbf{G}_{ff}$ ,  $\mathbf{G}_{mf}$ ,  $\mathbf{G}_{fm}$ , and  $\mathbf{G}_{mm}$ , the contributions from males to the 0th age classes are no longer zeros since both sexes contribute genes to the offspring. The variances and covariances of the elements also are different since sampling of alleles from heterozygotes generates additional stochasticity.

We assume that the numbers of offspring from fe-

males in the  $i$ th age class are independent, identically distributed variables with mean  $b_{f,i}$  and variance  $\sigma_{f,i}^2$  and write  $B_{f,i} = B_{f,m,i} + B_{f,f,i}$  for the realized mean number of offspring actually produced by the finite number of females in age class  $i$ . The offspring are of three types: individuals without the rare allele, daughters with the rare allele, and sons with the rare allele, occurring with probabilities  $\frac{1}{2}$ ,  $\frac{1}{2}q$ , and  $\frac{1}{2}(1 - q)$ , respectively. Hence, conditioning on  $B_{f,i}$ , the numbers of individuals in these categories produced by females in age class  $i$  have a multinomial distribution with parameters  $[X_i B_{f,i}, \frac{1}{2}, \frac{1}{2}q, \frac{1}{2}(1 - q)]$ . Using conditional expectations, it follows that the expected numbers of daughters and sons with the rare allele produced by females in age group  $i$  are  $\frac{1}{2}q b_{f,i} X_i$  and  $\frac{1}{2}(1 - q) b_{f,i} X_i$ . Although the male contributions may have a complex structure of variances depending on the mating system, the same argument applies for the expected contributions from males. Writing  $\mathbf{g}$  for the expectation of the genetic projection matrix  $\mathbf{G}$  and using the same decomposition gives

$$\mathbf{g}_{ff} = \begin{bmatrix} \frac{1}{2} q b_{f,0} & \frac{1}{2} q b_{f,1} & \dots & \frac{1}{2} q b_{f,k-1} & \frac{1}{2} q b_{f,k} \\ s_{f,0} & 0 & \dots & 0 & 0 \\ 0 & s_{f,1} & \dots & 0 & 0 \\ \vdots & \ddots & & \vdots & \\ 0 & 0 & \dots & s_{f,k-1} & 0 \end{bmatrix} \quad (9a)$$

$$\mathbf{g}_{mf} = \begin{bmatrix} \frac{1}{2} q b_{m,0} & \frac{1}{2} q b_{m,1} & \dots & \frac{1}{2} q b_{m,k} \\ 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix} \quad (9b)$$

$$\mathbf{g}_{fm} = \begin{bmatrix} \frac{1}{2} (1 - q) b_{f,0} & \frac{1}{2} (1 - q) b_{f,1} & \dots & \frac{1}{2} (1 - q) b_{f,k} \\ 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix} \quad (9c)$$

$$\mathbf{g}_{mm} = \begin{bmatrix} \frac{1}{2} (1 - q) b_{m,0} & \frac{1}{2} (1 - q) b_{m,1} & \dots & \frac{1}{2} (1 - q) b_{m,k-1} & \frac{1}{2} (1 - q) b_{m,k} \\ s_{m,0} & 0 & \dots & 0 & 0 \\ 0 & s_{m,1} & \dots & 0 & 0 \\ \vdots & \ddots & & \vdots & \\ 0 & 0 & \dots & s_{m,k-1} & 0 \end{bmatrix} \quad (9d)$$

Since females and males produce the same numbers of offspring of each sex, there are constraints on the parameters defining the male contributions. Conditioned

on the population vector  $\mathbf{N}$  the expected number of offspring also must be the same,  $\sum_{i=0}^k b_{f,i} F_i = \sum_{i=0}^k b_{m,i} M_i$ . Dividing both sides by the total population size and substituting the sex-age distribution obtained from the deterministic model (using expectations) yields  $q \sum_{i=0}^k b_{f,i} l_{f,i} \lambda^{-i} = (1 - q) \sum_{i=0}^k b_{m,i} l_{m,i} \lambda^{-i}$ , where  $l_{m,i}$  is the survival of males defined as for females.

We proceed to find the dominant eigenvalue of the expected genetic projection matrix  $\mathbf{g}$  satisfying  $\mathbf{g}\mathbf{Z} = \lambda\mathbf{Z}$ , leading to the relation

$$\frac{1}{2} q \sum_{i=0}^k b_{f,i} l_{f,i} \lambda^{-i} + \frac{1}{2} (1 - q) \sum_{i=0}^k b_{m,i} l_{m,i} \lambda^{-i} = \lambda.$$

Employing the above constraint we see that the dominant eigenvalue for the total population also satisfies this equation and that both the sums must equal  $\lambda/2$ . Consequently,  $\lambda$  should be computed from

$$q \sum_{i=0}^k l_{f,i} b_{f,i} \lambda^{-i-1} = 1, \quad (10a)$$

which is identical to the equation for the dominant eigenvalue of the expected female projection matrix  $\mathbf{E}\mathbf{A}_{ff}$  (Equation 8d; APPENDIX B), while the scaling of the expected birth rates for males is determined by

$$(1 - q) \sum_{i=0}^k l_{m,i} b_{m,i} \lambda^{-i-1} = 1. \quad (10b)$$

We use the term “female preference” to describe the age distribution of males chosen as mates by all females independent of female age and assume that in each time unit all offspring of a given female are fathered by a single male (see APPENDIX C).

Now consider the mean generation time for genes. Because we assume a constant sex ratio at birth, the mean age of mothers of newborn offspring is identical to the generation time of the female population,

$$T_f = q \sum_{i=0}^k (i + 1) l_{f,i} b_{f,i} \lambda^{-i-1}, \quad (11a)$$

where  $l_{f,i} = \prod_{j=0}^{i-1} s_{f,j}$  for  $i = 1, 2, \dots, k$  is the female survival to age  $i$  and  $l_{f,0} = 1$  (CASWELL 1989, 2001). Similarly, the mean age of fathers of newborn offspring is the same as the generation time of the male population,

$$T_m = (1 - q) \sum_{i=0}^k (i + 1) l_{m,i} b_{m,i} \lambda^{-i-1}. \quad (11b)$$

Thus the genetic generation time is  $T = (T_m + T_f)/2$  (EMIGH and POLLAK 1979).

**Effective population size:** To simplify calculation of the demographic variance in the genetic projection matrix  $\mathbf{G}$ , we initially assume no environmental stochasticity, which we later show has no direct influence on fluctuations in the frequency of a rare neutral allele and hence no impact on the momentary  $N_e$  calculated from a diffusion approximation. Results of ENGEN *et al.* (2005) can be employed to derive the diffusion approximation for the sum of the components of  $\mathbf{Z}$ , denoted as

$Z$ . If the demographic variance-covariance terms  $\text{Cov}(G_{i,l}, G_{j,l})$  are proportional to  $Z_l^{-1}$  and the others are 0, then the infinitesimal variance in the diffusion approximation for  $Z$  is  $\approx \sigma_{d,g}^2 Z$ , where the variance  $\sigma_{d,g}^2$  is a constant. In APPENDIX C we derive the demographic variances and covariances of elements in the genetic projection matrix  $\mathbf{G}$ , as well as sensitivity coefficients of the expected genetic projection matrix  $\mathbf{g}$ , from which this variance can be calculated.

In the absence of environmental stochasticity the diffusion approximation for  $Z$  has infinitesimal mean  $rZ$  and infinitesimal variance  $\sigma_{d,g}^2 Z$ , with

$$\sigma_{d,g}^2 \approx \sum_{l=0}^{2k+1} \frac{\lambda^{-2}}{u_l} \sum_{ij} \frac{\partial \lambda}{\partial g_{i,l}} \frac{\partial \lambda}{\partial g_{j,l}} \text{Cov}(G_{i,l}, G_{j,l}) Z_l, \quad (12)$$

where  $i$  and  $j$  run from 0 to  $2k + 1$  and  $\mathbf{u} = (u_0, u_1, \dots, u_{2k+1})^T$  is the stable age-sex distribution given by the right eigenvector of the expected genetic projection matrix  $\mathbf{g}$  (APPENDIX C). The frequency of the rare allele  $p = Z/(2N)$  can now also be approximated as a diffusion with infinitesimal mean 0 and infinitesimal variance  $V_p \approx p\sigma_{d,g}^2/(2N)$ . For a dioecious diploid population the variance effective population size per generation is defined by  $V_p T = p(1 - p)/(2N_e)$ , where  $T$  is the genetic generation time (after Equations 11). With  $p$  assumed to be small, this produces the effective population size per generation,

$$N_e = \frac{N}{\sigma_{d,g}^2 T}. \quad (13)$$

Although this derivation is based on the assumption of a small allele frequency, the results can be applied for any allele frequency, by the same argument as that given for a monoecious population (after Equation 7).

**Constraints on environmental fluctuations in  $\mathbf{G}$ :** In the previous section individuals carrying the rare neutral allele always mate with others not bearing this allele. Hence, for these individuals there are no constraints linking the number of offspring produced by males and females. When considering environmental fluctuations, however, by definition, stochastic fluctuations in the genetic projection matrix  $\mathbf{G}$  exert the same effect on all individuals of a given sex and age. This implies that  $\sum B_{f,i} F_i = \sum B_{m,i} M_i$  exactly at each time step, where the deviations in the birth rates, such as  $\Delta B_{f,i} = B_{f,i} - b_{f,i}$ , are purely environmental fluctuations, assuming that the population is large enough to ignore demographic stochasticity. Then, because  $\mathbf{Z}$  will be close to the stable age-sex distribution for  $Np$  sufficiently large, we also have the constraint  $\sum B_{f,i} X_i = \sum B_{m,i} Y_i$ .

In contrast, the demographic fluctuations in the transition matrix  $\mathbf{G}$ , arising in finite populations, are under no such constraint, since demographic fluctuations in  $\mathbf{X}$  and  $\mathbf{Y}$  occur independently. Inserting the above constraint in the projection equation and eliminating the  $B_{m,i}$  (which are determined by annual realizations of the  $B_{f,i}$ ) we find for populations sufficiently large to neglect demographic stochasticity ( $N \gg \sigma_d^2/\sigma_c^2$ ) that

$$\mathbf{G} \begin{bmatrix} \mathbf{X} \\ \mathbf{Y} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_{ff}\mathbf{X} + \mathbf{G}_{mf}\mathbf{Y} \\ \mathbf{G}_{fm}\mathbf{X} + \mathbf{G}_{mm}\mathbf{Y} \end{bmatrix} = \mathbf{A} \begin{bmatrix} \mathbf{X} \\ \mathbf{Y} \end{bmatrix}.$$

This implies that stochastic environmental effects on the subpopulation bearing the rare allele are perfectly correlated with those influencing the total population since their changes are defined exactly by the same realization of  $\mathbf{A}$  at each time. Environmental stochasticity therefore has no direct impact on the frequency of a neutral allele and influences  $N_e$  only indirectly through fluctuations in population size that it causes.

### $N_e$ OVER LONGER TIME INTERVALS

**Two-dimensional diffusion process for  $p$  and  $\ln N$ :** Figure 1 illustrates numerical simulations of the two-dimensional diffusion approximation for the frequency of a neutral allele,  $p$ , and log total population size,  $\ln N$ , in an age-structured population with two sexes in a fluctuating environment. In the diffusion approximation the process for  $p$  has infinitesimal mean 0 and infinitesimal variance  $p(1 - p)\sigma_{d,g}^2/(2N)$  (Equations 12 and 13), the process for  $\ln N$  has infinitesimal mean  $r - \sigma_c^2/2 - \sigma_d^2/(2N)$  and infinitesimal variance  $\sigma_c^2 + \sigma_d^2/N$ , and there is no infinitesimal covariance between  $p$  and  $\ln N$ . Along each sample path of this process the effective population size changes with time as the total population size changes (Equation 13) due to a combination of deterministic factors and demographic and environmental stochasticity. Sample paths for the bivariate diffusion process were generated numerically in discrete time by using the infinitesimal means to produce the expected changes at each time step, to which were added random normal deviates with means 0 and variances equal to the infinitesimal variances, updating the values of  $p$  and  $\ln N$  at each time step.

Stochastic simulations also were performed for the full age-structured model describing the dynamics of numbers of the three genotypes. Comparison of the results from these two approaches demonstrates that the two-dimensional diffusion approximation accurately predicts the distribution of  $\ln N$  and  $p$  over a substantial time interval of many generations. In the full age-structured model the total population size undergoes transient oscillations due to initial and stochastic deviations from the deterministic stable age distribution (CASWELL 1989, 2001). These oscillations are absent from the diffusion approximation, as reflected in quantiles of the distribution of  $\ln N$  in Figure 1, which display oscillations in the full age-structured model, but are smooth for the diffusion approximation. In contrast, the two-dimensional diffusion rather accurately describes the distribution of allele frequency,  $p$ , in the full age-structured model.

The next section develops a separate, analytical approach to extend the formulas for  $N_e$  to longer time intervals by accounting for deterministic changes and environmentally driven fluctuations in total population size.

**Extension of analytical formulas for  $N_e$  to longer times:**

Our formulas for  $N_e$  thus far are expressed as variance effective population sizes per generation, derived by multiplying the generation time by the infinitesimal variance in a diffusion approximation for the frequency of a neutral allele (Equations 4, 7, and 13). These formulas therefore describe the current rate of random genetic drift per generation under prevailing conditions, including total population size, rather than across a longer time during which the population size may change or fluctuate considerably. Despite our assumption of density-independent growth in deriving these formulas, these effective population sizes nevertheless are applicable to density-dependent populations, because conditions prevailing at a given time also can include the current population density. We now show how to extend these formulas for  $N_e$  to account for changes in population size over longer time intervals.

We first evaluate the effective population size given the process  $N(t)$  over some time interval  $\Delta t$ . Following WRIGHT (1931, 1969) we assume that this interval is sufficiently short ( $< 2N_e$  generations) so that the allele frequency does not change much,  $\Delta t \ll 2N_e T$ . Writing  $p = Z/(2N)$  for the allele frequency, the variance of the change in frequency is then

$$\text{Var}(\Delta p) \approx \sigma_{\text{dg}}^2 p(1-p) \int_0^{\Delta t} \frac{dt}{2N(t)}.$$

The drift per generation is  $\text{Var}(\Delta p) T/\Delta t$ , which we equate to  $p(1-p)/(2N_e)$ , giving

$$N_e = \frac{N_h(\Delta t)}{\sigma_{\text{dg}}^2 T}, \quad \text{where } N_h(\Delta t) = \left[ \frac{1}{\Delta t} \int_0^{\Delta t} \frac{dt}{N(t)} \right]^{-1}. \quad (14)$$

$N_h(\Delta t)$  is the harmonic mean of the population sizes over the time interval.

If we know only the population size at time  $t = 0$  we must extend the expression for effective population size to include unknown future population sizes during a certain time interval. This can be accomplished by considering the unconditional variance of  $\Delta p$  rather than the above, which is conditioned on a particular series of population sizes during the time interval. Writing  $\tilde{N}$  for the population process from time 0 to  $\Delta t$  we then have

$$\text{Var}(\Delta p) = E \text{Var}(\Delta p | \tilde{N}) + \text{Var} E(\Delta p | \tilde{N}) = E \text{Var}(\Delta p | \tilde{N})$$

because  $E(\Delta p | \tilde{N}) = 0$  for a selectively neutral allele. This establishes that if the harmonic mean is redefined as

$$N_h(\Delta t) = \left[ \frac{1}{\Delta t} \int_0^{\Delta t} E \frac{1}{N(t)} dt \right]^{-1},$$

then the formula for the effective population size remains the same as in Equation 14.

In the following formulas we assume for simplicity that the population is not very small, so that fluctuations in  $N$  are caused primarily by environmental stochasticity

rather than by demographic stochasticity,  $N(t) \gg \sigma_d^2/\sigma_c^2$  (LANDE *et al.* 2003). Then, in a density-independent age-structured population in a stochastic environment, with an initial total population size  $N(0)$ , the logarithm of total population size is asymptotically normally distributed (COHEN 1977, 1979). The one-dimensional diffusion approximation for  $\ln N(t)$  has infinitesimal mean  $r - \sigma_c^2/2$  and infinitesimal variance  $\sigma_c^2$ , which are constants; this identifies the diffusion approximation as a Wiener process, the solution of which is normal with mean  $\ln N(0) + (r - \sigma_c^2/2)t$  and variance  $\sigma_c^2 t$  (LANDE and ORZACK 1988). Using standard relationships between the moments of normal and lognormal distributions (JOHNSON and KOTZ 1970) this leads to

$$E \frac{1}{N(t)} \approx \frac{1}{N(0)} e^{-(r-\sigma_c^2)t}.$$

Integrating this from 0 to  $\Delta t$  and substituting the result into Equation 14 yields the effective population size per generation during the time interval  $\Delta t$ ,

$$N_e \approx \frac{N(0)}{\sigma_{\text{dg}}^2 T} \frac{(\sigma_c^2 - r)\Delta t}{e^{(\sigma_c^2 - r)\Delta t} - 1}, \quad (15)$$

which differs from the effective population size at time 0 (Equation 13) by the last factor that includes deterministic growth and environmental stochasticity in total population size.

To ensure accuracy of the correction factor in Equation 15 over longer time intervals, three conditions should apply. First, the population cannot be very small, because of the assumption that fluctuations in  $N$  are dominated by environmental stochasticity rather than by demographic stochasticity, which typically implies that  $N \geq 100$  individuals (LANDE *et al.* 2003). Second, as in classical formulas for effective population size that account for temporal fluctuations in  $N$  (WRIGHT 1931, 1969), Equation 15 holds only over time intervals  $\ll 2N_e$  generations, during which the frequency of a neutral allele does not change much. Finally, as in classical formulas for  $N_e$  that depend on the mean and variance of lifetime reproductive success (WRIGHT 1931, 1969; CROW and KIMURA 1970; HILL 1972, 1979), the population growth rate in the average environment, as well as the demographic and environmental variances, may be density dependent rather than being constants (LANDE *et al.* 2003), restricting the application of Equation 15 to time intervals during which  $N$  does not change greatly.

DISCUSSION

Previous theories on the effective size of age-structured populations assumed a constant population size and constant age-sex structure (FELSENSTEIN 1971; HILL 1972, 1979; EMIGH and POLLAK 1979; POLLAK 1980, 2000; NUNNEY 1991, 1993; ORIVE 1993). This severely limits their applicability to natural populations in which all of these quantities fluctuate due to a combination of

demographic and environmental stochasticity (LANDE *et al.* 2003). From simple models without age structure, and from their application to empirical data, it is known that fluctuating population size is the most important factor in reducing the ratio of effective to actual population size (WRIGHT 1931, 1969; CROW and KIMURA 1970; FRANKHAM 1995).

Recent demographic results have approximated the stochastic density-independent growth of an age-structured population as a one-dimensional diffusion process with two or three parameters, the deterministic growth rate in the average environment,  $r = \ln \lambda$ , and the environmental variance,  $\sigma_e^2$  (LANDE and ORZACK 1988), as well as the demographic variance,  $\sigma_d^2$  (ENGEN *et al.* 2005). We utilized these results to derive the effective size of a fluctuating age-structured population.

Our basic formulas for  $N_e$  are derived from the infinitesimal variance of a diffusion approximation, giving the sampling variance in the frequency of a neutral allele per unit time. Multiplying this by the generation time and equating to the sampling variance of allele frequency in an ideal population with nonoverlapping generations produce the effective population size per generation (Equations 4, 7, and 13). It is therefore necessary to interpret these basic formulas as the effective population size per generation applying under conditions prevailing at a given time, including the current population size. These effective population sizes depend on demographic stochasticity and (in diploid populations) Mendelian segregation, but not on environmental stochasticity, which by definition affects the vital rates of all genotypes in the same way and therefore has no direct influence on neutral allele frequency. Over longer time intervals of a generation or more, deterministic population growth and environmental stochasticity impact effective population size by causing changes in the actual population size. The effective population size at a given time, obtained from a diffusion approximation, can be extended to account for population growth and environmental stochasticity over longer time intervals (Equation 15).

It has long been understood from deterministic models that a close connection exists between the population growth rate used by ecologists and demographers and the mean fitness used by population geneticists. Our results demonstrate that this connection extends to stochastic models since the demographic and environmental variances in vital rates are key factors influencing not only stochastic population dynamics (TULJAPURKAR 1990; CASWELL 2001; LANDE *et al.* 2003), but also the genetic effective size of fluctuating age-structured populations (Equations 4, 7, 13, and 15).

Our formulas are consistent with previous results derived under simplified conditions of a constant environment, constant population size and age structure, and no demographic covariance between age-specific survival and reproduction within years. Further assuming that

reproduction occurs by random sampling of gametes from within each age class, producing a Poisson distribution of family size from parents of each age, Equation 4b for a haploid population is equivalent to formulas of Felsenstein (1971) and Hill (1979). For a monoecious population of constant size with discrete nonoverlapping generations ( $s_i = 0$ ,  $u_0 = 1$ ,  $\lambda = b_0 = b_{m0} = 1$ ) Equation 7 reduces to  $N_e = 4N / (2 + \sigma_0^2 + \sigma_{m0}^2)$ , where  $\sigma_0^2 + \sigma_{m0}^2$  is variance in family size through female plus male function. This agrees with the classical formula of Wright (1931, 1969), neglecting second-order terms ( $N \gg 1$ ), and under reproduction by random sampling of gametes (variance in family size = 2) we recover the ideal population with  $N_e = N$ . For a simplified life history with sex- and age-independent vital rates, the Euler-Lotka equation for a stable population shows that the birth rate equals the death rate,  $b = 1 - s$ , and the generation time is  $T = 1 / (1 - s)$ ; further assuming Poisson distributions of annual family sizes, Equation 7 reduces to  $N_e = N / (2 - 1/T)$ , which approaches  $N_e = N/2$  as the generation time becomes long. This agrees with a result derived under the same assumptions by Nunney (1991) from a formula of Hill (1979).

We established by simulations that our general expressions also can be employed to model a complex life history with population growth and environmentally driven fluctuations in population size and age structure. Our two-dimensional diffusion approximation accurately predicts the joint distribution of the frequency of a selectively neutral allele,  $p$ , and the total population size,  $N$ , in a fluctuating age-structured population over several or many generations, as illustrated for a diploid population with separate sexes in Figure 1. This applies for stochastic density-independent population growth, under which the coefficients describing demographic, environmental, and genetic stochasticity remain constant, while the effective population size continually changes with deterministic growth and stochastic fluctuations in total population size. This theory should therefore be useful for studies of evolution in finite populations when it is desirable to account for stochastic population dynamics and life history.

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#### APPENDIX A: TRANSFORMATION OF A DIFFUSION PROCESS

Suppose the variables  $\mathbf{x} = (x_1, x_2, \dots)$  obey a diffusion process with infinitesimal means  $M_i(\mathbf{x}) = (1/dt)E(dx_i|\mathbf{x})$  and infinitesimal variances and covariances  $V_{ij}(\mathbf{x}) = (1/dt)\text{Cov}(dx_i, dx_j|\mathbf{x})$ . The transformation formulas for a univariate diffusion can be derived by taking the mean and variance of a Taylor expansion of the transformed variables (KARLIN and TAYLOR 1981) and are readily generalized to a bivariate diffusion process.

For example, consider the univariate diffusion process for the natural log of population of size  $x = \ln N$ , discussed after Equation 3. Denoting  $r = \ln \lambda$ , this has infinitesimal mean  $M_x = r - \sigma_c^2/2 - \sigma_d^2/(2N)$  and infinitesimal variance  $V_x = \sigma_c^2 + \sigma_d^2/N$  (LANDE *et al.* 2003). Transforming to the scale of actual population size,  $N = e^x$ , the infinitesimal mean and variance are given by

$$\mu_N = \frac{\partial N}{\partial x} M_x + \frac{1}{2} \frac{\partial^2 N}{\partial x^2} V_x \quad \text{and} \quad \sigma_N^2 = \left( \frac{\partial N}{\partial x} \right)^2 V_x$$

(Karlin and Taylor 1981). Using  $\partial N/\partial x = e^x = N$  and  $\partial^2 N/\partial x^2 = e^x = N$  produces

$$\mu_N = rN \quad \text{and} \quad \sigma_N^2 = \sigma_d^2 N + \sigma_c^2 N^2.$$

As a second example, in the derivation of Equation 4 for a haploid population start with the original variables  $Y$  and  $Z$  for the numbers of two selectively neutral genotypes. These have infinitesimal means  $M_Y =$

$rY$  and  $M_Z = rZ$ , infinitesimal variances  $V_Y = \sigma_d^2 Y + \sigma_c^2 Y^2$  and  $V_Z = \sigma_d^2 Z + \sigma_c^2 Z^2$ , and infinitesimal covariance  $C_{YZ} = \sigma_c^2 YZ$ . The new variables of population size and gene frequency,  $N = Y + Z$  and  $p = Z/(Y + Z)$ , have infinitesimal means

$$\mu_N = \frac{\partial N}{\partial Y} M_Y + \frac{\partial N}{\partial Z} M_Z + \frac{1}{2} \frac{\partial^2 N}{\partial Y^2} V_Y + \frac{1}{2} \frac{\partial^2 N}{\partial Z^2} V_Z + \frac{\partial^2 N}{\partial Y \partial Z} C_{YZ}$$

$$\mu_p = \frac{\partial p}{\partial Y} M_Y + \frac{\partial p}{\partial Z} M_Z + \frac{1}{2} \frac{\partial^2 p}{\partial Y^2} V_Y + \frac{1}{2} \frac{\partial^2 p}{\partial Z^2} V_Z + \frac{\partial^2 p}{\partial Y \partial Z} C_{YZ},$$

infinitesimal variances

$$\sigma_N^2 = \left( \frac{\partial N}{\partial Y} \right)^2 V_Y + \left( \frac{\partial N}{\partial Z} \right)^2 V_Z + 2 \frac{\partial N}{\partial Y} \frac{\partial N}{\partial Z} C_{YZ}$$

$$\sigma_p^2 = \left( \frac{\partial p}{\partial Y} \right)^2 V_Y + \left( \frac{\partial p}{\partial Z} \right)^2 V_Z + 2 \frac{\partial p}{\partial Y} \frac{\partial p}{\partial Z} C_{YZ},$$

and infinitesimal covariance

$$C_{Np} = \frac{\partial N}{\partial Y} \frac{\partial p}{\partial Y} V_Y + \frac{\partial N}{\partial Z} \frac{\partial p}{\partial Z} V_Z + \frac{\partial N}{\partial Y} \frac{\partial p}{\partial Z} C_{YZ} + \frac{\partial N}{\partial Z} \frac{\partial p}{\partial Y} C_{YZ}.$$

Evaluating these formulas produces for the population size the intuitively obvious infinitesimal mean and variance  $\mu_N = rN$  and  $\sigma_N^2 = \sigma_d^2 N + \sigma_c^2 N^2$  and for the gene frequency the obvious infinitesimal mean  $\mu_p = 0$  with the infinitesimal variance  $\sigma_p^2 = p(1-p)\sigma_d^2/N$  and no infinitesimal covariance,  $C_{Np} = 0$ .

## APPENDIX B: CLASSICAL DEMOGRAPHIC FORMULAS

Results from the classical Leslie matrix model (LESLIE 1945; KEYFITZ 1968; DEMETRIUS 1969) for the deterministic dynamics of a density-independent age-structured population can be applied to the expected dynamics of a haploid (asexual) population, a monoecious population, or a population with separate sexes counting only females, as if the population were growing deterministically in the average environment (TULJAPURKAR 1982, 1990; CASWELL 1989, 2001). Assuming that the expected reproductive rates of any two sequential age classes are nonzero, the population asymptotically approaches a stable expected age distribution and a constant expected growth rate. The vital rates for individuals in the  $i$ th age class in the average environment are the expected reproductive rate,  $b_i$ , and probability of survival,  $s_i$ , per unit time. The dominant eigenvalue,  $\lambda$ , of expected projection matrix,  $EL$ , gives the asymptotic multiplicative growth rate of the expected population size per unit time when the expected age structure has achieved a stable distribution;  $\lambda$  is the unique real (and nonnegative) solution of the Euler-Lotka equation

$$\sum_{i=0}^k l_i b_i \lambda^{-i-1} = 1,$$

where  $l_i = \prod_{j=0}^{i-1} s_j$  for  $i = 1, 2, \dots, k$  is the probability of survival to age  $i$  and  $l_0 = 1$ .

The stable age distribution (column) vector  $\mathbf{u} = (u_0, u_1, \dots, u_k)^T$  and the reproductive value (row) vector  $\mathbf{v} = (v_0, v_1, \dots, v_k)$ , are, respectively, the right and left dominant eigenvectors of the expected Leslie matrix,  $(EL)\mathbf{u} = \lambda\mathbf{u}$  and  $\mathbf{v}(EL) = \lambda\mathbf{v}$ .

The stable age distribution has elements

$$u_i = \bar{b} l_i \lambda^{-i-1}, \quad \text{where } \bar{b} = 1 / \left( \sum_{i=0}^k l_i \lambda^{-i-1} \right),$$

which is normalized so that the elements sum to 1. In view of the Euler-Lotka equation,  $\bar{b}$  is the expected per capita reproductive rate per unit time in the population.

The generation time,  $T$ , is defined as the average of parents of newborn individuals when the population is in the stable age distribution,

$$T = \sum_{i=0}^k (i+1) l_i b_i \lambda^{-i-1}.$$

Fisher's reproductive value (FISHER 1958; CASWELL 1989, 2001) for an individual of a given age represents the expected contribution of that individual to future growth of the population, assuming  $v_0 = 1$ ,

$$v_i = \frac{\lambda^i}{l_i} \sum_{j=i}^k l_j b_j \lambda^{-j-1}.$$

Sensitivities of  $\lambda$  to small changes in the age-specific vital rates are

$$\frac{\partial \lambda}{\partial b_i} = \frac{l_i \lambda^{-i}}{T} \quad \text{and} \quad \frac{\partial \lambda}{\partial s_i} = \frac{l_i \lambda^{-i} v_{i+1}}{T}.$$

For a population with two sexes, similar formulas can be defined within each sex, by counting survival of mothers and their reproduction of daughters (the usual female-biased demographic model), separately from survival of fathers and their reproduction of sons.

## APPENDIX C

**Sensitivity coefficients of the expected genetic projection matrix  $\mathbf{g}$ :** Denote the left and right eigenvectors of the expected female matrix,  $\mathbf{a}_f = E\mathbf{A}_f$ , respectively, as  $\mathbf{v}_f = (v_{f,0}, v_{f,1}, \dots, v_{f,k})$  and  $\mathbf{u}_f = (u_{f,0}, u_{f,1}, \dots, u_{f,k})^T$ . These satisfy the eigenvalue equations  $\mathbf{v}_f \mathbf{a}_f = \lambda \mathbf{v}_f$  and  $\mathbf{a}_f \mathbf{u}_f = \lambda \mathbf{u}_f$ . The solutions are unique if we require that the elements of the right eigenvector sum to 1, as well as that  $\sum u_{f,i} v_{f,i} = 1$ . Then  $\mathbf{u}_f$  is the stable age distribution and  $\mathbf{v}_f$  is proportional to the reproductive value vector. Further, the sensitivities are  $\partial \lambda / \partial a_{f,ij} = v_{f,i} u_{f,j}$  (CASWELL 1978, 1989, 2001). Eigenvectors of the pure male matrix,  $\mathbf{a}_m$ , obtained by omitting the factor  $1/2$  in the first line of  $\mathbf{g}_m$ , are denoted similarly as  $\mathbf{v}_m$  and  $\mathbf{u}_m$ .

We have already seen that the dominant eigenvalue of  $\mathbf{g}$  is also  $\lambda$ . The right eigenvector of  $\mathbf{g}$  then defines the stable sex-age distribution. Because the proportion of females among newborns is  $q$ , it can be seen that the right eigenvector is  $[\mathbf{Q}\mathbf{u}_f^T, (1-Q)\mathbf{u}_m^T]^T$ , where  $Q = qu_{f,0}/$

$[qu_{f,0} + (1 - q)u_{m,0}]$ . To find the left eigenvector write the solution in the form  $\mathbf{w} = (\mathbf{w}_f, \mathbf{w}_m)$ , where  $\mathbf{w}_f$  and  $\mathbf{w}_m$  each have  $k + 1$  components. The set of equations to be solved is

$$w_{f,0} \frac{1}{2} qb_{f,i} + w_{f,i+1}s_{f,i} + w_{m,0} \frac{1}{2}(1 - q)b_{f,i} = \lambda w_{f,i}$$

$$w_{f,0} \frac{1}{2} qb_{m,i} + w_{f,i+1}s_{f,i} + w_{m,0} \frac{1}{2}(1 - q)b_{m,i} = \lambda w_{m,i}$$

for  $i = 0, 1, \dots, k - 1$  and

$$w_{f,0} \frac{1}{2} qb_{f,k} + w_{m,0} \frac{1}{2}(1 - q)b_{f,k} = \lambda w_{f,k}$$

$$w_{f,0} \frac{1}{2} qb_{m,k} + w_{m,0} \frac{1}{2}(1 - q)b_{m,k} = \lambda w_{m,k}$$

If we replace  $\frac{1}{2}(1 - q)w_{m,0}$  by  $\frac{1}{2}qw_{f,0}$  in the first and third equations it appears that the equations for the  $w_{f,i}$  are identical to those for  $v_f$ . Making the same kind of substitution in the second and fourth equations, but with  $f$  and  $q$  in place of  $m$  and  $1 - q$ , these produce the set of equations for  $\mathbf{v}_m$ . Hence, applying the same scaling of the eigenvectors as before, the solution takes the form  $\mathbf{w} = (\mathbf{w}_f, \mathbf{w}_m) = (\alpha\mathbf{v}_f, \beta\mathbf{v}_m)$  with the requirement that  $\alpha qv_{f,0} = \beta(1 - q)v_{m,0}$  and  $\alpha q + \beta(1 - q) = 1$ . This yields

$$\alpha = \frac{v_{m,0}}{q(v_{f,0} + v_{m,0})} \quad \text{and} \quad \beta = \frac{v_{f,0}}{(1 - q)(v_{f,0} + v_{m,0})}$$

Sensitivity coefficients in the full two-sex model can be compared to those in the pure male and pure female models. For an element with both indices  $\leq k$

$$\frac{\partial \lambda}{\partial g_{ij}} = \alpha^2 \frac{\partial \lambda}{\partial a_{ff,ij}}$$

and similarly for elements with both indices  $\geq k + 1$

$$\frac{\partial \lambda}{\partial g_{ij}} = \beta^2 \frac{\partial \lambda}{\partial a_{mm,ij}}$$

Other elements have nonzero sensitivities only if the first index is 0 or  $k + 1$  for which we have for  $i = 0, 1, \dots, k$

$$\frac{\partial \lambda}{\partial g_{0,k+i}} = \alpha\beta v_{f,0} u_{m,i} \quad \text{and} \quad \frac{\partial \lambda}{\partial g_{k+1,i}} = \alpha\beta v_{m,k+1} u_{f,i}$$

**Demographic stochasticity in the genetic projection matrix G:** *Stochasticity from females:* Assuming that the numbers of offspring from different females are independent, for parents heterozygous for the rare allele we first condition on the total number of offspring from females of age  $i$  and use a multinomial distribution among the three categories of offspring (without the allele, daughters with the allele, and sons with the allele). Then we apply standard formulas for conditional means and expectations to find the unconditional variances of female reproduction valid for  $l = 0, 1, \dots, k$ ,

$$\text{Var}(G_{0,l}) = Z_l^{-1} \frac{1}{4} [q(2 - q)b_{fl} + q^2\sigma_{f,l}^2]$$

$$\text{Var}(G_{k+1,l}) = Z_l^{-1} \frac{1}{4} [(1 - q)(1 + q)b_{fl} + (1 - q)^2\sigma_{f,l}^2]$$

There will also be a covariance between the production of daughters and sons,

$$\text{Cov}(G_{0,l}, G_{k+1,l}) = Z_l^{-1} \frac{1}{4} q(1 - q)(\sigma_{f,l}^2 - b_{f,l})$$

The demographic variance in female survival is given simply by the binomial distribution,

$$\text{Var}(G_{l+1,l}) = Z_l^{-1} s_{f,l}(1 - s_{f,l})$$

for  $l = 0, 1, \dots, k - 1$  (since  $s_{f,k} = 0$ ).

Finally, the reproduction and survival of females may be correlated through allocation of resources. Writing  $c_{f,i}$  for the covariance between a female's reproduction of daughters (or sons) when she is in age class  $i$  and her survival to the next age (indicator variable taking value 1 if she survives and 0 otherwise), this gives for  $l = 0, 1, \dots, k - 1$

$$\text{Cov}(G_{0,l}, G_{l+1,l}) = Z_l^{-1} \frac{1}{2} qc_{f,l}$$

for daughters and

$$\text{Cov}(G_{k+1,l}, G_{l+1,l}) = Z_l^{-1} \frac{1}{2} (1 - q)c_{f,l}$$

for sons.

*Stochasticity from males:* We assume in the deterministic model (using the expected matrices) that there are some initial female preferences for males of different ages. These preferences are finally scaled to give the mean number of offspring  $b_{m,i}$  produced by males of age  $i$ . These are proportional to the initial female preferences. Now consider a group of females that independently chose a particular male in age class  $i$  with probability  $b_{m,i}/(\sum M_i b_{m,i})$  and suppose that the chosen male fathers all offspring produced by these females this year. The probability of choosing a male in this age class bearing the rare allele is consequently  $Y_i b_{m,i}/(\sum M_i b_{m,i})$ . Because the population is large and the allele is rare, the number of females mating with males in age class  $i$  with the rare allele is Poisson distributed with mean  $Y_i \omega_i = Y_i b_{m,i} \sum F_i / (\sum M_i b_{m,i})$ . Since the population is large,  $M_i$  and  $F_i$  can be replaced by the stable sex-age distribution obtained from the deterministic model when computing the  $\omega_i$  giving  $\omega_i = (Q/(1 - Q))b_{m,i}/(\sum u_{m,i} b_{m,i})$ . Since  $(1 - Q) \sum u_{m,i} b_{m,i} = Q \sum u_{f,i} b_{f,i}$  we see that  $\omega_i = b_{m,i}/\bar{b}_f$ , where  $\bar{b}_f = \sum u_{f,i} b_{f,i}$  is the mean female fecundity in the population. It follows from these assumptions that the variance of the number of offspring produced by males in age class  $i$  is  $Y_i \omega_i (\sigma_f^2 + \tau_{f,b}^2)$ , where  $\tau_{f,b}^2$  denotes the variance of  $b_{f,i}$  among all females in the population and  $\sigma_f^2$  is the variance of the number of offspring produced by a randomly selected female from the population. Hence, the variance in the male contributions is  $\sigma_{m,i}^2 = \omega_i (\sigma_f^2 + \tau_{f,b}^2) = \omega_i \sum u_{f,i} (\sigma_{f,i}^2 + b_{f,i}^2)$ . The covariances between contributions from different age classes can be ignored for a rare allele. Male contributions split into the same three categories of offspring as for the females, yielding the variances for  $l = k + 1, k + 2, \dots, 2k + 1$ ,

$$\text{Var}(G_{0,l}) = Z_l^{-1} \frac{1}{4} [q(2 - q)b_{m,l-k-1} + q^2 \sigma_{m,l-k-1}^2]$$

$$\text{Var}(G_{k+1,l}) = Z_l^{-1} \frac{1}{4} [(1 - q)(1 + q)b_{m,l-k-1} + (1 - q)^2 \sigma_{m,l-k-1}^2]$$

while the covariance between the production of daughters and sons is

$$\text{Cov}(G_{0,l}, G_{k+1,l}) = Z_l^{-1} \frac{1}{4} q(1 - q)(\sigma_{m,l-k-1}^2 - b_{m,l-k-1}).$$

The demographic variance in male survival is given simply by the binomial distribution,

$$\text{Var}(G_{l+1,l}) = Z_l^{-1} s_{m,l-k-1}(1 - s_{m,l-k-1})$$

for  $l = k + 1, k + 2, \dots, 2k$ . We assume that the covariance between male survival and reproduction is 0 although such covariance terms can easily be added as for females.