The influence of persistent individual differences and age at maturity on effective population size

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Ratios of effective populations size, N_e, to census population size, N, are used as a measure of genetic drift in populations. Several life-history parameters have been shown to affect these ratios, including mating system and age at sexual maturation. Using a stochastic matrix model, we examine how different levels of persistent individual differences in mating success among males may affect N_e/N, and how this relates to generation time. Individual differences of this type are shown to cause a lower N_e/N ratio than would be expected when mating is independent among seasons. Examining the way in which age at maturity affects N_e/N, we find that both the direction and magnitude of the effect depends on the survival rate of juveniles in the population. In particular, when maturation is delayed, lowered juvenile survival causes higher levels of genetic drift. In addition, predicted shifts in N_e/N with changing age at maturity are shown to be dependent on which of the commonly used definitions of census population size, N, is employed. Our results demonstrate that patterns of mating success, as well as juvenile survival probabilities, have substantial effects on rates of genetic drift.

Keywords: effective population size; reproductive success; individual quality; age at maturity

1. INTRODUCTION

Genetic diversity is of central importance in evolutionary biology and conservation. Random genetic drift is a major cause of loss of this diversity, and a lot of studies have focused on the rates at which this loss can be expected to occur in natural populations (reviewed in [1]). Wright [2] introduced the concept of effective population size, N_e, defined as the size of an ideal population that would experience the same amount of genetic drift as the population in question. An ideal population refers to a population of constant size with discrete, non-overlapping generations and reproduction by random sampling of gametes. In a diploid population, the expected rate of allele frequency change owing to drift, and the loss of (selectively neutral) heterozygosity, is proportional to $1/(2N_e)$ per generation.

Most real populations have an effective population size which is lower than their census size (N), and thus experience higher levels of genetic drift [3–6]. It has proven difficult to find any general relationship between the effective population size and the actual size of populations [4], but a number of factors that influence the effective population size have been identified. Some of the most important of these are fluctuations in population size [2,4], variation in reproductive success [7,8] and unequal sex ratios [2,9]. Different mating systems give rise to different patterns of male mating success. When the distribution of mating success is skewed, like in harem polygyny, the effective population size is lower. This has been demonstrated both theoretically [7–12] and experimentally [13]. Other factors that affect the variance in reproductive success, and thus N_e, are multiple paternity within broods [14], population subdivision [15] and variance in female

fecundity [16–18]. Nunney [16] examined different types of variation in female fecundity and found that consistent individual effects decreased the effective population size more than random effects or age-related effects. The effects of mating system on N_e can be influenced by other factors [19–22], and may often be overwhelmed by stronger effects, such as fluctuating population size [23]. However, many species have life-history characteristics that allow N_e to be substantially affected by mating system [5,23–25].

Values of N_e/N have been reported for a number of populations of different species (e.g. [3,4,6]). The range of values reported is extensive (studies reviewed by [4] include values of N_e/N from 10^{-6} to 1.07), and techniques for obtaining these estimates vary [3,4,26]. One problem with these numbers is that several different definitions of N are used [3]. Sometimes N is reported as the census size of the entire population, sometimes it refers to the adult population only and sometimes only breeding individuals are counted. Nunney & Elam [3] discussed this issue, and concluded with a recommendation that N be counted as the number of adults in the population.

There are two main types of effective population size. Inbreeding effective size focuses on the rate of increase of identity by descent, whereas the variance effective size is concerned with the sampling variance in allele frequency from one generation to the next [27,28]. These two types of effective population size can differ substantially in populations of increasing or decreasing size [8,29], but are identical when populations are of constant size with stable stage distributions, as is the case in this paper [30].

The study of effective population size is often complicated by the presence of overlapping generations [1,31]. Several authors have addressed this point, and presented formulas for calculating the effective population size in

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populations in which generations overlap ([10,11,31–36], among others). As shown by Hill [32], it is the variance in *lifetime* reproductive success that matters when determining effective size in such populations. Fluctuations in age structure make the problem even more complex. Engen *et al.* [37] showed how diffusion theory and matrix models can be used to derive the effective population size in populations subject to fluctuations in age structure. Studying a subpopulation of individuals carrying a selectively neutral allele allows calculation of the sampling variance in the frequency of this allele per time step [37]. Thus, this method can be used to study genetic drift per time step, and when it is combined with the generation time, it gives N_e/N per generation.

Generation time has been shown to influence the effects of other factors on the effective population size. For example, a skewed sex ratio tends to cause N_e/N to decrease more when the generation time is short than when it is long [10,38]. Also, Nunney [10,11] found that although some mating systems have the potential to lower N_e/N significantly, this effect all but disappeared as the generation time in their model was lengthened, and N_e approached $N/2$ regardless of mating system. This was explained by a decrease in the variance in male mating success as the generation time increased. When each male participated in several mating seasons they had more chances to be successful, and reproductive success could even out among them. This assumes that male mating success is independent each season, which is not necessarily the case. Several recent studies have highlighted the importance of recognizing that populations consist of individuals with different vital parameters, and that the individual differences may be persistent over time [39–47]. Mating success is one area in which persistent individual differences may exist in some species (e.g. [44,48–50]), thus potentially causing correlations in individual success from year to year.

Delayed maturity has been shown to increase the effective population size [11,51–53]. In fact, Waite & Parker [51] found that the convergence of N_e/N to 0.5 at long generation times reported by Nunney [11] was dependent on a low ratio of age at maturity to adult lifespan. When the age at maturity was increased in relation to the adult lifespan, N_e/N was found to increase linearly. Both age at maturity, adult lifespan and the relationships between the two vary among species and taxonomic groups, making this particularly relevant [51].

In this paper, we use a stochastic matrix model to investigate how the effective population size is influenced by the presence of persistent individual differences in mating success among males, and how this may depend on generation time. We also examine how juvenile survival rates influence the effects of delayed maturity. In addition, we demonstrate that the definition of N used to calculate N_e/N when studying age at maturity has the potential to influence the results in ways not previously considered.

2. THE MODEL

Consider a diploid population with two sexes. Based on well-known theory, we use a matrix model to study a subpopulation of heterozygote individuals carrying a certain rare allele (e.g. [8,37,54,55]). The number of individuals in this subpopulation will be called X. Pre-reproductive individuals are divided into classes according to age and sex. Adult males are classed according to mating success (number of mates, from 0 to d), and adult females are all assumed to have the same individual parameters (survival probability and expected number of offspring) and are therefore collected in a single group. This means that there are a total of $(r_m + d + r_f)$ classes in the model, where r_m is the age at sexual maturity of males, d is the maximum number of mates a single male can obtain and r_f is the female age at maturity. The population vector can then be written as $\mathbf{X} = (X_{ym1}, \ldots, X_{ym(r_{m-1})}, X_{am0}, \ldots, X_{amd}, X_{yf1}, \ldots, X_{yf(r_{f-1})}, X_{af})^T$ where the superscript T indicates matrix transposition. Subscripts denote young (pre-reproductive) males of age 1 to $r_m - 1$ (ym1, ..., ym($r_m - 1$)), adult males who obtain 0 to d mates (am0, ..., am$d$), young females of age 1 to $r_f - 1$ (yf1, ..., yf($r_f - 1$)), and adult females (af). Note that offspring are not included in the model until they reach 1 year of age (any individuals that die before that age are ignored). The population vector for the next time step is obtained from the current population vector by matrix multiplication with the stochastic projection matrix, $\mathbf{G}$. Thus, $\mathbf{X}_{t+1} = \mathbf{G}\mathbf{X}_t$. The stochastic projection matrix can be partitioned into four parts,

$$G = \begin{bmatrix} G_{mm} & G_{mf} \\ G_{fm} & G_{ff} \end{bmatrix},$$

where G_{mm} is the contribution from the male part of the population to next time step's males, G_{mf} is the contribution from females to males, G_{fm} from males to females and G_{ff} is the contribution from females to next time step's females.

If all individuals become sexually mature at age 1 ($r_m = r_f = 1$), the stochastic projection matrix can be written as a composite of the following submatrices:

$$\mathbf{G}_{mm} = \begin{bmatrix} \bar{S}_{am0}\bar{T}_{am0,am0} & \bar{S}_{am1}\bar{T}_{am0,am1} + \bar{Z}_{am1}\bar{A}_{am0,am1} \\ \bar{S}_{am0}\bar{T}_{am1,am0} & \bar{S}_{am1}\bar{T}_{am1,am1} + \bar{Z}_{am1}\bar{A}_{am1,am1} \\ \bar{S}_{am0}\bar{T}_{am2,am0} & \bar{S}_{am1}\bar{T}_{am2,am1} + \bar{Z}_{am1}\bar{A}_{am2,am1} \\ \vdots & \vdots \\ \bar{S}_{am0}\bar{T}_{amd,am0} & \bar{S}_{am1}\bar{T}_{amd,am1} + \bar{Z}_{am1}\bar{A}_{amd,am1} \end{bmatrix}$$

$$\begin{matrix} \bar{S}_{am2}\bar{T}_{am0,am2} + \bar{Z}_{am2}\bar{A}_{am0,am2} & \cdots \\ \bar{S}_{am2}\bar{T}_{am1,am2} + \bar{Z}_{am2}\bar{A}_{am1,am2} & \cdots \\ \bar{S}_{am2}\bar{T}_{am2,am2} + \bar{Z}_{am2}\bar{A}_{am2,am2} & \cdots \\ \vdots & \ddots \\ \bar{S}_{am2}\bar{T}_{amd,am2} + \bar{Z}_{am2}\bar{A}_{amd,am2} & \cdots \end{matrix}$$

$$\begin{matrix} \bar{S}_{amd}\bar{T}_{am0,amd} + \bar{Z}_{amd}\bar{A}_{am0,amd} \\ \bar{S}_{amd}\bar{T}_{am1,amd} + \bar{Z}_{amd}\bar{A}_{am1,amd} \\ \bar{S}_{amd}\bar{T}_{am2,amd} + \bar{Z}_{amd}\bar{A}_{am2,amd} \\ \vdots \\ \bar{S}_{amd}\bar{T}_{amd,amd} + \bar{Z}_{amd}\bar{A}_{amd,amd} \end{matrix}$$

$$\mathbf{G}_{mf} = (\bar{Z}_{af}\bar{A}_{am0,af}, \bar{Z}_{af}\bar{A}_{am1,af}, \bar{Z}_{af}\bar{A}_{am2,af}, \ldots, \bar{Z}_{af}\bar{A}_{amd,af})^T.$$

$$\mathbf{G}_{fm} = (0, \bar{Z}_{am1}\bar{A}_{af,am1}, \bar{Z}_{am2}\bar{A}_{af,am2}, \ldots, \bar{Z}_{amd}\bar{A}_{af,amd}).$$

$$\mathbf{G}_{ff} = \bar{S}_{af} + \bar{Z}_{af}\bar{A}_{af,af}.$$

In these matrices

$$\bar{S}_i = \frac{1}{x_i}\sum_{k=1}^{x_i} S_{i,k},$$

where $S_{i,k}$ is an indicator variable for survival of individual k in group i,

$$\bar{T}_{i,j} = \frac{1}{S_j} \sum_{k=1}^{S_j} T_{i,j,k},$$

where $T_{i,k}$ is an indicator variable indicating which of the S_j survivors from group j move to group i,

$$\bar{Z}_i = \frac{1}{x_i} \sum_{k=1}^{\alpha_i x_i} Z_{i,k},$$

where $Z_{i,k}$ is the number of offspring produced by individual k in group i,

$$\bar{A}_{i,j} = \frac{1}{Z_j} \sum_{k=1}^{Z_j} A_{i,j,k},$$

where $A_{i,j,k}$ is an indicator variable indicating which of th Z_j offspring from group j move to group i (based on presence of the rare allele, sex and mating probability).

We assume a constant environment, so the stochastic projection matrix G includes demographic stochasticity but not environmental stochasticity. Adult males are assumed to have a survival probability s_m (s_f for females). The probability of a male obtaining v mates, and thus being in class am$v$ is called t_v. Since the variance effective population size is defined by the variance in allele frequency, the actual distribution of females among males does not need to be known. It is the variance in reproductive success among males (or females) that matters. In order to find t-values that give a particular variance in male mating success, we have used the model from Lee *et al.* [56]. The t-values represent the probability of a new male in the population ending up in a certain class (and mating a certain number of times) in his first season. If there are no permanent individual differences among males, these are also the probabilities of surviving males moving to each class in later seasons. However, the mating probability of a male in a given season is not necessarily independent from his mating success in previous seasons. This is incorporated by introducing a parameter c. This parameter can increase the probability of obtaining the same number, one more or one less mate than the previous season. At the limits, if $c = 0$, mating is independent among seasons. If $c = 1$, a surviving male is guaranteed to end up in the same class, or one of the neighbouring classes (one more or one less mate) the next season. The adjusted probabilities of these three classes are $\mathrm{E}(\bar{T}_{am v, am\omega}) = t_v(1-c) + c/3$ (for $v = \omega - 1$, ω, $\omega + 1$). The only exception is the group of unmated males, where we assume that c affects only the probability of staying unmated the next season (without increasing the probability of obtaining a single mate). Thus, $\mathrm{E}(\bar{T}_{am0,am0}) = t_0(1-c) + c$. All other classes have an adjusted probability of $\mathrm{E}(\bar{T}_{am v, am\omega}) = t_v(1-c)$. In this way, the ratio between the other classes is not altered. It would also be possible for c to be negative, but we have not considered that here.

We assume that survival and reproduction are independent within years, and can therefore treat the survival and reproduction terms separately. We also assume independence among columns as we are studying a small group of individuals found in a much larger population. Within

columns, however, there must be some covariance. To see this, consider the surviving males from adult class one at a given time step. At the next time step, each of these survivors will be in one and only one of the d classes of adult males. A single individual cannot move to more than one class. Thus, survival terms in $\mathbf{G}_{mm}$ have a multinomial distribution in which the $S_{am\omega}$ survivors from group $j = am\omega$ have probabilities $\mathrm{E}(\bar{T}_{am v, am\omega})$ of ending up in each of the $d + 1$ classes of adult males. Equivalently, the reproduction terms also have a multinomial distribution in which the Z_j offspring from class j have a probability $\mathrm{E}(\bar{A}_{am v, j}) = 1/2(1-q)t_v$ of ending up in class $i = am v$ (this is the probability of an offspring having the rare allele, being male and ending up in quality group $am v$), as well as a probability $\mathrm{E}(\bar{A}_{af, j}) = 1/2q$ of being female. Assuming that females produce a mean of μ_z offspring each, the number of offspring produced in group j can be written as: $\mathrm{E}(Z_j) = \mathrm{E}(\sum_{k=1}^{\alpha_j x_j} Z_{j,k}) = \mu_z x_j \alpha_j$, where α_j is equal to v for $am v$, $v = 0, \ldots, d$ and equal to 1 for adult females. For simplicity, we assume that the number of offspring produced per female per time step has a Poisson distribution. The total number of offspring produced in the population at a given time step, and the total number of offspring produced by a single female over her entire lifetime, are then also Poisson-distributed.

When r_m and/or r_f are greater than 1, offspring of each sex are born into a single class. Male offspring pass through $r_m - 1$ pre-reproductive classes (and females pass through $r_f - 1$ pre-reproductive classes) before entering an adult class. Survival probability in these pre-reproductive classes is called s_{ym} for males and s_{yf} for females. The projection matrix $\mathbf{G}$ for this case is presented in appendix A.

Ignoring environmental stochasticity, the demographic variance of the subpopulation of heterozygotes with the rare allele can be written as [37]:

$$\sigma_{dg}^2 = \frac{X}{\lambda^2} \sum_{ijk} v_i v_k u_j^2 \mathrm{ECov}(G_{ij}, G_{kj}), \tag{1.1}$$

where λ is the growth rate of the subpopulation, found as the dominant eigenvalue of the expected projection matrix, v_i is the reproductive value of class i (found from the left eigenvector), u_j is the proportion of individuals found in class j once a stable stage distribution has been reached (found from the right eigenvector), and G_{ij} is the entry in the ith row and jth column of $\mathbf{G}$. The stable stage distribution is scaled such that $\sum u_j = 1$, and the reproductive values are scaled to get $\sum u_j v_j = 1$. We use u_{ad} to denote the proportion of a population that is found in adult classes (as opposed to pre-reproductive classes).

Assuming $x_j = X u_j$, equation (1.1) becomes

$$\sigma_{dg}^2 = \frac{1}{\lambda^2} \sum_{ijk} v_i v_k u_j \mathrm{Cov}(G_{ij}, G_{kj}) x_j. \tag{1.2}$$

Expressions for $\mathrm{Cov}(G_{ij}, G_{kj})$ in the different cases described above can be found in appendix B. These covariances are all proportional to $1/x_j$, causing the x_j's in equation (1.2) to cancel out. Thus, $\sigma_{d,g}^2$ is independent of the size of the subpopulation, X.

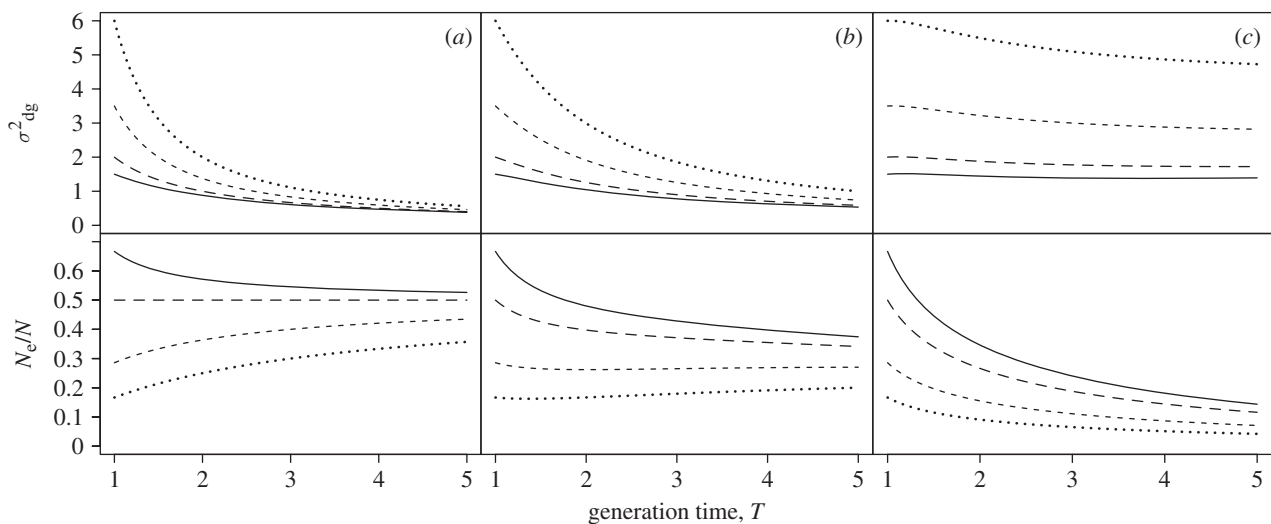As shown by Engen *et al.* [37], the ratio of effective population size to census population size can be

Figure 1. Effects of generation time, T, on the genetic drift per time step, σ_{dg}^2, and the ratio of effective population size to census (total) population size, N_e/N, in populations with different mating systems and different levels of persistent individual differences in mating success among males; (*a*) $c = 0$ (no persistent differences), (*b*) $c = 0.5$ and (*c*) $c = 1$. See §2 for a more detailed description of the parameter c. Different mating systems are represented by the variance in annual male mating success, which is equal to 1 (solid lines), 2 (long dash), 5 (short dash) and 10 (dotted). Generation time is increased by increasing the annual survival probability, s from 0 ($T = 1$) to 0.8 ($T = 5$), simultaneously decreasing the expected number of offspring per female from 2 to 0.4. Other parameters are sex ratio at birth, $q = 0.5$, and age at maturity, $r = 1$.

calculated as:

$$\frac{N_e}{N} = \frac{1}{\sigma_{d.g}^2 T}, \tag{1.3}$$

where T is the generation time (defined as the average age of parents of newborn offspring), and N is the total population size. Given age-independent survival and reproduction in adults, the average generation time, T, can be written as $T = (T_m + T_f)/2$, where $T_m = r_m + s_m /(\lambda - s_m)$ and $T_f = r_f + s_f/(\lambda - s_f)$ [38,57].

In equation (1.3), N is the total number of individuals in the population. In order to find N_e/N for an alternate definition of N (e.g. only adults or only mated individuals), one can simply multiply equation (1.3) by N/N_{alt}. This ratio can be found from the relevant values of u_j (the stable stage distribution).

This model is used here to study genetic drift by looking at the sampling variance in allele frequency per time step, and the effective population size (per generation). The growth rate of the subpopulation X is held constant at $\lambda = 1$ at all times. The effect of persistent differences in mating probability among individual males is examined by adjusting the parameter c while holding all other parameters constant. We look at three specific cases, with $c = 0$, 0.5 and 1, which span the gradient from completely independent mating success among seasons ($c = 0$) to permanent individual differences ($c = 1$). We also look at four different levels of variance in male mating success (1, 2, 5 and 10). By increasing survival probabilities, we also investigate the effect of generation time on these populations. As survival is increased, female fecundity is decreased such that the growth rate stays constant at 1.

We look at how age at maturity affects $\sigma_{d.g}^2$ and N_e/N, and how this effect may vary depending on the survival probability of pre-reproductive individuals. We assume that males and females mature at the same age ($r_m = r_f$), and adjust female fecundity in such a way that a stable

population size is maintained. Finally, we examine whether the outcome of these analyses is dependent on the definition of N used when calculating the ratio N_e/N.

3. RESULTS

In the absence of persistent individual differences among males, the mating success of each individual male is independent among years. In this situation, the ratio of effective population size to adult or census population size becomes less affected by differences in mating system as the generation time increases (figure 1*a*). Differences in mating system are here defined by differences in the variance in male mating success. Mean male mating success is constant at 1 (the sex ratio is even and all females mate), and age at maturity is set to 1, so all individuals in the population are assumed to be adults. Nunney [11] has previously shown that the ratio of effective population size to adult population size converges towards 0.5 as the generation time increases. This result was confirmed by Waite & Parker [51] and is supported by our figure 1. In fact, the graph shown in figure 1*a* can be exactly reproduced by inserting our parameters into the equations of Nunney [10]. However, if there are persistent individual differences among males, N_e/N approaches a lower value than 0.5 (figure 1*b*,*c*). Effects of mating system differences on N_e/N still decrease with increasing generation time, and the speed with which this happens does not seem to differ much from the case with no persistent individual differences. The demographic variance, on the other hand changes much more slowly as individual differences become more persistent (top panel in figure 1). Thus, the fact that differences in mating system become less important as the generation time increases does not seem to be caused by a reduction in the variance in male reproductive success (as suggested by Nunney [11]). Such a reduction in the variance is
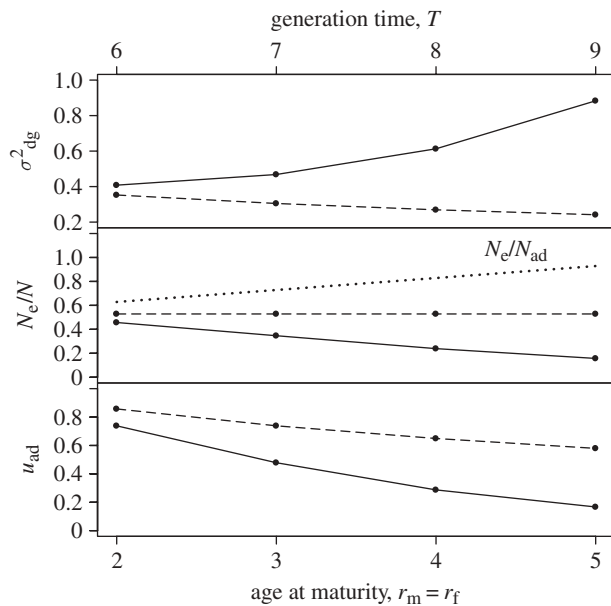
Figure 2. Effects of age at maturity, r, on the genetic drift per time step, σ^2_{dg}, the ratio of effective population size to census (total) population size, N_e/N, and the proportion of adults at stable stage structure, u_{ad}, in populations with different levels of juvenile survival. Annual survival probability of prereproductive individuals, $s_{ym} = s_{yf}$, is equal to 0.5 (solid lines) and 1 (dashed lines). In the middle panel, the dotted line shows the ratio N_e/N_{ad}, where N_{ad} is the adult population size (as opposed to the total population size used in the ratio N_e/N represented by the solid and dashed lines). Variance in annual male mating success is equal to 2, the sex ratio, q, is equal to 0.5, and the expected number of offspring is adjusted to maintain a growth rate, λ, of 1.

Figure 3. Effects of annual juvenile survival probability on the genetic drift per time step, σ^2_{dg}, the ratio of effective population size to census (total) population size, N_e/N, and the proportion of adults at stable stage structure, u_{ad}. Parameters are age at maturity, $r = 5$, generation time, $T = 9$ and sex ratio, $q = 0.5$. Variance in annual male mating success is equal to 2. The expected number of offspring is adjusted to maintain a growth rate, λ, of 1. The dotted line in the middle panel shows the ratio N_e/N_{ad}, where N_{ad} is the adult population size, whereas the solid line shows N_e/N, where N is the total population size.

expected when the mating success of males is independent from year to year, allowing different males to be successful at different times, thereby reducing the variance in lifetime reproductive success when compared with the variance in reproductive success in a single season. However, even when the probability of the same males being successful year after year is very high, causing the demographic variance to stay high as the generation time is increased, N_e/N still seems to converge (figure 1c). This suggests that the convergence is a result of the way the effective population size is defined. This can be seen from equation (1.3). As T becomes large, changes in σ^2_{dg} become less influential. Analogously, when σ^2_{dg} is large, changes in T have less effect on N_e/N.

Increasing the age at maturity also affects N_e/N (figure 2). The direction and magnitude of this effect depends on the survival probability of pre-reproductive individuals, s_{ym}, as well as the definition of N used in the calculation of N_e/N. When the annual survival probability of juveniles is close to 1, an increase in the age at maturity causes σ^2_{dg} to decrease (figure 2). At lower juvenile survival probabilities, on the other hand, σ^2_{dg} increases as the age at maturity increases (figure 2). This increase becomes greater as the survival probability decreases (figure 3). Changes in the age at maturity are also reflected in the average generation time, T. When N is defined as the (total) census population size, changes in σ^2_{dg} and T described above cause N_e/N to decrease as the age at maturity increases
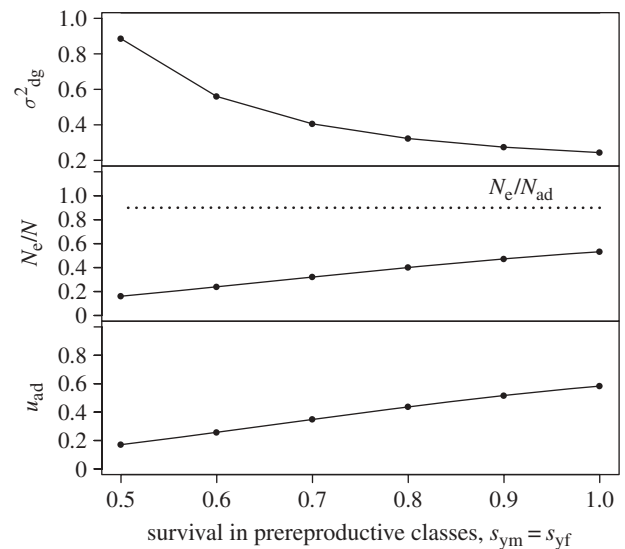
(figure 2). When s_{ym} is close to 1, the observed decrease in N_e/N is very slight. On the other hand, if N_{ad} denotes the size of the adult population only, N_e/N_{ad} increases linearly with age at maturity. With this definition of population size, the ratio N_e/N_{ad} is also not affected by changes in juvenile survival rate (figure 3). The substantial difference between the behaviour of the two ratios N_e/N and N_e/N_{ad} can be explained by the changes in stage structure that accompany changes in the age at maturity and/or juvenile survival rate. Since the denominator of N_e/N_{ad} includes only adult individuals, changing the proportion of the population that is in the adult state (u_{ad}) will alter this ratio. Thus, a decrease in u_{ad} causes N_e/N_{ad} to increase with age at maturity, even when both σ^2_{dg} and T increase (figure 2). When juvenile survival is altered, the resulting change in σ^2_{dg} is cancelled out by the change in u_{ad}, leaving N_e/N_{ad} unchanged, while N_e/N is shifted.

4. DISCUSSION

Effective population size, N_e, is influenced by a number of different factors, including mating system and generation time. In a study on the influence of mating systems on N_e, Nunney [11] found that the effective population size should approach half the size of the adult population, $N_{ad}/2$, as generation time becomes large. Later, Waite & Parker [51] showed that the result of Nunney only held when the age at maturity was low when compared with the adult lifespan. Using a matrix model, we have re-examined these ideas, taking persistent individual differences and juvenile survival probabilities into account.

Persistent individual differences in mating success among males cause N_e/N to converge to a value lower than 0.5 as the generation time increases (figure 1). There is evidence to support the existence of such persistent individual differences in natural populations (e.g. [43,44,48–50,58,59]). Basically, when male mating success is dependent on certain male traits and the expression of these traits is not independent among breeding seasons, mating success will not be independent among seasons either. Some physical attributes that may affect mating success are permanent, like colour morph [58,60–62], while the expression of other traits may vary from season to season but still be correlated. One such trait is male body weight. In species where males engage in physical combat over females or territories, body weight may be important in determining reproductive success. Accordingly, body weight (at birth or capture) is positively correlated with lifetime reproductive success of males in some studied populations [49,63–68]. If there is strong site fidelity in a population, the distribution of territories may cause correlations in reproductive success among years, even without persistent differences in fighting ability [48,69–71].

A common pattern, especially in birds, is that lifespan is the main predictor of lifetime reproductive success [72,73]. However, even in long-lived seabirds, a considerable part of the variation in lifetime reproductive success can be traced back to factors other than lifespan, and reproductive parameters are often found to be consistent between years [43]. Sometimes traits that increase annual reproductive success also promote longevity, intensifying the effect [44,48,50,59,74,75]. In other cases reproduction is costly. This can cause negative correlation in reproductive success among years [76], or negative effects of reproduction on survival [77–80]. The model presented in this paper can easily be extended to include both of these cases.

It has previously been demonstrated that increasing the age at maturity in relation to the adult lifespan causes an increase in N_e/N [51]. We have shown that this result is very dependent on the definition of N used. Waite & Parker [51] used the number of adults, N_{ad}, as their measure of population size, following recommendations from Nunney & Elam [3]. When the pre-reproductive part of the life cycle is lengthened when compared with the adult part, the proportion of individuals found in the pre-reproductive state also increases. Thus, N_{ad} then represents a smaller proportion of the population, and N_e/N_{ad} increases. This does not necessarily mean, however, that the amount of genetic drift decreases. In fact, depending on the survival probability of juveniles, the genetic drift per time step (measured by σ_{dg}^2) may increase substantially (figure 2). This is reflected in N_e/N if N is counted as the total population size (both adults and juveniles).

The use of different definitions of N when reporting values of N_e/N has previously been discussed by Nunney & Elam [3]. They called attention to the fact that estimates of N_e/N become impossible to compare when different definitions of N are used. The total census number was deemed an impractical measure of population size because it is often difficult to obtain and is also prone to fluctuations (juvenile numbers are more likely to vary with seasonal conditions). Thus, practical considerations make the number of adults a better choice [3]. This is not a problem as long as the consequences of this choice are kept in mind. As we have shown, the definition of N used is not only an issue when comparing ratios of N_e/N from different studies. Results from theoretical analyses must also be interpreted in light of the definition used.

Waite & Parker [51] mention that having delayed maturity could restrict the genetic effects of a catastrophic (short-term) loss of adults. Any possible advantage of having a large proportion of the population in a juvenile state during catastrophic events is obviously dependent on the relative vulnerability of juveniles and adults to such events. In figure 3, we have shown that σ_{dg}^2 increases as the survival probability of juveniles decreases. Koons *et al.* [81] demonstrated that environmental uncertainty can drive the evolution of delayed maturity in iteroparous populations if juveniles have a higher survival probability than adults. However, environmental uncertainty did not have the same effect in the more common case of juvenile survival being lower than that of adults.

In general, low juvenile survival would be expected to oppose the evolution of delayed maturation [82]. What would be considered 'low' in this context is however dependent on the benefits that delayed maturation confer. In a study using data from 109 populations of snakes, lizards and turtles, Pike *et al.* [83] found that juvenile survival in these species did not differ substantially from adult survival. These are taxa in which the age at maturity is often quite high in relation to their lifespan [51]. Survival probabilities shown in figure 3 are within the range presented by Pike *et al.* [83]. Thus, these combinations of age at maturity and juvenile survival rate seem to be realistic.

In figures 1–3 mating systems are represented by their variance in male mating success (with mean mating success constant at 1). This is in accordance with previous studies [10,11,51] and accommodates comparison with other results. It is worth noting, however, that the mean number of recruits per season is changed as the generation time is altered (in order to maintain a stable population size), so the variance in reproductive success does not necessarily stay constant even if the mating system (mating success) does.

The model presented here assumes that survival rate and fecundity are independent of age once adulthood is reached. However, it is not uncommon for these parameters to be age-specific (e.g. [72]), and there is a possibility that this may affect patterns of genetic drift. Although we have chosen not to include adult age classes as an additional complicating factor in this study, the model can easily be expanded to accommodate this.

As shown by Hill [32], it is the variance in *lifetime* reproductive success that is important when estimating the effective size of populations with overlapping generations, and most formulas for N_e contain this parameter (e.g. [1,11,32,84]). However, estimates are often available for reproductive success in single seasons only [11]. Using seasonal measures for estimating N_e could be a problem if fecundity varies with age, but Nunney [11] and Nunney & Elam [3] demonstrated that corrections can be made to minimize this problem. Our results highlight another potential problem using seasonal estimates. We have shown that persistent individual differences in mating success over time can have a strong influence on genetic drift.

Establishing the presence or absence of such differences will therefore be an important step in the venture to quantify genetic drift in natural populations.

APPENDIX A. PROJECTION MATRIX FOR THE CASE OF DELAYED MATURATION

If one or both sexes have delayed maturation (i.e. r_f or r_m, or both, are greater than 1), the projection matrix **G** consists of the following submatrices:

$$G_{mm} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ \bar{S}_{ym1} & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & \bar{S}_{ym(r_m-2)} & 0 \\ 0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{am0,ym(r_m-1)} \\ 0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{am1,ym(r_m-1)} \\ 0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{am2,ym(r_m-1)} \\ & & & \vdots \\ 0 & 0 & 0 & \bar{S}_{ym(r_m-1)}\bar{T}_{amd,ym(r_m-1)} \end{bmatrix}$$

$$\begin{bmatrix} 0 & \bar{Z}_{am1}\bar{A}_{ym1,am1} & \bar{Z}_{am2}\bar{A}_{ym1,am2} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ \bar{S}_{am0}\bar{T}_{am0,am0} & \bar{S}_{am1}\bar{T}_{am0,am1} & \bar{S}_{am2}\bar{T}_{am0,am2} \\ \bar{S}_{am0}\bar{T}_{am1,am0} & \bar{S}_{am1}\bar{T}_{am1,am1} & \bar{S}_{am2}\bar{T}_{am1,am2} \\ \bar{S}_{am0}\bar{T}_{am2,am0} & \bar{S}_{am1}\bar{T}_{am2,am1} & \bar{S}_{am2}\bar{T}_{am2,am2} \\ \vdots & \vdots & \vdots \\ \bar{S}_{am0}\bar{T}_{amd,am0} & \bar{S}_{am1}\bar{T}_{amd,am1} & \bar{S}_{am2}\bar{T}_{amd,am2} \end{bmatrix}$$

$$\begin{bmatrix} \cdots & \bar{Z}_{amd}\bar{A}_{ym1,amd} \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ \cdots & \bar{S}_{amd}\bar{T}_{am0,amd} \\ \cdots & \bar{S}_{amd}\bar{T}_{am1,amd} \\ \cdots & \bar{S}_{amd}\bar{T}_{am2,amd} \\ \ddots & \vdots \\ \cdots & \bar{S}_{amd}\bar{T}_{amd,amd} \end{bmatrix}$$

$$G_{mf} = \begin{bmatrix} 0 & 0 & 0 & 0 & \bar{Z}_{af}\bar{A}_{ym1,af} \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$G_{fm} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & \bar{Z}_{am1}\bar{A}_{yf1,am1} & \bar{Z}_{am2}\bar{A}_{yf1,am2} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\begin{bmatrix} \cdots & \bar{Z}_{amd}\bar{A}_{yf1,amd} \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{bmatrix}$$

$$G_{ff} = \begin{bmatrix} 0 & 0 & 0 & 0 & \bar{Z}_{af}\bar{A}_{yf1,af} \\ \bar{S}_{yf1} & 0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & \bar{S}_{yf(r_f-2)} & 0 & 0 \\ 0 & 0 & 0 & \bar{S}_{yf(r_f-1)} & \bar{S}_{af} \end{bmatrix}.$$

Expected values of the entries in these submatrices are basically the same as in the case with $r_m = r_f = 1$, except that the survival and reproduction terms are separate. A few things that must be noted are that pre-reproductive survival may differ from adult survival and that the mating success of male offspring does not come into play until they enter the adult population at age r_m. Thus, $E(\bar{T}_{amv,ym(r_m-1)}) = t_v$. It would also be possible to let mating probabilities be lower for these first-year males.

APPENDIX B. VARIANCES AND COVARIANCES OF G

Survival and reproduction are assumed to be independent within years. We can therefore treat survival and reproduction terms separately.

$\text{Var}(G_{i,j,\text{survival}} \times x_j)$ is simply the variance in a multinomial distribution in which the x_j individuals from class j have probabilities $s_j E(\bar{T}_{i,j})$ of surviving and moving to class i. Here, s_j is either s_m (for males) or s_f (for females). Thus,

$$\text{Var}(G_{i,j,\text{survival}} \times x_j) = s_j E(\bar{T}_{i,j})(1 - s_j E(\bar{T}_{i,j}))x_j.$$

In order to calculate $\text{Var}(G_{i,j,\text{reproduction}} \times x_j)$, we first find the conditional variance given Z_j (the number of offspring produced in class j), and then use the law of total variance to obtain

$$\text{Var}(G_{i,j,\text{reproduction}} \times x_j) = E(\bar{A}_{i,j})(1 - E(\bar{A}_{i,j}))E(Z_j) + E(\bar{A}_{i,j})^2 \text{Var}(Z_j).$$

The expressions for s_j, $E(Z_j)$, $\text{Var}(Z_j)$, $E(\bar{T}_{i,j})$ and $E(\bar{A}_{i,j})$ for different values of i and j are all presented in the main text. Note that $E(\bar{A}_{af,af}) = 1$.

Since the x_j values are known, we have

$$\text{Var}(G_{i,j}) = \frac{\text{Var}(G_{i,j} \times x_j)}{x_j^2}$$

$$= \frac{\text{Var}(G_{i,j,\text{survival}} \times x_j) + \text{Var}(G_{i,j,\text{reproduction}} \times x_j)}{x_j^2}$$

As explained in the main text, there are no covariances between columns. Within columns we have

$$\mathrm{Cov}(G_{i,j} \times x_j, G_{k,j} \times x_j | Z_j) = -s_j^2 x_j \mathrm{E}(\bar{T}_{i,j})\mathrm{E}(\bar{T}_{k,j})$$
$$- Z_j \mathrm{E}(\bar{A}_{i,j})\mathrm{E}(\bar{A}_{k,j}).$$

This means that

$$\mathrm{Cov}(G_{i,j} \times x_j, G_{k,j} \times x_j) = -s_j^2 x_j \mathrm{E}(\bar{T}_{i,j})\mathrm{E}(\bar{T}_{k,j})$$
$$- \mathrm{E}(Z_j)\mathrm{E}(\bar{A}_{i,j})\mathrm{E}(\bar{A}_{k,j})$$
$$+ \mathrm{Var}(Z_j)\mathrm{E}(\bar{A}_{i,j})\mathrm{E}(\bar{A}_{k,j})$$
$$= -s_j^2 x_j \mathrm{E}(\bar{T}_{i,j})\mathrm{E}(\bar{T}_{k,j})$$
$$+ \mathrm{E}(\bar{A}_{i,j})\mathrm{E}(\bar{A}_{k,j})[\mathrm{Var}(Z_j) - \mathrm{E}(Z_j)]$$

and

$$\mathrm{Cov}(G_{i,j}, G_{k,j}) = \frac{\mathrm{Cov}(G_{i,j} \times x_j, G_{k,j} \times x_j)}{x_j^2}.$$

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