Note

Random Mating With a Finite Number of Matings

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ABSTRACT

Random mating is the null model central to population genetics. One assumption behind random mating is that individuals mate an infinite number of times. This is obviously unrealistic. Here we show that when each female mates a finite number of times, the effective size of the population is substantially decreased.

RANDOM mating is the null model central to population genetics theory. Parameters such as *F*-statistics are defined as deviations from expectations under random mating. It is also at the heart of the definition of the effective population size, the parameter summarizing the amount of drift to which a population is subjected. Indeed, effective population size is quantified as the number of idealized randomly mating individuals, which experience the same amount of random fluctuations at neutral loci as the population under scrutiny.

The strictest form of random mating, random union of gametes, is not possible in self-incompatible organisms, as the fraction of homozygotes produced through self-fertilization is excluded. This translates into an excess of heterozygotes ($F_{IS} = -1/(2N+1)$). The effective population size N_e will also be slightly increased and approximately equal to $N + 0.5$ (WRIGHT 1969). This approximation also holds for the effective population size of a random-mating population of dioecious organisms with an even sex ratio (WRIGHT 1969).

An assumption behind the random-mating model is that individuals mate an infinite number of times. This condition is necessary since in classical models, once the first gamete is drawn from an individual, the second gamete still has an equal chance to stem from any individual in the population. This implies that all individuals within the population must have mated together previously. This assumption may be reasonable for some plants producing large amounts of pollen or some marine broadcast spawners. It is, however, highly unrealistic for most animals with internal fertilization, where females must minimize the various fitness costs fre-

quently associated with mating repeatedly (CHAPMAN *et al.* 1995; BLANCKENHORN *et al.* 2002) and tend to have their offspring sired by one or a few fathers. We therefore build a model where we relax this assumption by allowing females to mate an arbitrary number of times.

Genetic identities and coalescence times: We consider a single dioecious population of diploid individuals. Sexual reproduction in the model follows random union of gametes with an arbitrary number of matings. We further assume stable census sizes and no selection. The life cycle involves nonoverlapping generations. As we focus on a single undivided population, only the two following probabilities of identity by descent are needed to describe the apportionment of genetic variation:

F: The inbreeding coefficient, defining the probability that two alleles drawn at random from a single individual are identical by descent.

θ: Coancestry of individuals drawn at random, defined as the probability that two randomly sampled alleles from two different individuals within a subpopulation are identical by descent.

We first have to define the probabilities that two alleles come from the same mother or from the same father, which we denote P_f and P_m, respectively. Under an infinite number of matings, we have $P_f = 1/n_f$ and $P_m = 1/n_m$, where n_f and n_m represent the numbers of females and males, respectively. While the probability of drawing two alleles from the same mother remains unchanged with a finite number of matings, we have to modify the probability for fathers. We denote l as the number of matings. Assuming internal fertilization, paternal alleles are sampled from the females with whom males have mated earlier. Thus we draw with probability $1/n_f$ the same female, and with probability $1/l$ the two alleles stem from the same mating event, and with the

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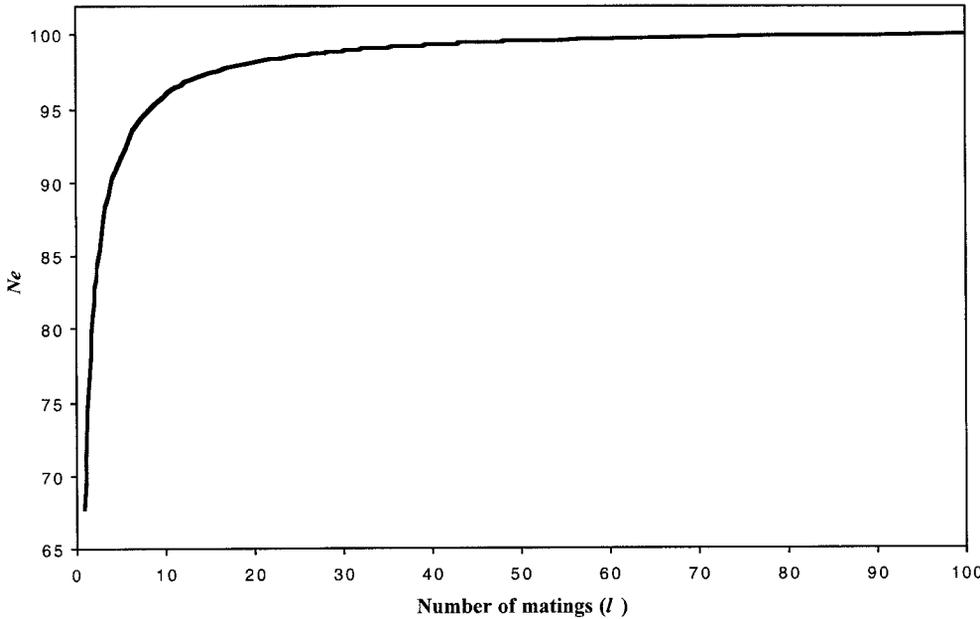
FIGURE 1.—Effective population size in a dioecious population of size $N = 100$ with an even sex ratio ($N = n_f + n_m$), as a function of the number of times each female mates.

corresponding probability $1 - 1/l$ they stem from a different mating event. In the latter case there is still the probability $1/n_m$ that both alleles come from the same father. With probability $(1 - 1/n_f)$ the two alleles originate from different mothers; in this case they still have a probability $1/n_m$ to originate from the same male. Collecting terms we obtain

$$P_m = \frac{1}{n_f}\left(\frac{1}{l} + \left(1 - \frac{1}{l}\right)\frac{1}{n_m}\right) + \left(1 - \frac{1}{n_f}\right)\frac{1}{n_m}. \quad (1)$$

We can then express the identities of the present generation as functions of identities in the previous generation. Both mutation and the reproductive system will affect the genetic identities. The mutation rate is u for all alleles and therefore the probability of two alleles identical by descent before mutation still being identical after mutation will be $\gamma \equiv (1 - u)^2$. Inbreeding (F_{t+1}) will be the parental coancestry (θ_t):

$$F_{t+1} = \gamma\theta_t. \quad (2)$$

Coancestry will be a function of both inbreeding and coancestry at the previous generation and will depend on P_f and P_m. For coancestry, there is a $1/4$ chance to draw two maternal alleles. In this case, with probability P_f they stem from the same female. There is a $1/2$ chance to draw the same allele and a $1/2$ chance to draw the alternate allele, which will be identical by descent with probability F_t. With complementary probability $1 - P_f$, the alleles come from different mothers and have a probability of identity by descent of θ_t. The logic is the same when drawing two paternal alleles with probability $1/4$. Finally, when drawing one paternal and maternal allele with probability $1/2$, their coancestry will be θ_t. Collecting the different probabilities gives us the following recurrence equations for identities at equilibrium:

$$\theta_{t+1} = \gamma\left(\frac{1}{4}\left(P_f\frac{1 + F_t}{2} + (1 - P_f)\theta_t\right)\right.$$
$$\left. + \frac{1}{4}\left(P_m\frac{1 + F_t}{2} + (1 - P_m)\theta_t\right) + \frac{1}{2}\theta_t\right). \quad (3)$$

Following ROUSSET (2002) and BALLOUX et al. (2003), we obtain the mean coalescence times:

$$\bar{t}_F = \frac{2(4 + P_f + P_m)}{P_f + P_m} \quad (4)$$

$$\bar{t}_\theta = \frac{8 + P_f + P_m}{P_f + P_m}. \quad (5)$$

Effective population size: We take advantage of the coalescence effective population size as defined in BALLOUX et al. (2003), as it is probably the most direct definition for effective population size. In a single unsubdivided population coalescence effective population size is defined as

$$N_e = \left(\frac{1}{2}\right)\left(\frac{1}{N}\bar{t}_F + \left(1 - \frac{1}{N}\right)\bar{t}_\theta\right), \quad (6)$$

where ($N = n_f + n_m$). Substituting coalescence times in the previous equation yields the following equation for the effective population size with an arbitrary number of mating events:

$$N_e = \frac{4n_m n_f l}{lN + nm - 1} + \frac{1}{2} + \frac{1}{2N}. \quad (7)$$

For an infinite number of matings, taking the limit when $l \to \infty$, we get the classical result for N_e under random mating

$$N_e = \frac{4n_m n_f}{N} + \frac{1}{2} + \frac{1}{2N} \quad (8)$$

(WRIGHT 1969).
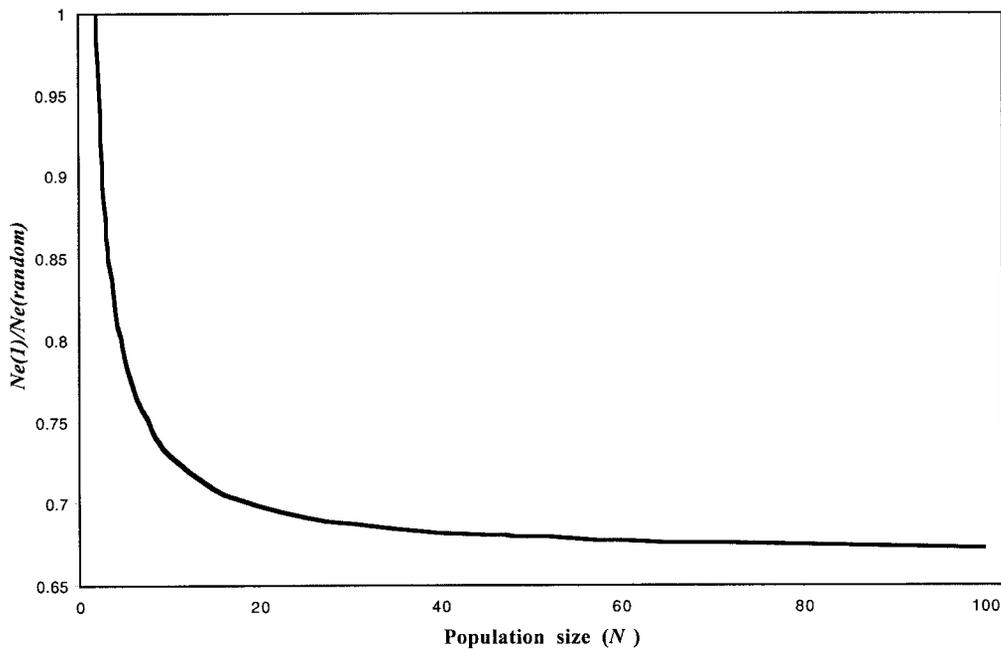
FIGURE 2.—Ratio of the effective population size achieved when females mate only once over the effective size when females mate an infinite number of times. The ratio is given as a function of population size N with an even sex ratio.

In Figure 1 we plot the effective population size for a varying number of mating events for a population of size 100 with an even sex ratio. When each female mates only once the effective population size is reduced to approximately two-thirds of the effective size the population would have if individuals mated an infinite number of times. The effective population size first rapidly increases with additional mating events and then asymptotically reaches its value under strict random mating. Random mating with singly mated females is not equivalent to monogamy. In a monogamous breeding system with an even sex ratio, each individual is involved in a single bond and the effective population size will be undistinguishable from a random-mating breeding system with an infinite number of matings (BASSET et al. 2001).

In Figure 2 we give for increasing population size the ratio of the effective population size when females mate once over the effective population size achieved with an infinite number of mating events. Trivially when only two individuals (one female and a male) comprise the population one mating event is sufficient for random mating. When population size increases the effective size for a population with singly mated females rapidly decreases to the asymptotic value of two-thirds of the effective size observed under an infinite number of matings. In reasonably large populations, the decrease in effective population size is substantial when females mate with one or a few males.

Whether this decrease in effective size is of importance will depend on lifetime polyandry of females in natural populations. Lifetime polyandry will be affected by both the effective number of males siring each single clutch and the probability that the same male sires a female's successive clutches. The number of males siring each litter is expected to be low, as even in species where females mate with many males, a single male generally sires most offspring (frequently the last). Variation in polyandry will be more strongly affected by the number of successive litters sired by different males. It is therefore expected that decrease in effective population size due to a finite number of matings should be more severe in species where females produce a limited number of successive clutches.

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