

# Differences in the effective population sizes of males and females do not require differences in their distribution of offspring number



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## ABSTRACT

Difference in male and female effective population sizes has, at times, been attributed to both sexes having unequal variance in their number of offspring. Such difference is paralleled by the relative effective sizes of autosomes, sex chromosomes, and mitochondrial DNA. I develop a simple framework to calculate the inbreeding effective population sizes for loci with different modes of inheritance. In this framework, I separate the effects due to mating strategy and those due to genetic transmission. I then show that, in addition to differences in the variance in offspring number, skew in the male/female effective sizes can also be caused by family composition. This approach can be used to illustrate the effect of induced behaviors on the relative male and female effective population sizes. In particular, I show the impact of the one-child policy formerly implemented in the People's Republic of China on the relative male and female effective population sizes. Furthermore, I argue that, under some strong constraints on family structure, the concepts of male and female effective population sizes are invalid.

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## 1. Introduction

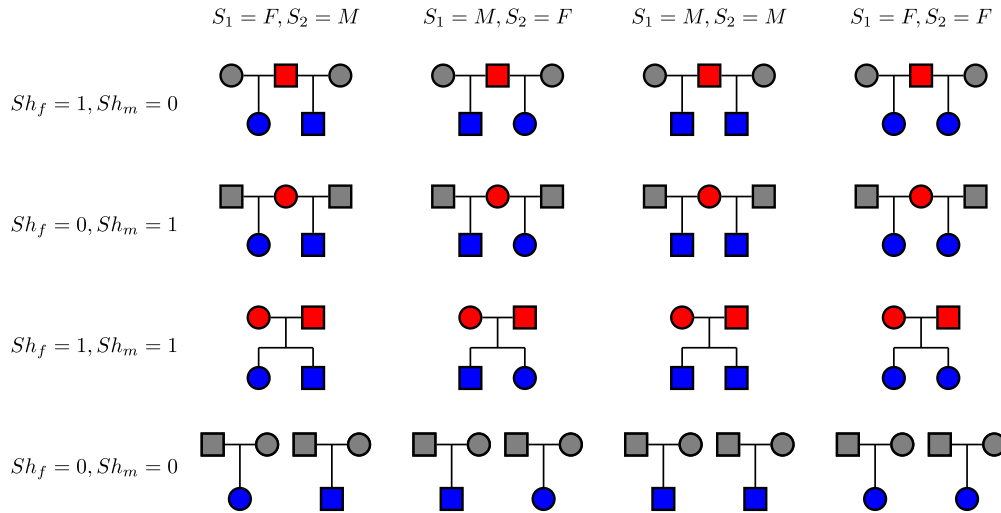
The concept of effective population size provides a natural way to formalize the effect of genetic drift on the evolution of populations. In populations with larger effective size, genetic drift proceeds more slowly, resulting in longer times to fixation of neutral polymorphisms and higher overall diversity levels. In dioecious species, it is also possible to define distinct effective population sizes for each of the two sexes. The strength of genetic drift at a given locus depends both on the mode of inheritance and on the effective population sizes of the two sexes; thus, different neutral loci may experience different levels of genetic drift. For instance, genetic drift at loci with cytoplasmic inheritance depends only on the female effective population size, while genetic drift at autosomal loci depends on effective sizes of both males and females. Consequently, demographic processes have the potential to affect relative levels of polymorphism and population differentiation at loci with different inheritance modes. This effect is even more pronounced for processes that affect males and females differently (Schaffner, 2004; Hammer et al., 2008; Ellegren, 2009; Keinan et al., 2009). For instance, in structured populations, differences in migration rates for males and females affect relative times to coalescence (and levels of diversity) for autosomes and sex-linked loci (Ramachandran et al., 2008). In humans, the prevalence and importance of patrilocality and matrilocality in shaping local and global patterns of nucleotide diversity has been a matter of

intense debate (Seielstad et al., 1998; Oota et al., 2001; Wilder et al., 2004a; Wilkins, 2006; Keinan et al., 2009; Bustamante and Ramachandran, 2009). In addition, changes in size that affect the population as a whole may also have a different impact on polymorphism levels at loci with different modes of inheritance (Fay and Wu, 1999; Pool and Nielsen, 2007). A crucial component of this last effect is that when sequence diversity is out of equilibrium, the rate of recovery depends on the effective population size of the locus, which differs depending on the mode of inheritance of the locus.

One intuitive way to understand the effect of genetic drift on patterns of population genetic diversity is through the concept of inbreeding effective population size, which for a diploid population can be defined as half the reciprocal of the probability that two distinct randomly chosen lineages will coalesce into a single lineage in the previous generation (Crow and Kimura, 1970; Ewens, 2004). The inbreeding effective population size is a key parameter in the coalescent process, where it provides a natural scale for time (Kingman, 1982). In part due to its importance for conservation, inbreeding effective population sizes of autosomal and hemizygous loci (e.g., X-linked in mammals and *Drosophila*) have been studied extensively over several decades for a range of mating structures (reviewed in Caballero (1994)).

Specific mating strategies, like polygyny or serial monogamy, can lead to a skew in the relative levels of polymorphism on the X chromosome versus autosomes (Hammer et al., 2008; Keinan et al., 2009). More generally speaking, this skew may be the result of differential variance in offspring numbers for males and females,

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**Fig. 1.** Potential pedigrees for two sampled individuals. The sexes of the two sampled individuals (in blue) are indicated with  $S_1$  and  $S_2$ . The individuals can share just their father, just their mother, both parents, or none of them; this is indicated with the values for the variables  $Sh_f$  and  $Sh_m$ . Shared parents are indicated in red and non-shared parents are in gray. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a more general concept that is meaningful for a wide range of mating strategies (Schuster and Wade, 2003). This phenomenon has naturally led to the interpretation of observed skews as a direct consequence of differences in the number of “breeding males” and “breeding females” (Wilder et al., 2004b; Hammer et al., 2008; Keinan et al., 2009). However, as shown below, deviations from standard expectations of the relative amounts of genetic drift between autosomes and X-chromosome may also be caused by a lack of independence between family size and sex of the offspring.

I present a simple framework to calculate the inbreeding effective population size. This framework allows a straightforward demonstration that even some strictly monogamous systems may result in different effective sizes for males and females. I illustrate the application of these calculations with an example from human populations, the one-child policy, as it was implemented for rural families in the People’s Republic of China. This analysis does not take into consideration differences in the fractions of boys and girls due to selective abortions or infanticide (which did affect relative numbers of males and females), but shows the policy would still have an effect on the relative effective sizes for males and females, even if the relative numbers of total male and female births were not affected. Skews in the relative effective population sizes of males and females can also be the consequence of conditions that affect pregnancies, if they influence reproductive behavior (e.g. decision to stop reproducing) and their prevalence depends on the sex of the fetus. I also show that an aggregate of populations with well-defined ratios of male to female effective sizes also has a well-defined ratio of male to female effective sizes. However, for some family structures with tight regulations, it is also possible to have situations in which the concepts of male and female effective population sizes are not meaningful.

## 2. Methods

First, I provide a framework to calculate coalescence rates for different kinds of loci under the assumptions of two separate sexes, neutrality, non-overlapping generations, and single births. Following Ewens (2004), we define the inbreeding effective population size ( $N_e$ ) at a locus as half the reciprocal of the coalescence rate of two randomly sampled allele copies, which we define formally in Appendix A. This definition considers the potential genetic contribution of individuals to future generations; for instance, mitochondria would not be sampled in males, because they do not contribute

their mitochondria to the following generation. Our goal is to find the rates of coalescence for loci with different inheritance patterns and the relationship of these rates with the reproductive strategy in the population. We use the law of total probability to calculate rates of coalescence. For each locus and pair of lineages, we consider six random variables, which we use to partition the sample space:  $S_1$  and  $S_2$  are the sexes of the two individuals carrying the sampled lineages, which take as values  $M$  (male) or  $F$  (female);  $T_1$  and  $T_2$  are the respective parents where the lineages originate and take values  $f$  (father) or  $m$  (mother); and  $Sh_f$  and  $Sh_m$  indicate whether the individuals share (value 1) or do not share (value 0) their father or mother, respectively (Fig. 1). Denoting the coalescence of the two lineages in the previous generation as  $c$ , we have

$$\frac{1}{2N_e} = P(c) = \sum P(c, T_1, T_2, Sh_f, Sh_m, S_1, S_2)$$

on which the summation goes over all possible values of each of the random variables. For the non-zero terms in the summation, we have

$$\begin{aligned} &P(c, T_1, T_2, Sh_f, Sh_m, S_1, S_2) \\ &= P(c|T_1, T_2, Sh_f, Sh_m, S_1, S_2) \cdot P(T_1, T_2, Sh_f, Sh_m, S_1, S_2) \\ P(T_1, T_2, Sh_f, Sh_m, S_1, S_2) &= P(T_1, T_2, Sh_f, Sh_m|S_1, S_2) \cdot P(S_1, S_2) \\ P(T_1, T_2, Sh_f, Sh_m|S_1, S_2) &= P(T_1, T_2|Sh_f, Sh_m, S_1, S_2) \cdot P(Sh_f, Sh_m|S_1, S_2) \\ P(S_1, S_2) &\simeq P(S_1) \cdot P(S_2) \\ P(T_1, T_2|Sh_f, Sh_m, S_1, S_2) &\simeq P(T_1|S_1) \cdot P(T_2|S_2). \end{aligned}$$

The approximate equalities result from excluding the possibility that the two lineages are the same in the given generation, which also implies that if the two lineages are found in the same individual, they derive from different parents. In what follows, we may write the sign of equality out of convenience. We note that  $P(Sh_f, Sh_m|S_1, S_2)$  may depend on factors like mating system and strategy, population history, or the underlying population pedigree (Wakeley et al., 2012), but not on the mode of inheritance of the locus. On the other hand,  $P(c|T_1, T_2, Sh_f, Sh_m, S_1, S_2)$ ,  $P(T_1|S_1)$ , and  $P(T_2|S_2)$  depend only on the inheritance of the locus. I list the non-zero values for  $P(c|T_1, T_2, Sh_f, Sh_m, S_1, S_2)$  in Table 1, and values for  $P(T_1|S_1)$  and  $P(S_1)$  in Table 2. For two lineages to coalesce, they must come from the same individual in the previous generation, thus for  $P(c|T_1, T_2, Sh_f, Sh_m, S_1, S_2) \neq 0$ , we have  $T_1 = T_2$ . We can

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