APPENDIX E

EFFECTIVE POPULATION SIZE DISCUSSION

Genetic Effective Population Size (N_e)

In discussing minimum viable population size, geneticists refer to "genetic effective size" of populations (N_e), not the census size (N) of populations. For example, Equation 1 describes how inbreeding will occur in an ideal population. Population geneticists define an ideal population having the following characteristics: even sex ratio, non-overlapping generations, random (Poisson) variation in family size, and constant population size. GUSG populations do not fit any of the characteristics of such a genetically ideal population, and this will cause the genetic effective size of GUSG populations to be less than the census size. For example, in GUSG populations, small numbers of males are usually responsible for most of the mating at a lek. Assume for purposes of illustration that 1 male is responsible for all of the matings in a GUSG population. In this population, all of the offspring would be half-siblings, and subsequent inbreeding would be unavoidable.

Relatively simply formulae describe simple departures from the ideal population described above. For example, the lek mating system of GUGS will cause the number of breeding males to be less than the number of breeding females. If GUSG populations were ideal in all respects except sex ratio, then the genetic effective population size would be

$$(1) \qquad N_e = \frac{4N_m N_f}{N_m + N_f}$$

where N_m is the number of breeding males and N_f is the number of breeding females (Hedrick 2000).

However, estimating the genetic effective size of populations is not a simple matter of plugging terms into formulae such as Equation 1. In most cases, species depart from the idealized model described above in multiple ways, and equations that account for all of these departures are difficult to formulate. Accommodating overlapping generations is especially problematic. Furthermore, metapopulation dynamics can have a critical effect upon genetic effective population size but are difficult to resolve analytically.

One alternative to using analytical approaches for estimating genetic effective population size is to estimate the genetic effective population size (N_e) from the census size (N) of the population using N_e/N ratios obtained from similar populations or species. However, the ratio between the genetic effective size and census size of populations is determined by many aspects of a species' biology, and N_e/N ratios vary accordingly (Frankham 1995). A review of N_e/N ratios found a mean of approximately 0.1. This means that the average genetic effective size of population is approximately 10% of the average census size.

Deciding whether GUSG populations have a higher or lower N_e/N ratio than 0.1 is difficult. The genetic effective population size of populations that fluctuate in size is strongly reduced by the generations with low sizes (Hedrick 2000) and only weakly increased by generations with large sizes. If GUSG populations do not fluctuate in size as much as the populations reviewed by Frankham (1995), then N_e/N may be higher than 0.1. For example, Frankham's (1995) review suggests that N_e/N is approximately 0.4 for populations that do not fluctuate in size. If GUSG populations fit this criterion, 1,250 individuals would be needed to achieve an genetic effective population size of 500 individuals. On the other hand, the lek mating system of GUSG may lead to an N_e/N that is less than average. Evaluating how these processes interact is difficult to predict without research specifically attempting to estimate genetic effective population size.

There are 2 general approaches for estimating genetic effective population size. First, genetic data can be used to evaluate how much genetic drift there is in a population. Genetic drift is stronger in small populations. This method works well for estimating the genetic effective size of small populations (Fig. 1), but is much less accurate for estimating the genetic effective size of large populations. There is little genetic drift in large populations, and estimating the slight changes in heterozygosity or allele frequencies requires prohibitively large amounts of data. Demographic data can also be used. Until recently, this was done with formulae that attempted to summarize how a natural population compared to the idealized model. Now, however, the genetic effective size of natural populations can be estimated from individual-based population dynamics models (e.g., Harris and Allendorf 1989; Basset et al. 2001). Such models are difficult to parameterize, but they are also useful for examining population demographics.

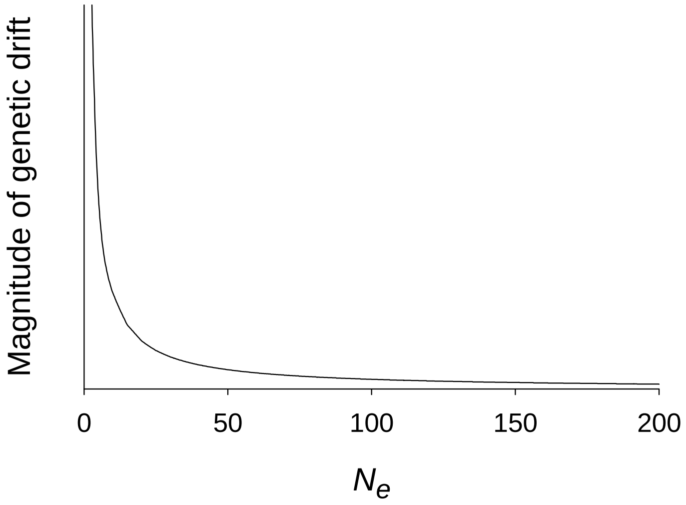

Fig. 1. The relationship between genetic effective population size (N_e) and the magnitude of genetic drift. The amount of genetic drift experienced by a population can be measured by the decline in heterozygosity, variance of allele frequencies, or amount of gametic disequilibrium, and each of these measures is related to genetic effective size in a similar way.