APPENDIX (see pp. 183-190)

EFFECTIVE POPULATION SIZE WITH OVERLAPPING GENERATIONS

Consider an allele at a locus and denote its frequency by \( p \) in a population in which generations are overlapped. Following Kimura and Crow (1963), the variance effective size is defined as

\[
N_s = \frac{p(1-p)}{2V_{ap}}
\]

where \( V_{ap} \) is the variance of the change in gene frequency in a period of time equal to one generation. Let \( N_md\tau \) be the number of individuals who are born during a time interval \( d\tau \) and able to reach the mean reproductive age or, more accurately, participate in the reproduction. The variance of the change in gene frequency during \( d\tau \) is then given approximately by

\[
p(1-p)^2N_md\tau/4(\tau N_m)^2
\]

assuming, as Kimura and Crow (1963) did, that gene frequency changes are slow enough that \( p \) is nearly the same for the period of one generation. In the above expression \( \tau \) represents the generation time. Note that the denominator \( 4(\tau N_m)^2 \) is approximate since individuals of all age groups do not mate at random. In practice, marriages are contracted more frequently between individuals whose ages are close with each other than those whose ages are far apart. However, if generations are completely overlapped for a sufficiently long time, the genes possessed by young and old individuals in a certain generation are finally mixed up. Therefore, the above approximation appears to lead to no serious error, though the variance of the change in gene frequency is slightly overestimated.

At any rate, the above expression should be equated to \( V_{ap}d\tau/\tau \). Thus,

\[
V_{ap} = \frac{p(1-p)}{2\tau N_m}
\]

Hence,

\[
N_s = \tau N_m.
\]

In the derivation of an equivalent formula, Kimura and Crow (1963) used the total population number in place of \( \tau N_m \). Since, however, \( V_{ap} \) has been defined as the variance of the change in gene frequency during one generation time, the total number cannot be used. This is especially so when the effective size referring to a long time change in gene frequency is considered.