Copyright © 1993 by the Genetics Society of America

Effective Sizes for Subdivided Populations

Ronald K. Chesser,[*,†] **Olin E. Rhodes, Jr.,**[*] **Derrick W. Sugg**[*] **and Andrew Schnabel**[*]

[*]*Savannah River Ecology Laboratory, Aiken, South Carolina 29802, and* [†]*Department of Genetics and Institute of Ecology, University of Georgia, Athens, Georgia 30602*

Manuscript received August 24, 1992
Accepted for publication August 26, 1993

ABSTRACT

Many derivations of effective population sizes have been suggested in the literature; however, few account for the breeding structure and none can readily be expanded to subdivided populations. Breeding structures influence gene correlations through their effects on the number of breeding individuals of each sex, the mean number of progeny per female, and the variance in the number of progeny produced by males and females. Additionally, hierarchical structuring in a population is determined by the number of breeding groups and the migration rates of males and females among such groups. This study derives analytical solutions for effective sizes that can be applied to subdivided populations. Parameters that encapsulate breeding structure and subdivision are utilized to derive the traditional inbreeding and variance effective sizes. Also, it is shown that effective sizes can be determined for any hierarchical level of population structure for which gene correlations can accrue. Derivations of effective sizes for the accumulation of gene correlations within breeding groups (coancestral effective size) and among breeding groups (intergroup effective size) are given. The results converge to traditional, single population measures when similar assumptions are applied. In particular, inbreeding and intergroup effective sizes are shown to be special cases of the coancestral effective size, and intergroup and variance effective sizes will be equal if the population census remains constant. Instantaneous solutions for effective sizes, at any time after gene correlation begins to accrue, are given in terms of traditional F statistics or transition equations. All effective sizes are shown to converge upon a common asymptotic value when breeding tactics and migration rates are constant. The asymptotic effective size can be expressed in terms of the fixation indices and the number of breeding groups; however, the rate of approach to the asymptote is dependent upon dispersal rates. For accurate assessment of effective sizes, initial, instantaneous or asymptotic, the expressions must be applied at the lowest levels at which migration among breeding groups is nonrandom. Thus, the expressions may be applicable to lineages within socially structured populations, fragmented populations (if random exchange of genes prevails within each population), or combinations of intra- and interpopulation discontinuities of gene flow. Failure to recognize internal structures of populations may lead to considerable overestimates of inbreeding effective size, while usually underestimating variance effective size.

THE effective size of populations is a concept of paramount importance to biologists. The importance of accurate effective sizes lies in their utility for predicting the dynamics of genetic variation within and among populations of organisms. Effective population size can be operationally defined as the size of an ideal population that would undergo the same amount of genetic change, via random union of gametes, as the actual population (Wright 1969; Lande and Barrowclough 1987). Traditionally, two types of effective size have been recognized; one that reflects the accumulation of gene correlations within individuals (inbreeding effective size, N_{eI}) and one that reflects effects of gene-frequency drift (variance effective size, N_{eV}; Crow 1954; Crow and Kimura 1970; Crow and Denniston 1988). The concept of effective population size is central to much of population genetics theory primarily because it incorporates those characteristics that affect the conservation or loss of genetic diversity within and among populations or subdivisions of populations (Wood 1987; Chesser 1991b).

Numerous mathematical treatments, involving variables such as the proportions and ages of males and females within populations, the mean and variance in reproductive contributions by each sex, and the covariance in male and female progeny contributed by each sex have been used to provide realistic formulations with which to calculate N_{eI} and N_{eV} (Kimura and Crow 1963; Crow and Kimura 1970; Crow and Denniston 1988). Models for estimation of effective population size often differ in their treatment of generation interval as either discrete or overlapping (Choy and Weir 1978; Hill 1979). Further models have been derived to account for systems of mating between relatives (Pollak 1987; Caballero and Hill 1992a,b). It is not surprising, therefore, that the various estimates vary in complexity, information con-

Genetics **135**: 1221–1232 (December, 1993)

content, and interpretability (WOOD 1987; HARRIS and ALLENDORF 1989).

A common shortcoming of most existing formulations, beyond the general lack of convergence (HARRIS and ALLENDORF 1989), is their failure to address population organization (CHESSER 1991b). There is evidence that many organisms are arrayed into complexes of breeding units or subpopulations (EHRLICH 1965; SELANDER 1970; CHESSER 1983a). For the purposes of this paper we will define a population as a network of social units, breeding groups, or subpopulations (*e.g.*, CHESSER 1991a,b) and genetic exchange may take place within and among the groups. Regardless of geographic scale, subdivided populations can be maintained by means of intrinsic factors, such as behavioral segregation, or extrinsic factors, such as geographic distance and habitat fragmentation. Given the impact of structure on the gene diversity of breeding groups or subpopulations (CROW and KIMURA 1970; CHESSER 1991a,b), the importance to inbreeding and variance effective population sizes is irrefutable.

Changes in N_{eI} and N_{eV} under conditions of incomplete migration by males or females have been previously assessed (CHESSER 1991b). Models used to approximate values for N_{eI} and N_{eV} were based on populations composed of varying numbers of social units and incorporated the number of breeding females within each unit, the rates of migration by each sex, and potential polygynous breeding tactics. This work demonstrated that N_{eI} and N_{eV} were approximately equal under conditions of complete migration by males or females and that N_{eI} and N_{eV} differ markedly under various conditions of incomplete migration by both sexes.

The present work adds to the original models of CHESSER (1991a,b) by integrating the concept of effective population size into a theoretical framework for the assessment of genetic variation in subdivided populations. Specifically, we will extend the formulas of CHESSER (1991b) to include variance in progeny numbers, random sex of progeny, and the mean and variance in the number of mates per male. We also provide solutions for N_{eI} and N_{eV} when breeding groups are changing in size and a new derivation of WRIGHT's (1969) island model that is appropriate to any scale. Throughout the text the terms breeding group and subpopulation will be defined as the lowest level of structure at which nonrandom exchange of genes occurs.

TRANSITION OF GENE CORRELATIONS

The expressions needed to derive equations for effective population sizes will be developed through methods similar to those presented in CHESSER (1991a,b). To circumvent restrictive assumptions, however, it will be necessary to rederive the following variables:

F = average correlation of genes within individuals (inbreeding coefficient)
θ = average correlation of genes between random progeny within breeding groups (coancestry)
α = average correlation of genes of random individuals from different breeding groups

The parameters used to derive the state of the critical variables are:

n = number of breeding females within a breeding group for a given generation
s = number of breeding groups within the population
k = average number of progeny, which survive to reproduce, produced by each female
σ_k^2 = variance in number of progeny/female surviving to reproduce
d_m and d_f = migration rates for males and females, respectively
ϕ = probability that random females within a breeding group mate with the same male.

CHESSER (1991a,b) defined the parameter ϕ as

$$\phi = \frac{\sum_{i=1}^{m} (b_i^2 - b_i)}{n^2 - n} \tag{1}$$

where m is the number of males per breeding group, and b_i is the number of females mated by the ith male ($\sum_i b_i = n$). This parameter, however, can be expanded to include the mean and variance of the number of females mated by each male (b and σ_b^2, respectively). Because $\sum b_i^2 = m(\sigma_b^2 + b^2)$, the expression for ϕ becomes

$$\phi = \frac{m[\sigma_b^2 + b(b - 1)]}{n(n - 1)} \tag{2}$$

and $b = (\sum_i b_i)/\mathrm{m} = n/m$. It should be noted that m may represent either the number of mating or potentially mating males, provided σ_b^2 is determined from the corresponding pool of males. In the instance when a single male mates with all of the females in a group, if the number of *potentially* breeding males is used, then $m = n$, $b = 1$ and $\sigma_b^2 = (n - 1)$ because $n - 1$ males per subpopulation breed with zero females and one male in each subpopulation breeds with n females. Such a situation results in $\phi = 1$. Alternatively, if the *actual* number of breeding males is used, m is set to one, $b = n$ and $\sigma_b^2 = 0$ because there is only one actual male breeder per subpopulation that mates with n females. This scenario also results in $\phi = 1$.

CHESSER (1991a,b) assumed that each female produced exactly two progeny, one male and one female. This assumption dictated that two variables were necessary to denote gene correlations (coancestry) within breeding groups, θ_{mm} for the correlation of genes among male progeny within breeding groups (which is identical to that among female progeny) and θ_{mf} for the coancestry between male and female progeny. However, if we permit the sex of the progeny to be determined randomly (each sex produced with a probability of ½), we find that $\theta_{mm} = \theta_{ff} = \theta_{mf}$, and there is no need to differentiate between the coancestries of like-sexed and different-sexed progeny. Hence, we will designate the average coancestry of progeny born within breeding groups as simply θ.

The average coancestries of progeny born within subpopulations (or breeding groups) can be determined from a triangular matrix. For example, if there are kn progeny born within a breeding group, then the average coancestry is the mean of the values for progeny pairs ($\theta_{i,j}$ denotes the coancestry between the ith and jth progeny born within a subpopulation)

$$\begin{array}{cccc} \theta_{1,2} & \theta_{1,3} & \cdots & \theta_{1,kn} \\ & \theta_{2,3} & \cdots & \theta_{2,kn} \\ & & \cdots & \cdots \\ & & & \theta_{kn-1,kn} \end{array} \tag{3}$$

The expected proportion of full siblings represented in this matrix is

$$\epsilon(\text{sibs}) = \frac{\frac{1}{2}\sum_{i=1}^{n}[k_i^2 - k_i]}{kn(kn-1)/2} = \frac{\sum_{i=1}^{n}[k_i^2] - kn}{kn(kn-1)} \tag{4}$$

with k_i denoting the number of progeny produced by the ith female within a subpopulation. Because $\sum k_i^2 = n[\sigma_k^2 + k^2]$, Equation 4 simplifies to

$$\epsilon(\text{sibs}) = \frac{\sigma_k^2 + k(k-1)}{k(kn-1)}. \tag{5}$$

The expected coancestry of full siblings is

$$\epsilon[\theta(\text{sibs})]_{t+1} = \frac{1}{4}(1 + F_t + 2F_{t+1}) \tag{6}$$

(CHESSER 1991a, Equation 15) where t references the generation. The gene correlations among the remainder of the progeny (non-sibs) within the subpopulation will be equal to the average coancestry of their parents (γ_t; CHESSER 1991b). Therefore, the expectation for the average coancestry within subpopulations is

$$\theta_{t+1} = \frac{[\sigma_k^2 + k(k-1)]\,[\frac{1}{4}(1 + F_t + 2F_{t+1})]}{k(kn-1)} + \left[1 - \frac{[\sigma_k^2 + k(k-1)]}{k(kn-1)}\right]\gamma_t. \tag{7}$$

The coancestry of non-siblings, γ_t, is determined using Equations A.7 through A.9 of CHESSER (1991b, p. 583) and substituting θ_{t+1} for $\theta_{mm(t+1)}$,

$$\begin{aligned}\gamma_t = {} & \frac{\phi(1 + F_t)}{8} \\ & + \frac{2 - \phi - \left(1 - \frac{kn-1}{kns-1}\right)(d_m(1-\phi) + d_f)}{4}\theta_t \\ & + \frac{F_{t+1}}{2} + \frac{\left(1 - \frac{kn-1}{kns-1}\right)(d_m(1-\phi) + d_f)}{4}\alpha_t.\end{aligned} \tag{8}$$

The expression for F_{t+1} can be derived from equations presented by CHESSER (1991b, Equation A.1) with the stipulation that now the sex of progeny is randomly determined;

$$\begin{aligned}F_{t+1} = {} & \left[1 - \left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)\right]\theta_t \\ & + \left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)\alpha_t.\end{aligned} \tag{9}$$

Using Equations 8 and 9, expression (7) can be expanded, giving the average coancestry among progeny born within a subpopulation,

$$\begin{aligned}\theta_{t+1} = {} & (1 + F_t)\left[\frac{(2-\phi)\sigma_k^2 + 2k(k-1) + \phi k^2(n-1)}{8k(kn-1)}\right] \\ & + \theta_t\left[\frac{1 - \left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)}{2} + \left(\frac{k^2(n-1) - \sigma_k^2}{4k(kn-1)}\right)\right. \\ & \qquad \left.\cdot\left[2 - \phi - \left(\frac{kn(s-1)}{kns-1}\right)(d_m(1-\phi) + d_f)\right]\right] \\ & + \alpha_t\left[\frac{\left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)}{2} + \left(\frac{k^2(n-1) - \sigma_k^2}{4k(kn-1)}\right)\right. \\ & \qquad \left.\cdot\left(\frac{kn(s-1)}{kns-1}\right)(d_m(1-\phi) + d_f)\right].\end{aligned} \tag{10}$$

Finally, the transition for the correlation of genes among subpopulations can be expressed as

$$\begin{aligned}\alpha_{t+1} = {} & \frac{2(d_m + d_f - d_m d_f)/s + \frac{kn-1}{kns-1}(d_m + d_f)}{4}\theta_t \\ & + \left[1 - \frac{1}{2s}(d_m + d_f - d_m d_f) - \frac{kn-1}{4(kns-1)}(d_m + d_f)\right]\alpha_t.\end{aligned} \tag{11}$$

The transition matrix for the changes in correlations of genes within individuals (F), within subpopulations (θ), and among subpopulations (α) can be constructed from Equations 9, 10 and 11

$$T = \begin{bmatrix} 0 & 1 - \left(1 - \frac{1}{s}\right)A & \left(1 - \frac{1}{s}\right)A \\ \frac{(2 - \phi)\sigma_k^2 + 2k(k - 1) + \phi k^2(n - 1)}{8k(kn - 1)} & \frac{1 - \left(1 - \frac{1}{s}\right)A}{2} + G\left(2 - \phi - \left(\frac{kn(s - 1)}{kns - 1}\right)B\right) & \frac{\left(1 - \frac{1}{s}\right)A}{2} + G\left(\frac{kn(s - 1)}{kns - 1}\right)B \\ 0 & \frac{2A/s + \frac{kn - 1}{kns - 1}(d_m + d_f)}{4} & \frac{4 - 2A/s - \frac{kn - 1}{kns - 1}(d_m + d_f)}{4} \end{bmatrix} \quad (12)$$

with A, B, and G denoting $(d_m + d_f - d_m d_f)$, $(d_m(1 - \phi) + d_f)$, and $[k^2(n - 1) - \sigma_k^2]/(4k(kn - 1))$ respectively. A constant vector,

$$C = \begin{bmatrix} 0 \\ \frac{(2 - \phi)\sigma_k^2 + 2k(k - 1) + \phi k^2(n - 1)}{8k(kn - 1)} \\ 0 \end{bmatrix} \quad (13)$$

must be included such that $\{F_{t+1}, \theta_{t+1}, \alpha_{t+1}\} = T\{F_t, \theta_t, \alpha_t\} + C$.

EFFECTIVE POPULATION SIZES

Eigenvalue solutions to the matrix T would provide implicit solutions to the transitions of gene correlations. A single eigenvalue solution is possible, however, only if the population remains in a steady state. When the population is either growing ($k > 2$) or declining ($k < 2$) the numbers of breeding females (n) and males (m) change each generation. Given an equal sex ratio of breeding individuals, n and m would change according to

$$n_{t+1} = m_{t+1} = \frac{n_t k}{2}. \quad (14)$$

Likewise, if R represents a constant proportion of males in the subpopulations, $R = m/(m + n)$, then

$$n_{t+1} = n_t k(1 - R); \quad m_{t+1} = m_t kR$$
$$n_t = n_0[k(1 - R)]^t; \quad m_t = m_0[kR]^t. \quad (15)$$

With changing population size, unique eigenvalues would be found for each generation. Additionally, numerical solutions would necessarily incorporate the changes of n and m each iteration.

The derived eigenvalue solutions for steady state population sizes are extremely lengthy and complex and will not be presented here. We will derive expressions for effective numbers in three stages. First, the initial effective numbers will be presented and our results will be compared to formulas derived for single, isolated populations with random mating. COCKERHAM (1970), however, showed that with nonrandom mating, the values for effective population size change over generations. COCKERHAM (1970) and CABALLERO and HILL (1992b) derived expressions applicable to the asymptotic value of effective population size. Therefore, we subsequently will derive instantaneous effective numbers that are accurate for any generation, whether or not asymptote has been attained. Last, we derive approximations for the asymptotic effective population size.

Initial effective numbers: Using the constant value of coancestry transition in the vector C (Equation 13) the recursions for F and α are

$$F_{t+1} = \left[\frac{(2 - \phi)\sigma_k^2 + 2k(k - 1) + \phi k^2(n - 1)}{8k(kn - 1)} \cdot \left[1 - \left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)\right] + \left(1 - \frac{(2 - \phi)\sigma_k^2 + 2k(k - 1) + \phi k^2(n - 1)}{8k(kn - 1)} \cdot \left[1 - \left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)\right]\right)F_t \right] \quad (16)$$

and

$$\alpha_{t+1} = \left[\frac{(2 - \phi)\sigma_k^2 + 2k(k - 1) + \phi k^2(n - 1)}{8k(kn - 1)} \cdot \frac{2(d_m + d_f - d_m d_f)/s + \frac{kn - 1}{kns - 1}(d_m + d_f)}{4} + 1 - \frac{(2 - \phi)\sigma_k^2 + 2k(k - 1) + \phi k^2(n - 1)}{8k(kn - 1)} \cdot \frac{2(d_m + d_f - d_m d_f)/s + \frac{kn - 1}{kns - 1}(d_m + d_f)}{4} \alpha_t. \right] \quad (17)$$

Furthermore, because $F_{t+1} = {}^1\!/\!{}_2 N_{eI} + (1 - {}^1\!/\!{}_2 N_{eI})F_t$ Equation 16 can be alternatively expressed in terms of the initial inbreeding effective size as [using the expanded expression (2) for ϕ]

$$N_{eI} = \frac{4k(kn-1)}{\left[2\sigma_k^2 + 2k(k-1) + \frac{m(\sigma_b^2 + b(b-1))}{n(n-1)}[k^2(n-1) - \sigma_k^2]\right]\left[1 - \left(1 - \frac{1}{s}\right)(d_m + d_f - d_m d_f)\right]}. \tag{18}$$

Equation 17 can likewise be expressed as the "intergroup effective size," $N_{e\alpha}$, which reflects the overall accumulation of gene correlations among breeding groups,

$$N_{e\alpha} = \frac{4k(kn-1)}{\left[2\sigma_k^2 + 2k(k-1) + \frac{m(\sigma_b^2 + b(b-1))}{n(n-1)}[k^2(n-1) - \sigma_k^2]\right]\left[\frac{\mathrm{d}_m + \mathrm{d}_f - \mathrm{d}_m\mathrm{d}_f}{2\mathrm{s}} + \frac{(\mathrm{kn}-1)(\mathrm{d}_m + \mathrm{d}_f)}{4(\mathrm{kns}-1)}\right]}. \tag{19}$$

Figure 1 depicts some general effects of male (d_m) and female (d_f) migration rates on the relative values of N_{eI} and $N_{e\alpha}$. Regardless of the number of breeding groups, when d_m and d_f are small, the inbreeding effective size is much smaller than the intergroup effective size ($N_{eI}/N_{e\alpha} \ll 1$). The two sizes attain nearly equivalent values ($N_{eI}/N_{e\alpha} \approx 1$) only when migration of one or the other sex is very high, but under no conditions is N_{eI} greater than $N_{e\alpha}$.

Although the expression for $N_{e\alpha}$ in (19) is equivalent to that defined as variance effective size (N_{eV}) by CHESSER (1991b), this equivalence holds only under certain circumstances. For example, because N_{eV} depends on the number of progeny, whereas $N_{e\alpha}$ depends on the number of parents (*cf.* CROW and KIMURA 1970, p. 361), the relative values of N_{eV} and $N_{e\alpha}$ will be affected by changing population size. When this occurs, the value of N_{eV} is readily determined from expression (19) by substitution of n_{t+1} and m_{t+1} for n and m. Assuming that sex ratio of breeding individuals (m/n) is not changing over generations, its value can be represented by $R/(1-R)$. Substituting $R/(1-R)$ for m/n and $nk(1-R)$ for n in Equation 19, the variance effective size is determined to be

$$N_{eV} = \frac{4k[k^2n(1-R) - 1]}{\left[(2-\phi)\sigma_k^2 + 2k(k-1) + \frac{Rk^2}{1-R}\left[[\sigma_b^2 + b(b-1))\right]\right]\left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(k^2n(1-R)-1)(d_m + d_f)}{4(k^2n(1-R)s - 1)}\right]}. \tag{20}$$

If the population is rapidly growing ($k \gg 2$) or declining ($k \ll 2$) N_{eV} may be considerably different from $N_{e\alpha}$ (larger or smaller, respectively).

CROW and DENNISTON (1988) determined inbreeding and variance effective numbers for single, isolated populations as (using our parameter symbols)

$$N_{eI} = \frac{kN_{t-2} - 2}{k - 1 + (\sigma_k^2/k)} = \frac{k(kN_{t-2} - 2)}{\sigma_k^2 + k(k-1)} \tag{21}$$

and

$$N_{eV} = \frac{2(N_{t-1} - 1)}{1 + (\sigma_k^2/k)} = \frac{2k(N_t - 1)}{\sigma_k^2 + k}. \tag{22}$$

Our equations for initial effective sizes can be expressed in terms that are consistent with those used by CROW and DENNISTON (1988). The variance in numbers of progeny produced by females, σ_k^2, is explicitly included in all measures of effective numbers whereas variance in progeny sired by males is not. However, it can be shown that the variance in progeny produced by males is

$$\sigma_{k(m)}^2 = \phi k^2(n-1) + (1-\phi)\sigma_k^2 \tag{23}$$

and the variance in progeny number produced by parents (regardless of sex) is

$$\sigma_{kT}^2 = \sigma_{k(m)}^2 + \sigma_k^2 + 2\sigma_{k,k(m)}. \tag{24}$$

If the covariance ($\sigma_{k,k(m)}$) of sire and dam progeny numbers is assumed to be zero [a reasonable assumption (CROW and DENNISTON 1988, p. 491)], then

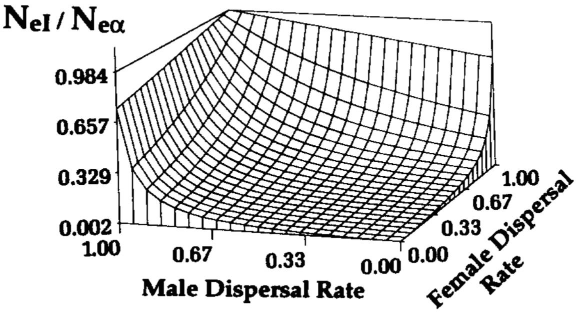

FIGURE 1.—Three-dimensional diagram depicting the influence of migration rates by males (d_m) and females (d_f) on the ratio of the inbreeding effective size to the interpopulation effective size ($N_{eI}/N_{e\alpha}$). The graph was generated using 15 females per breeding group, 20 breeding groups, and values of 2, 2, and 0.1 for k, σ_k^2, and ϕ, respectively.

Equation 24 can be expressed as

$$\sigma_{kT}^2 = (2 - \phi)\sigma_k^2 + \phi k^2(n - 1). \tag{25}$$

Substituting Equation 25 into our measures of primary effective numbers

$$N_{eI} = \frac{4k(kn - 1)}{[\sigma_{kT}^2 + 2k(k - 1)][1 - (1 - (1/s))(d_m + d_f - d_m d_f)]} \tag{26}$$

$$N_{e\alpha} = \frac{4k(kn - 1)}{[\sigma_{kT}^2 + 2k(k - 1)]\left[\dfrac{d_m + d_f - d_m d_f}{2s} + \dfrac{(kn - 1)(d_m + d_f)}{4(kns - 1)}\right]} \tag{27}$$

$$N_{eV} = \frac{4[k^2 n(1 - R) - 1]}{[\sigma_{kT}^2 + 2k(k - 1)]\left[\dfrac{d_m + d_f - d_m d_f}{2s} + \dfrac{(k^2 n(1 - R) - 1)(d_m + d_f)}{4(k^2 n(1 - R)s - 1)}\right]}. \tag{28}$$

These equations can be compared to those of CROW and DENNISTON (1988) by assigning $s = 1$ (a single population), $d_m = d_f = 1$ (all individuals disperse back into their native population), and random mating (thus $m = n$, $b = 1$, and $\sigma_b^2 = 0$). With these stipulations $\sigma_{kT}^2 = 2\sigma_k^2$, and our equations become

$$N_{eI} = \frac{2k(kn - 1)}{\sigma_k^2 + k(k - 1)} \tag{29}$$

$$N_{eV} = N_{e\alpha} = \frac{2k(kn - 1)}{\sigma_k^2 + k(k - 1)} \tag{30}$$

Remembering that $2n = N$, it can be seen that Equations 21 and 29 for N_{eI} are identical whereas those for N_{eV}, (22) and (30), are convergent as N becomes large. Furthermore, when $k = 2$, indicating constant population number, then Equations 21, 22, 29 and 30 become

$$N_{eI} = N_{eV} = N_{e\alpha} = \frac{4N - 4}{\sigma_k^2 + 2}. \tag{31}$$

Thus, our expressions for primary effective numbers are either equal to or are close approximations of those of CROW and DENNISTON (1988) when applied to a single isolated population. Our results also confirm that CROW and DENNISTON's (1988) equations are relevant to initial rather than ultimate effective population sizes (*cf.* CABALLERO and HILL 1992a,b).

The large number of parameters in Equations 18–20 makes it difficult to discern clearly the relative importance of male and female contributions to effective population sizes. It could be argued that because the distribution of possible values for σ_k^2 is bounded for particular values of n and k, and the value of σ_b^2 is limited by m and b, that we should not present all of these as parameters. Indeed, if we assign ϕ_m as equivalent to ϕ (Equation 2) and ϕ_f to Equation 5, the inbreeding effective population size can be represented as

$$N_{eI} = \frac{4}{[2\phi_f + \phi_m(1 - \phi_f)][1 - (1 - (1/s))(d_m + d_f - d_m d_f)]}. \tag{32}$$

Here ϕ_m and ϕ_f are defined as the probabilities that random progeny were the product of a particular adult male or female, respectively, and each may vary from essentially zero (progeny produced by many parents of a particular sex) to unity (all progeny produced by a single mother or father). Although Equation 32 is operationally identical to Equation 18, the relative roles of male and female contributions are more clearly envisioned by this reduced expression. Figure 2 shows that for a given number of subgroups, number of breeding females per group, and male and female dispersal rates, the inbreeding effective size is

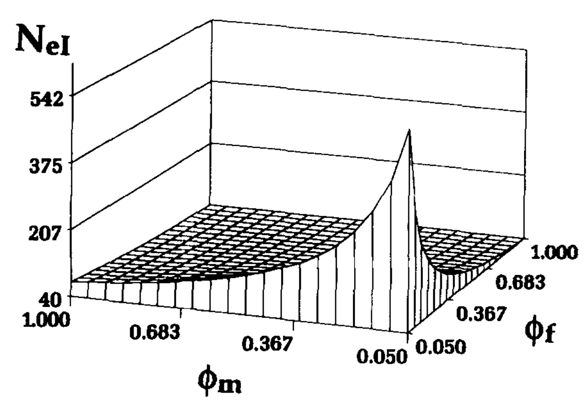

FIGURE 2.—Three dimensional diagram depicting the influence of the probabilities that random progeny are a product of a particular adult male (ϕ_m) or female (ϕ_f) on inbreeding effective size (N_{eI}). The graph was generated using 5 females per breeding group, 20 breeding groups, and $d_m = d_f = 1$. The graph for $N_{e\alpha}$ is essentially identical (because migration rates are unity) and will not be shown.

smallest when either ϕ_m or ϕ_f is large and increases dramatically as both ϕ_m and ϕ_f approach zero. Similarly, the intergroup effective size can be reduced to

$$N_{e\alpha} = \frac{16s}{[2\phi_f + \phi_m(1 - \phi_f)][3(d_m + d_f) - 2d_m d_f]} \tag{33}$$

if it is assumed that $(kn - 1)/(kns - 1) \approx 1/s$. Unfortunately, such reductions are not easily extended to N_{eV} when populations are growing or diminishing in size.

Instantaneous effective numbers: Perhaps the greatest utility of the effective sizes is for the prediction of changes in gene diversity within individuals and within populations over successive generations. Traditionally, recursive equations such as

$$\begin{aligned} F_t &= \frac{1}{2N_{eI}} + \left(1 - \frac{1}{2N_{eI}}\right)F_{t-1} \\ \alpha_t &= \frac{1}{2N_{e\alpha}} + \left(1 - \frac{1}{2N_{e\alpha}}\right)\alpha_{t-1} \\ V_t &= \frac{1}{2N_{eV}} + \left(1 - \frac{1}{2N_{eV}}\right)V_{t-1} \end{aligned} \tag{34}$$

would be used to estimate the value of inbreeding (F), correlations among groups (α) and genetic variance (V) for any generation. The solution for N_{eI} provided in Equation 18, however, is for an initial rate of inbreeding at any given beginning time zero. It is clear from Equation 9 that the rate of accumulation of inbreeding over successive generations must also include the correlations among groups (α) as well. Thus, the accumulation of inbreeding over generations may be represented as

$$\begin{aligned} F_{t+1} &= \frac{1}{2N_{eI}} + \left(1 - \frac{1}{2N_{eI}}\right)F_t + \left[1 - \frac{1}{2N_{eI}} - \left(1 - \frac{1}{2N_{eI}}\right)F_t\right]\alpha_t \\ &= \alpha_t + \left[\frac{1}{2N_{eI}} + \left(1 - \frac{1}{2N_{eI}}\right)F_t\right](1 - \alpha_t) \end{aligned} \tag{35}$$

which may be expanded using Equation 34 to

$$\begin{aligned} F_{t+1} = \alpha_{t-1} + \frac{1 - \alpha_{t-1}}{2N_{e\alpha}} + \left[\frac{1}{2N_{eI}} + \left(1 - \frac{1}{2N_{eI}}\right)F_t\right] \\ \cdot (1 - \alpha_{t-1})\left(1 - \frac{1}{2N_{e\alpha}}\right). \end{aligned} \tag{36}$$

Both N_{eI} and $N_{e\alpha}$ must be taken into account for accurate assessment of the dynamics of inbreeding in subdivided populations. Calculation of F from expression (36) over many generations is only slightly less tedious than numerical iterations of the matrices (Equations 12 and 13).

Cockerham (1970; also see Caballero and Hill 1992a,b) demonstrated that nonrandom mating changes the gene correlations over generations and alters the ultimate value of effective population size. As is demonstrated by equations 35 and 36, expressions for effective population numbers presented thus far apply to the rates of change at the initial generation ($t = 0$ to 1) of gene correlations within individuals (N_{eI}) and among groups ($N_{e\alpha}$); these rates will be altered as gene correlations accrue. Caballero and Hill (1992b) derived the asymptotic value of effective size as

$$\hat{N}_e = \frac{4N}{2(1 - F_{IS}) + \sigma_k^2(1 + 3F_{IS})} \tag{37}$$

which would be attained after several generations of consistent mating tactics (the "hat" is used to reference asymptotic values). Their approach, however, was considerably different than ours in that breeding groups and dispersal rates were not explicitly defined. As such, Caballero and Hill's (1992b) analyses could not incorporate all of the gene correlations necessary to define asymptotic effective sizes. In particular, lack of specific group definitions prevents inclusion of intragroup coancestry (θ) values, the most predominant gene correlation under many breeding and dispersal tactics in our expressions. The rate of change of inbreeding is defined as

$$\Delta F = \frac{F_{t+1} - F_t}{1 - F_t} \tag{38}$$

Falconer (1989). Using Equation 9 to replace F_{t+1}, Equation 38 becomes

$$\Delta F = \frac{\theta_t - F_t - (\theta_t - \alpha_t)(1 - (1/s))(d_m + d_f - d_m d_f)}{1 - F_t} \tag{39}$$

where the gene correlations (F_t, θ_t, and α_t) are given in equations (9–11). The F-statistics given by Chesser (1991a,b)

$$F_{ST} = \frac{\theta_t - \alpha_t}{1 - \alpha_t} \quad F_{IS} = \frac{F_t - \theta_t}{1 - \theta_t} \quad F_{IT} = \frac{F_t - \alpha_t}{1 - \alpha_t} \tag{40}$$

(using subscripts I, S, and T refer to individuals, breeding groups, and total array of breeding groups, respectively) can be substituted into Equation 39 to yield

$$\Delta F = \frac{[1 - (1 - (1/s))(d_m + d_f - d_m d_f)]F_{ST} - F_{IT}}{1 - F_{IT}}. \tag{41}$$

Because $N_{eI} = 1/(2\Delta F)$, the inbreeding effective number is determined to be

$$N_{eI} = \frac{1 - F_{IT}}{2[(1 - (1 - (1/s))(d_m + d_f - d_m d_f))F_{ST} - F_{IT}]}. \tag{42}$$

Similarly, $\Delta\alpha = (\alpha_{t+1} - \alpha_t)/(1 - \alpha_t)$, and using Equations 11 and 40 the rate of change of gene correlations among groups is

$$\Delta\alpha = F_{ST}\left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(kn-1)(d_m + d_f)}{4(kns-1)}\right] \tag{43}$$

and the intergroup effective population size is determined as

$$N_{e\alpha} = \frac{1}{2F_{ST}\left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(kn-1)(d_m + d_f)}{4(kns-1)}\right]} \tag{44}$$

$$\approx \frac{2s}{F_{ST}[3(d_m + d_f) - 2d_m d_f]}.$$

Equation 44 also suffices for N_{eV} if there is a constant census number. Interestingly, group (n) or total population size (N) and variance of progeny number (σ^2_{kT}) are absent from the derivations of effective numbers, although they are important in determining the ultimate values of the F statistics.

Expressions (42 and 44) for effective population sizes provide exact fits for the values obtained via iterations of Equations 12 and 13, as would be expected. Therefore, Equations 42 and 44 represent instantaneous effective population sizes that are applicable at any generation (other than $t = 0$). CHESSER (1991a,b) showed that with constant breeding and dispersal tactics the rates of change in gene correlations (F, θ, α) also become equal, and the F statistics attain steady-state values. When the asymptotic values of the fixation indices are acquired, the effective population numbers will likewise become asymptotic.

Asymptotic effective number: Although initial values of N_{eI} and N_{eV} (assuming stable census number) may be dramatically different, the instantaneous values of the effective sizes converge upon similar quantities when there is even slight genetic exchange among breeding groups ($d_f + d_m \neq 0$; Figure 3). The time required for convergence is dependent upon the rates of genetic exchange with low rates requiring more generations until convergence is achieved.

The asymptotic effective population size can be estimated readily using Equations 42 and 44. Assigning $D = d_m + d_f - d_m d_f$ in Equation 44, then

$$N_{e\alpha} \approx \frac{2s}{3DF_{ST}}. \tag{45}$$

At asymptote $N_{eI} \approx N_{e\alpha}$, therefore

$$\frac{2s}{3D\hat{F}_{ST}} \approx \frac{1 - \hat{F}_{IT}}{2\left[\left(1 - \left(1 - \frac{1}{s}\right)D\right)\hat{F}_{ST} - \hat{F}_{IT}\right]}. \tag{46}$$

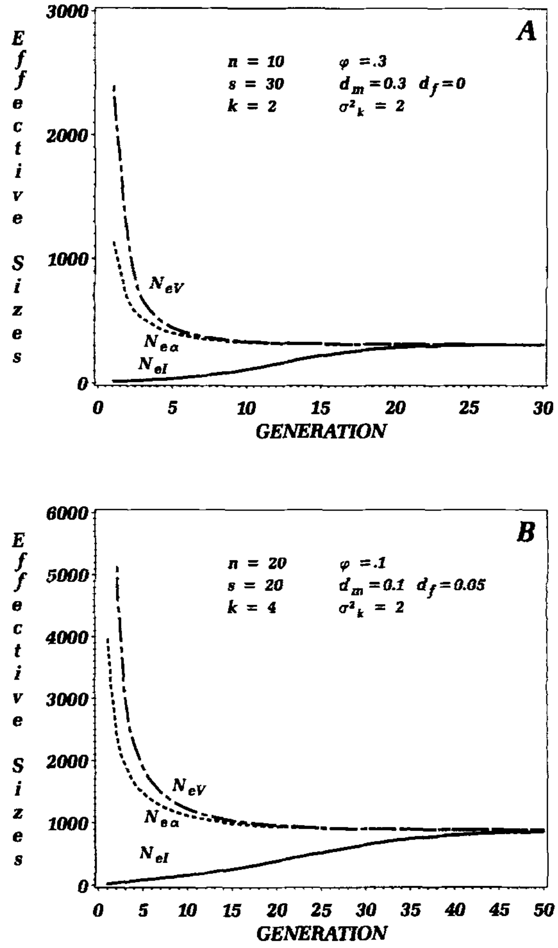

FIGURE 3.—Changes in inbreeding (N_{eI}), variance (N_{eV}), and intergroup ($N_{e\alpha}$) effective numbers over successive generations for two different breeding and dispersal scenarios. All converge on the same asymptotic value and the rate of convergence is dependent upon the rates of genetic exchange. Parameter values are explained in the text.

Solving Equation 46 for D yields

$$D = \frac{4s(\hat{F}_{ST} - \hat{F}_{IT})}{\hat{F}_{ST}(4s - 3\hat{F}_{IT} - 1)} \tag{47}$$

which when substituted into Equation 42 or 45 results in the asymptotic estimate for effective population size

$$\hat{N}_e \approx \frac{4s - 3\hat{F}_{IT} - 1}{6(\hat{F}_{ST} - \hat{F}_{IT})}. \tag{48}$$

THE ISLAND MODEL

CHESSER (1991b) showed that WRIGHT's (1969) island model did not account for variation at intrapopulational levels. CHESSER's (1991b) solutions indicated that breeding tactics may be much more important in determining genetic differentiation among breeding groups than gene flow over short geographic distances. The solution to the difference equation presented as expression (16) will result in a more complex form of the island model:

$$\hat{F} = \frac{[1 - (1 - (1/s))(d_m + d_f - d_m d_f)][2\phi_f + (\phi_m(1 - \phi_f)]}{8 - [8 - 2\phi_f - \phi_m(1 - \phi_f)][1 - (1 - (1/s))(d_m + d_f - d_m d_f)]}. \tag{49}$$

The value of F above is intended to represent the steady state value of inbreeding relative to the genetic variation remaining among groups and may not denote the value for genetic differentiation (F_{ST}) among groups as originally intended by WRIGHT (1969; see CHESSER 1991b). If there is one mate per male ($b = 1$, $\sigma_b^2 = 0$, and $m = n$), a very large number of subpopulations ($1/s \approx 0$), a constant population size ($k = 2$; $\sigma_k^2 = 0$), and equal migration rates by males and females ($d_m = d_f = d$), the result of Equation 45 will converge on WRIGHT's (1969, p. 291) original asymptotic solution

$$\hat{F} = \frac{(1 - d)^2}{2N - (2N - 1)(1 - d)^2} \tag{50}$$

as n becomes large (note that $N = 2n$). The reason that Equations 49 and 50 will not match exactly, given WRIGHT's assumptions above [as did CHESSER's (1991b) equation], is that not all progeny will have a sibling of the opposite sex as a potential mate. In WRIGHT's original derivations sex was not taken into account (random admixture of genes) and in CHESSER's (1991b) expressions each female produced a male and female offspring; thus, there was always a potential sibling mate.

If mating is not random then the island model will be biased by the accumulation of gene correlations just as were the effective sizes. Thus, Equations 49 and 50 represent overestimates of the asymptotic value of inbreeding, whereas Equations 41 and 43 are unbiased estimators of asymptotic changes in gene correlations. Rearrangement of Equation 44 presents an asymptotic estimate of the F_{ST} as

$$\hat{F}_{ST} \approx \frac{2s}{\hat{N}_{e\alpha}[3(d_m + d_f) - 2(d_m d_f)]}. \tag{51}$$

Furthermore, the total number of effective migrants per generation in the population is determined as

$$\hat{N}_{e\alpha}[3(d_m + d_f) - 2(d_m d_f)] = \frac{2s}{\hat{F}_{ST}} \tag{52}$$

and the average number of migrants per breeding group is found by dividing both sides by s (comparable to Nm of WRIGHT 1969). If dispersal is performed by only one sex ($d_m \cdot d_f = 0$), then $N_{e\alpha}d/s = 2/(3F_{ST})$ and if dispersal is performed equally by both sexes ($d_m = d_f = d$) yet is sufficiently low that terms with d^2 can be ignored (*e.g.*, WRIGHT 1969), the average number of migrants per breeding group ($N_{e\alpha}d/s$) is $1/(3F_{ST})$.

DISCUSSION

The expressions derived herein provide for the delineation of initial and instantaneous inbreeding and variance effective sizes for subdivided populations exhibiting varying degrees of isolation and with different mating tactics and progeny production. Although these equations include several parameters not found in previous derivations of N_{eI} and N_{eV} (WRIGHT 1922; CROW and KIMURA 1970; CROW and DENNISTON 1988), they permit the definition of critical values for complex population structures. Previous expressions for N_{eI} and N_{eV} were limited to single population values.

Initial effective numbers: Failure to recognize the contributions of incomplete migration (by either or both sexes) and nonrandom breeding tactics can lead to considerable bias in the estimation of inbreeding and variance effective sizes, especially in early generations. Consider, for example, a population that is organized into several breeding groups. The breeding groups may be characterized as harems for polygnous males ($\phi_m > 0$) and/or the groups may be somewhat isolated from other groups in the population ($d_m, d_f < 1$). If such groups are ignored in the determination of N_{eI}, as would be done using traditional equations, the resulting value would overestimate the inbreeding effective size. This overestimation is clearly depicted in Figure 4A, which shows the ratio of a traditionally calculated N_{eI} (CROW and KIMURA 1970, p. 351) to that of equation (18). In this particular example the traditional N_{eI} may overestimate the true value by over sixty times. The ratio of the traditional N_{eV} (CROW and KIMURA 1970, p. 359) and our expression (Equation 20) also shows a large potential bias (Figure 4B). The traditional N_{eV} is often an underestimate of the true value (ratio approaches zero). Traditional estimates have not included the potential for conservation of gene diversity among totally or partially isolated breeding groups.

Breeding tactics (ϕ_m) and migration rates (d_m, d_f) differ in their influence on the ratios for initial values of inbreeding and variance effective sizes (Figure 4). In instances of complete migration (d_m, $d_f \approx 1$), there is little bias of traditional and newly derived values of inbreeding effective size regardless of the value for ϕ_m. When migration is complete there is little or no

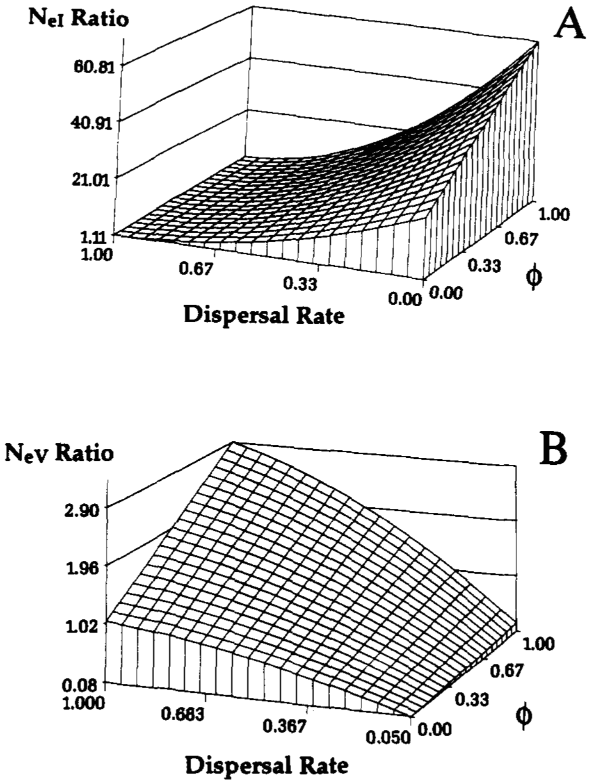

FIGURE 4.—Three dimensional diagrams depicting the influence of dispersal rate and the probability that random females within a breeding group mate with the same male (ϕ) on the ratios of traditionally calculated values for N_{eI} and N_{eV} (CROW and KIMURA 1970) to our estimates for N_{eI} (A) and $N_{e\alpha}$ (B). The graphs were generated using 5 females per breeding group, 20 breeding groups, $k = \sigma_k^2 = 2$, and $\phi = 1.0$.

partitioning of genetic variation among breeding groups; that is, the population functions as a single unit and the rate of inbreeding approaches that estimated by traditional methods. When groups become isolated (d_m, $d_f < 1$) the influence of breeding structure takes on greater importance in the calculation of N_{eI}. In contrast, the effects of breeding tactics are greater when migration rates are high if traditional N_{eV} values are compared to those derived herein. As groups become isolated, N_{eV} approaches infinity regardless of the breeding tactics employed whereas traditional values remain finite. However, if even minute levels of genetic exchange persist among groups the effective numbers for N_{eI} and N_{eV} will converge.

The expressions for N_{eI}, $N_{e\alpha}$, and N_{eV} are applicable at any hierarchical scale, including breeding groups within populations, among populations within regions, etc. As one progresses up the hierarchical scale, the effects of breeding tactics rapidly diminish (n increases while b and σ_b^2 remain fixed) yet rates of exchange (d_m and d_f) remain of paramount importance. It is important to note, however, that regardless of the scale at which calculations are made, estimates will not be accurate unless all lower hierarchical levels exhibit random exchange of genes. Discontinuities in genetic exchange lead to relatively rapid rates of inbreeding within groups yet conserve variation among groups. Thus, calculations of inbreeding and variance effective population sizes need to be determined at the lowest level at which these discontinuities take place.

The concept of effective population size can be extended to any unit for which gene correlations may accrue. The number of random breeders that are necessary to produce expected intragroup gene correlations (coancestral effective size; $N_{e\theta}$) in initial generations can be defined as

$$N_{e\theta} = \frac{4k(kn-1)}{(2-\phi)\sigma_k^2 + 2k(k-1) + \frac{mk^2}{n}[\sigma_b^2 + b(b-1)]} = \frac{4}{2\phi_f + \phi_m(1-\phi_f)} \tag{53}$$

which is derived from the nonzero second term of Equation 13. With this definition, the N_{eI} and $N_{e\alpha}$ may be restated in terms of the $N_{e\theta}$ as

$$N_{eI} = \frac{N_{e\theta}}{1 - (1 - (1/s))(d_m + d_f - d_m d_f)}$$
$$N_{e\alpha} = \frac{N_{e\theta}}{\frac{(d_m + d_f - d_m d_f)}{2s} + \frac{(kn - 1)(d_m + d_f)}{4(kns - 1)}}. \tag{54}$$

Instantaneous effective numbers: The progression of gene correlation within groups over generations is determined from Equation 10 to be

$$\theta_{t+1} = \frac{1 + F_t}{2N_{e\theta}} + \left(1 - \frac{1}{2N_{e\theta}}\right)\theta_t - \left(1 - \frac{1}{s}\right)\left[\frac{(d_m + d_f - d_m d_f)}{2} + \frac{(k^2(n - 1) - \sigma_k^2)(d_m(1 - \phi_m) + d_f)}{4k(kn - 1)}\right](\theta_t - \alpha_t). \tag{55}$$

As before, the instantaneous change in coancestry can be represented as $\Delta\theta = (\theta_{t+1} - \theta_t)/(1 - \theta_t)$, which, using Equations 10, 18, and 19, becomes

$$\Delta\theta = \frac{1 + F_{IS}}{2N_{eI}} - \frac{1 - F_{ST}}{2F_{ST}N_{e\alpha}} \tag{56}$$

noting that N_{eI} and $N_{e\alpha}$ are for initial, rather than asymptotic, effective numbers. Therefore, the instantaneous coancestral effective size ($1/2\Delta\theta$) is

$$N_{e\theta} = \frac{F_{ST}N_{eI}N_{e\alpha}}{F_{ST}N_{e\alpha}(1 + F_{IS}) - N_{eI}(1 - F_{ST})}. \tag{57}$$

The expressions derived herein document that effective population numbers cannot be expressed as constant values over the range of generations commencing with the initiation of a population unless mating is completely panmictic. Although effective sizes do eventually attain steady state values, considerable accumulation of gene correlations may be transpired prior to asymptote. Complete characterization of Equations 12 and 13 into eigenvalues and eigenvectors would enable the dynamics of gene correlations to be determined using parameter assignments rather than by resultant F statistics and parameter combinations. Such characterization is intractable unless simplifying assumptions are made. Therefore, the most feasible way to depict accurately the dynamics of all relevant gene correlations is to iterate numerically Equations 12 and 13 using a simple computer program. In this manner, the F-statistics, inbreeding coefficients, coancestry values, correlations among groups, and all effective numbers, can be precisely tracked for each generation.

The definition of effective population sizes applicable to interacting breeding groups requires greater numbers of parameters for accurate description than traditional single population applications. Many simplifying assumptions are included in our derivations such as random migration (when present) among groups, discrete nonoverlapping generations, and a relatively large ($\geq$10) number of breeding groups. It is unlikely that substantial deviations from the numerical values will result if extensions of these scenarios are made to include overlapping generations (CHOY and WEIR 1978; HILL 1979). Other methods such as migration matrices and variance in group sizes can be used to account for specific scenarios that deviate from those presented herein.

Asymptotic effective number: Our derivations of asymptotic values for variance (or intergroup) effective population numbers were not consistent with those of CABALLERO and HILL (1992b; our Equation 37). It appears that the reason for the inconsistency is because CABALLERO and HILL's (1992b) approach did not permit the incorporation of intragroup coancestry (θ). Although they used the F_{IS} to account for deviations from random mating, their application is at the population level rather than that of the breeding groups; thus, their $F_{IS} = (F - \alpha)/(1 - \alpha)$ (*e.g.*, CHESSER 1991a,b) and not $(F - \theta)/(1 - \theta)$ as defined herein (their F_{IS} is equal to the F_{IT} in this paper). Our derivations of $N_{e\alpha}$ include both the F_{ST} and the F_{IT} and therefore incorporate gene correlation values for θ, F, and α. Interestingly, our equations for N_{eI}, $N_{e\alpha}$, and N_{eV} show that knowledge of population census (N) and means and variances of progeny numbers are not required if the F statistics are known. From a theoretical perspective, however, knowledge of these parameters is necessary to derive the expected F statistics (CHESSER 1991a,b).

Nonrandom mating and migration tactics have been documented both within and among populations for a large number of taxa (SELANDER 1970; CHESSER 1983a; RYMAN *et al.* 1980) and it has long been recognized that isolation of populations may act to conserve gene frequencies while promoting inbreeding (CHESSER, SMITH and BRISBIN 1980; CHESSER 1983b). Furthermore, knowledge of gene correlation values at various levels of population organization may elucidate the evolutionary significance of different breeding and dispersal tactics (CHESSER *et al.* 1993). Despite the ubiquity of population subdivision and its importance to gene conservation and evolutionary processes, previous models for effective population size have not taken such parameters into account. Our intent, in the development of expressions for population effective sizes, is to facilitate the inclusion of complex population structures into programs for genetic conservation and evolution.

This work was supported by funds from contract (DE-AC09-765R00-819) between the Department of Energy and the University of Georgia's Savannah River Ecology Laboratory. Thanks go to I. L. BRISBIN, JR., M. H. SMITH, K. B. WILLIS and three anonymous reviewers for their helpful comments and reviews of this manuscript.

LITERATURE CITED

CABALLERO, A., and W. G. HILL, 1992a A note on the inbreeding effective population size. Evolution **46:** 1969–1972.

CABALLERO, A., and W. G. HILL, 1992b Effective size of nonrandom mating populations. Genetics **130:** 909–916.

CHESSER, R. K., 1983a Genetic variability within and among populations of the black-tailed prairie dog. Evolution **37:** 320–331.

CHESSER, R. K., 1983b Isolation by distance: Relationship to the management of genetic resources, pp. 66–77, in *Genetics and Conservation. A Reference for Managing Wild Animal and Plant Populations*, edited by C. M. SHONEWALD-COX, S. M. CHAMBERS, B. MACBRYDE and L. THOMAS. Benjamin/Cummings Publ. Co., London.

CHESSER, R. K., 1991a Gene diversity and female philopatry. Genetics **127:** 437–447.

CHESSER, R. K., 1991b Influence of gene flow and breeding tactics on gene diversity within populations. Genetics **129:** 573–583.

CHESSER, R. K., M. H. SMITH and I. L. BRISBIN, JR., 1980 Management and maintenance of genetic variability in endangered species. Int. Zoo Ybk. **20:** 146–154.

CHESSER, R. K., D. W. SUGG, O. E. RHODES, JR., J. N. NOVAK and M. H. SMITH, 1993 Evolution of mammalian social structure. Acta Theriol. (in press).

CHOY, S. C., and B. S. WEIR, 1978 Exact inbreeding coefficients in populations with overlapping generations. Genetics **89:** 591–614.

COCKERHAM, C. C., 1970 Avoidance and rate of inbreeding, pp. 104–127, in *Biomathematics, Vol. 1, Mathematical Topics in Population Genetics*, edited by K. KOJIMA. Springer-Verlag, New York.

CROW, J. F., 1954 Breeding structure of populations. II. Effective population number, pp. 543–560, in *Statistics and Mathematics in Biology*, edited by O. KEMPTHORNE, T. A. BANCROFT, J. W.

GOWEN and J. L. LUSH. Iowa State College Press, Ames.

CROW, J. F., and C. DENNISTON, 1988 Inbreeding and variance effective population numbers. Evolution **42:** 482–495.

CROW, J. F., and M. KIMURA, 1970 *An Introduction to Population Genetics Theory*. Harper & Row, New York.

EHRLICH, P. R., 1965 The population biology of the butterfly *Euphydryas editha*. II. The structure of the Jasper Ridge Colony. Evolution **19:** 327–336.

FALCONER, D. A., 1989 *Introduction to Quantitative Genetics*, Ed. 3. Longman, London.

HARRIS, R. B., and F. W. ALLENDORF, 1989 Genetically effective population size of large mammals: an assessment of estimators. Conserv. Biol. **3:** 181–191.

HILL, W. G., 1979 A note on effective population size with overlapping generations. Genetics **92:** 317–322.

KIMURA, M., and J. F. CROW, 1963 The measurement of effective population number. Evolution **17:** 279–288.

LANDE, R., and G. F. BARROWCLOUGH, 1987 Effective population size, genetic variation, and their use in population management, pp. 86–123, in *Viable Populations for Conservation*, edited by M. E. SOULE. Cambridge University Press, New York.

POLLAK, E., 1987 On the theory of partially inbreeding finite populations. I. Partial selfing. Genetics **117:** 353–360.

RYMAN, N., C. REUTERWALL, K. NYGREN and T. NYGREN 1980 Genetic variation and differentiation in Scandinavian moose (*Alces alces*): are large mammals monomorphic? Evolution **34:** 1037–1049.

SELANDER, R. K., 1970 Behavior and genetic variation in natura populations. Am. Zool. **10:** 53–66.

WOOD, J. W., 1987 The genetic demography of the Gainj of Papua New Guinea. 2. Determinants of effective population size. Am. Nat. **129:** 165–187.

WRIGHT, S., 1922 Coefficients of inbreeding and relationship Am. Nat. **56:** 330–338.

WRIGHT, S., 1969 Evolution and the genetics of populations, Vol 4, *The Theory of Gene Frequencies*. University of Chicago Press, Chicago.

Communicating editor: B. S. WEIR