Effective Population Sizes With Multiple Paternity

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ABSTRACT

While the concept of effective population size is of obvious applicability to many questions in population genetics and conservation biology, its utility has suffered due to a lack of agreement among its various formulations. Often, mathematical formulations for effective sizes apply restrictive assumptions that limit their applicability. Herein, expressions for effective sizes of populations that account for mating tactics, biases in sex ratios, and differential dispersal rates (among other parameters) are developed. Of primary interest is the influence of multiple paternity on the maintenance of genetic variation in a population. In addition to the standard inbreeding and variance effective sizes, intragroup (coancestral) and intergroup effective sizes also are developed. Expressions for effective sizes are developed for the beginning of nonrandom gene exchanges (initial effective sizes), the transition of gene correlations (instantaneous effective sizes), and the steady-state (asymptotic effective size). Results indicate that systems of mating that incorporate more than one male mate per female increase all effective sizes above those expected from polygyny and monogamy. Instantaneous and asymptotic sizes can be expressed relative to the fixation indices. The parameters presented herein can be utilized in models of effective sizes for the study of evolutionary biology and conservation genetics.

THE effective size of populations is a concept of considerable interest to population biologists because of its relationship to genetic variation and rates of inbreeding. Operationally, the effective size of a population can be defined as the size of an ideal population that would lose genetic variability, due to random processes, at the same rate as the actual population (WRIGHT 1931; LANDE and BARROWCLOUGH 1987). The concept of effective size is useful because it offers insight into future levels of genetic variability within and among groups in a population and the parameters that are important for determining rates of change in genetic variability. Genetic variability can be partitioned into several hierarchical levels, each with a corresponding effective size (CHESSER *et al.* 1993b). Population attributes such as inbreeding, dispersal, and mating tactics influence effective sizes to varying degrees at each level (CHESSER 1991a,b; CHESSER *et al.* 1993b) and play an important role in the evolution of social structures (CHESSER *et al.* 1993a).

While the concept of effective size is of obvious applicability to many questions in population and conservation biology, its utility has suffered due to a lack of agreement among its various formulations (see HARRIS and ALLENDORF 1989). Many of these problems are related to oversimplification of biological processes and restrictive assumptions. Recently, several attempts have been made to alleviate these shortcomings (CROW and DENNISTON 1988; CHESSER 1991a,b; CABALLERO and HILL 1992a,b; CHESSER *et al.* 1993b) while preserving concordance with the classical models of WRIGHT (1969) and CROW and KIMURA (1970) when the same assumptions are

made (CHESSER *et al.* 1993b). While these studies have addressed the contributions of non random mating and incomplete isolation on effective population sizes, they need to be expanded to include more breeding systems.

Traditionally, multiple paternity has been used to describe mating systems where there are multiple sires for a given brood (HASKINS *et al.* 1962; BOROWSKY and KALLMAN 1976; BOROWSKY and KHOURI 1976; LESLIE and VRIJENHOEK 1977). Herein a broader definition is used to incorporate other systems of mating that result in more than one male sire for offspring produced during the lifetime of a single female. Using this definition, multiple paternity also can be achieved through a series of broods being inseminated by different males; *i.e.*, superfetation (SCRIMSHAW 1944) or serial monogamy. Regardless of how multiple paternity is achieved, it is expected to increase the effective size beyond that expected if adults did not practice multiple paternity (LESLIE and VRIJENHOEK 1977; VRIJENHOEK 1979; CHESSER *et al.* 1984; ROBBINS *et al.* 1987). The degree to which the effective size is influenced by the number of males mating with a female has been the subject of some debate largely because generalized predictive models have not been developed. ROBBINS *et al.* (1987) presented data that suggested increased numbers of sires contributing to brood increases effective sizes, but they failed to address several alternatives. WAPLES (1987, p. 1070) argued that increased effective sizes in their system was relatively unaffected by number of sires. Until mathematical models of effective size are extended to account for multiple paternity (and other systems of mating) the relative

contributions of these factors to effective sizes will be difficult to assess, and the genetic consequences of multiple paternity will be poorly understood.

The purpose of this manuscript is to extend the equations for effective sizes presented by CHESSER (1991a,b) and CHESSER *et al.* (1993b) to include multiple paternity. The methodologies employed here can provide a guide for extensions to other systems of matings. The results of these expressions will be compared to other models, and the relative influence of several parameters will be assessed. For the sake of brevity, extensions of previous models are explained in the text while modified expressions are presented in the APPENDIX.

GENE CORRELATIONS

To determine effective sizes for subdivided populations, it is necessary to obtain expressions for three variables (COCKERHAM 1969, 1973; CHESSER 1991a,b; CHESSER *et al.* 1993b). Since there is the potential for relationships beyond full and half siblings when multiple paternity is practiced, it is necessary to rederive expressions for the following variables:

- F = correlation of genes within individuals (inbreeding coefficient).
- θ = correlation of genes for random progeny within a breeding group (coancestry).
- α = correlation of genes for random individuals from different breeding groups.

The parameters necessary to derive transition states for these variables are:

- n, m = average number of breeding females and males, respectively, within a breeding group.
- ℓ = average number of males mated by each female.
- s = number of breeding groups.
- k = average of the number of progeny produced during the lifetime of a female that survive to reproduce.
- σ_k^2 = variance in the number of progeny produced during the lifetime of a female that survive to reproduce.
- b = average of the number of females mated by each male which result in progeny that survive to reproduce.
- σ_b^2 = variance in the number of females mated by each male which result in progeny that survive to reproduce.
- p = average of the number of progeny in a brood sired by a single male.
- σ_p^2 = variance in the number of progeny in a brood sired by a single male.
- d_m, d_f = rates of migration among breeding groups for males and females, respectively.

The probability that random progeny born within a breeding group are sired by the same male is defined as $\phi_m = m[\sigma_b^2 + b(b-1)]/\ell n(n-1)$ (*cf.* CHESSER *et al.*

1993b) and $\phi_f = (\sigma_k^2 + k(k-1))/k(kn-1)$ is defined as the probability that two randomly chosen progeny in a breeding group are the offspring of a given mother (Equation 5 of CHESSER *et al.* 1993b). The parameter ϕ_m represents the degree of polygyny with values of zero indicating complete monogamy and values of one indicating all progeny in a breeding group are sired by the same male. Values for ϕ_f likewise range from zero (all progeny have different mothers) to one (all progeny have the same mother). Because multiple paternity can lead to relationships in a brood that span the range from half to full siblings (in the absence of inbreeding, average coancestry of a brood can be 0.125 or 0.25), it is necessary to define a new parameter (ϕ_w) as the probability that randomly chosen progeny within a brood are the product of the same male.

$$\phi_w = \frac{\sum_{i=1}^{\ell} p_i^2 - p_i}{k(k-1)} = \frac{\ell[\sigma_p^2 + p(p-1)]}{k(k-1)}. \quad (1)$$

Values of zero indicate that each progeny in a single brood is the product of a different male ($p=1$), and values of one indicate progeny in a brood are the product of the same male ($p=k$). Because $\ell = k/p$,

$$\phi_w = \frac{\sigma_p^2 + p(p-1)}{p(k-1)}. \quad (2)$$

To determine how gene correlations accrue, it is necessary to develop transition equations for the critical variables across generations. CHESSER (1991a; Equation 15) has shown that the expected correlation of genes among full siblings is

$$\epsilon[\theta_{\text{sibs}}]_{t+1} = \frac{1 + F_t + 2F_{t+1}}{4}, \quad (3)$$

where t references the generation. Using the parameters for probabilities of sharing parents described above, the average coancestry within breeding groups due to full siblings can be expressed as

$$\theta(\text{full})_{t+1} = \frac{\phi_f}{4} \left[\frac{1 + F_t}{2} + 2F_{t+1} + \frac{\phi_w(1 + F_t)}{2} \right], \quad (4)$$

where F refers to the inbreeding coefficient. Additional gene correlations within breeding groups can be developed for siblings that share only one parent. Using the average coancestry of parents (γ ; CHESSER 1991b; Equation A.9), the average coancestry among half siblings is

$$\begin{aligned} \theta(\text{half})_{t+1} &= \frac{\phi_f}{4} (1 - \phi_w) \gamma_t \\ &= \frac{\phi_f}{4} (1 - \phi_w) \left[\left(1 - \left(1 - \frac{kn-1}{kns-1} \right) d_m \right) \theta_t \right. \\ &\quad \left. + \left(1 - \frac{kn-1}{kns-1} \right) d_m \alpha_t \right], \end{aligned} \quad (5)$$

where θ_t and α_t are the average coancestry within breeding groups and correlation of genes among groups, respectively. Gene correlations between non-sibling progeny can be determined using the average coancestry of breeding adults ($\bar{\gamma}$; CHESSER 1991b; Equation A.10)

$$\theta(\text{nonsib})_{t+1} = (1 - \phi_p)\bar{\gamma}$$

$$= \frac{(1 - \phi_p)}{4} \left\{ \frac{\phi_m(1 + F_t)}{2} + \left(2 - \phi_m - \left(1 - \frac{kn - 1}{kns - 1} \right) (d_m(1 - \phi_m) + d_p) \right) \theta_t \right. \\ \left. + 2F_{t+1} + \left(1 - \frac{kn - 1}{kns - 1} \right) (d_m(1 - \phi_m) + d_p) \alpha_t \right\}. \quad (6)$$

Thus, the average coancestry of progeny in a breeding group (Equation A.1) can be expressed by summing Equations 4–6. CHESSER *et al.* (1993b; Equations 9 and 11) define the transitions for gene correlations within individuals (F_{t+1}) and among groups (α_{t+1}), respectively. The complete transition for coancestry is obtained by substituting the expression for F_{t+1} into Equation A.1 to yield Equation A.2. Transition equations for the gene correlations can be used to develop a transition matrix (**T**) to predict average correlations of genes at any generation t . Such a transition matrix must satisfy the requirement that $\{F_{t+1}, \theta_{t+1}, \alpha_{t+1}\} = \mathbf{T}\{F_t, \theta_t, \alpha_t\} + \mathbf{C}$ (see Equations A.3 and A.4).

EFFECTIVE POPULATION SIZES

Accurate estimates for future levels of gene corre-

sions for instantaneous effective numbers that are accurate for any generation and a single expression for the asymptotic effective size. These expressions will be compared to those obtained under the assumption of single paternity.

Initial effective sizes: A critical effective size (identi-

fied by CHESSER *et al.* 1993b) is the number of random breeders that are necessary to produce the realized loss of genetic variation within breeding groups (coancestral effective size; $N_{e\theta}$). This parameter, expressed in terms of coancestry, is $\theta_{t+1} = 1/2N_{e\theta} + [1 - 1/2N_{e\theta}]\theta_t$ (*i.e.*, CROW and KIMURA 1970), where θ_{t+1} corresponds to the portion of coancestry influenced by gene correlations among individuals within breeding groups (COCKERHAM 1969, 1973; CHESSER 1991a,b). If it is assumed that contributions to θ_{t+1} by F and α are negligible (a good assumption for the first few generations), then the middle row of the transition matrix **T** (Equation A.3) becomes $\{0, 1 - (1/2N_{e\theta}), 0\}$, and the middle element of the vector **C** (Equation A.4) is $1/2N_{e\theta}$. Thus, $1/2N_{e\theta} = (\phi_f(1 + \phi_w) + (1 - \phi_p)\phi_m)/8$ and solving for the coancestral effective size

$$N_{e\theta} \cong \frac{4}{\phi_f(1 + \phi_w) + (1 - \phi_p)\phi_m} \\ = \frac{4k(kn - 1)}{(\sigma_k^2 + k(k - 1)) \left[1 + \frac{\sigma_p^2 + p(p - 1)}{p(k - 1)} \right] + [k(kn - 1) - \sigma_k^2 - k(k - 1)] \frac{m(\sigma_b^2 + b(b - 1))}{\ell n(n - 1)}}. \quad (7)$$

lations can be obtained with two methodologies; by iteration of the transition matrix (**T**; Equations A.3 and A.4), or by solving the transition matrix for eigenvalues. The former method is preferred because of the large and cumbersome expressions resulting from the eigenvalue solutions. However, good approximation for gene correlations can be obtained for short intervals of time by approximation of the eigenvalue solutions. We will derive expressions for effective sizes in the three stages described by CHESSER *et al.* (1993b). First, the initial effective sizes will be presented and results will be compared to formulas derived for single isolated populations with random mating and for subdivided populations with nonrandom mating and single paternity. Subsequently, we will derive expres-

Note that when all of the progeny of a brood are the product of a single male ($\phi_w = 1$), this expression reduces to that presented by CHESSER *et al.* (1993b; Equation 53) which assumes single paternity. It can readily be seen in Figure 1 that the effective size with multiple paternity ($N_{e\theta}$) is always as great or greater than the effective size based on the expression in CHESSER *et al.* (1993b; $N'_{e\theta}$). At its maximum value, the effective size with multiple paternity is twice that expected with single paternity.

The denominator in equations for coancestral effective size can be simplified by accounting for variance in the number of progeny as in traditional expressions for effective sizes (*cf.* CROW and DENNISTON 1988). CHESSER *et al.* (1993b; Equation 25) have given the variance in

FIGURE 1.—Three-dimensional surface plots for the ratio of coancestral effective sizes with ($N_{e\theta}$; Equation 7) and without ($N'_{e\theta}$; CHESSEY *et al.* 1993b) multiple paternity. In each plot, ratios greater than one indicate conditions under which expressions that account for multiple paternity result in coancestral effective size greater than that expected from systems that involve only one male mate. Plot A depicts the relative increase in effective size expected with changing probability that progeny within a brood are the product of the same male (ϕ_w) as a function of the probability that progeny in a breeding group share the same sire (ϕ_m). Plot B depicts the relative increase in effective size expected with changing probability that progeny within a brood are the product of the same male (ϕ_w) as a function of the probability that progeny in a breeding group share the same mother (ϕ_f). Note that $\phi_w = 1$ for the model presented by CHESSEY *et al.* (1993b).

the number of progeny produced by all breeding individuals when the covariance in male and female progeny number is negligible (see also CROW and DENNISTON 1988). The relationship between total variation in progeny numbers and effective sizes can be shown to hold for systems of mating that involve multiple paternity, specifically

$$\sigma_{kT}^2 = (1 + \phi_w)\sigma_k^2 - \phi_m[\sigma_k^2 - k^2(n-1)]. \quad (8)$$

Inspection of Equation 8 and Equation 25 of CHESSEY *et al.* (1993b) reveal that part of the total variation that had been attributed to males by CHESSEY *et al.* (1993b) is no longer simply a function of the variation in progeny of females (σ_k^2), but it is now also a function of the number of sires of a brood ($\phi_w\sigma_k^2$). Assuming that there is no multiple paternity ($\phi_w = 1$), Equations 8 and (25 of CHESSEY *et al.* 1993b) are equivalent. Util-

izing Equation 8, the initial coancestral effective size can be expressed as

$$N_{e\theta} = \frac{4k(kn-1)}{\sigma_{kT}^2 + (1 + \phi_w)k(k-1)}. \quad (9)$$

The equations for initial effective sizes can be compared to those of CROW and DENNISTON (1988) by utilizing their assumptions. Because CROW and DENNISTON's model deals with only one population, there is only one breeding group ($s = 1$), and dispersal is complete for both sexes ($d_m = d_f = 1$). Also, assuming that all males mate ($m = n$, $b = 1$, and $\sigma_b^2 = 0$), ϕ_m will be zero and the total variance in progeny number becomes

$$\sigma_{kT}^2 = (1 + \phi_w)\sigma_k^2 = \left(1 + \frac{\sigma_p^2 + p(p-1)}{p(k-1)}\right)\sigma_k^2. \quad (10)$$

These are not the only conditions under which ϕ_m will be zero (see CHESSEY *et al.* 1993b), but are used simply for illustrative purposes. When there is random union of gametes, then $p = 1$, $\sigma_p^2 = 0$ and $\sigma_{kT}^2 = \sigma_k^2$. However, if each female mates with only one male, then $p = k$, $\sigma_p^2 = 0$ and the total variance in progeny number reduces to $\sigma_{kT}^2 = 2\sigma_k^2$. In the case of random union of gametes, and remembering that $2n = N$ (total population size), the effective size becomes

$$N_{e\theta} = \frac{4k(kn-1)}{\sigma_k^2 + k(k-1)} = 2 \frac{k(kN-2)}{\sigma_k^2 + k(k-1)}, \quad (11)$$

which is twice the inbreeding effective size given by CROW and DENNISTON (1988) and coancestral effective size given by CHESSEY *et al.* (1993b), the same result obtained for Equation 7. Additionally, when there is only one mate per female, the effective size becomes

$$N_e = \frac{2k(kn-1)}{\sigma_k^2 + k(k-1)} = \frac{k(kN-2)}{\sigma_k^2 + k(k-1)}, \quad (12)$$

identical to the values presented by CROW and DENNISTON (1988) and CHESSEY *et al.* (1993b), as expected.

Initial inbreeding (N_{ei}) and intergroup (N_{ea}) effective sizes can be derived in a manner similar to coancestral effective size, or they can be expressed in terms of $N_{e\theta}$ (CHESSEY *et al.* 1993b). The inbreeding effective size determines the rate of accumulation of gene correlations within individuals (inbreeding) and can be expressed as

$$N_{ei} \cong \frac{4k(kn-1)}{[\sigma_{kT}^2 + (1 + \phi_w)k(k-1)] \times [1 - (1 - 1/s)(d_m + d_f - d_m d_f)]} \\ = \frac{N_{e\theta}}{1 - (1 - 1/s)(d_m + d_f - d_m d_f)}. \quad (13)$$

Likewise, the intergroup effective size determines the rate of accumulation of gene correlations among

individuals from different groups

$$N_{ea} \cong 4k(kn - 1) \left/ \left\{ [\sigma_{kT}^2 + (1 + \phi_w)k(k - 1)] \right. \right. \\ \times \left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(kn - 1)(d_m + d_f)}{4(kns - 1)} \right] \left. \right\} \\ = \frac{N_{e\theta}}{\frac{d_m + d_f - d_m d_f}{2s} + \frac{(kn - 1)(d_m + d_f)}{4(kns - 1)}}. \quad (14)$$

Low dispersal rates for either sex lead to low inbreeding effective size (and thus, rapid rates of inbreeding), when compared to intergroup effective size. Increasing the dispersal rate will increase the inbreeding effective size; however, the gene diversity conserved within breeding groups can never be greater than that among groups in structured populations. If dispersal is complete in both sexes ($d_m = d_f = 1$), then N_{ei} will approach the value of N_{ea} with increasing values of ns (see also CHESSER *et al.* 1993b).

The expression for N_{ea} is similar to the variance effective size (N_{ev}) defined by CHESSER (1991b); however, these effective sizes are equivalent only under certain conditions. Because N_{ev} depends on the number of progeny, while N_{ea} depends on the number of parents (CROW and KIMURA 1970), changing population size will lead to deviations in the respective effective sizes. By assuming that the sex ratio of breeding individuals (m/n) is constant over generations, even with changing population size, the ratio can be expressed as $R/(1 - R)$. Substituting $R/(1 - R)$ for $m/\ell n$ and $nk(1 - R)$ for n in Equation 14 gives the variance effective size

$$N_{ev} \cong \frac{4}{\left[\frac{\sigma_k^2 + k(k - 1)}{k(k^2 n(1 - R) - 1)} \left(1 + \frac{\sigma_p^2 + p(p - 1)}{p(k - 1)} \right) + \left(1 - \frac{\sigma_k^2 + k(k - 1)}{k(k^2 n(1 - R) - 1)} \right) \left(\frac{R(\sigma_s^2 + b(b - 1))}{(1 - R)(kn(1 - R) - 1)} \right) \right] \left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(k^2 n(1 - R) - 1)(d_m + d_f)}{4(k^2 n(1 - R)s - 1)} \right]} \\ = \frac{4k[k^2 n(1 - R) - 1]}{[\sigma_{kT}^2 + (1 + \phi_w)k(k - 1)] \left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(k^2 n(1 - R) - 1)(d_m + d_f)}{4(k^2 n(1 - R)s - 1)} \right]}. \quad (15)$$

When the population census is constant and sex ratios are even, N_{ev} will equal N_{ea} . Alternatively, if population size is increasing or decreasing, N_{ev} may be considerably greater than or less than N_{ea} , respectively with single and multiple paternity.

Instantaneous effective size: While equations for effective sizes presented thus far provide reasonable approximations for a few generations after gene correlation start to accrue, they can deviate considerably from true values because the contributions of inbreeding (F) and intergroup (α) correlations become increasingly important. CABALLERO and HILL (1992b; Equation 10) derived a value for the asymptotic effective size which is obtained after several generations of consistent mating tactics with F_{IS} representing the within-group inbreed-

ing coefficient of WRIGHT (1969). Their model does not explicitly define breeding groups and dispersal rates and, for this reason, does not account for all gene correlations (see CHESSER *et al.* 1993b). To determine instantaneous effective sizes, one must first determine the rates of change for all gene correlations. FALCONER (1989) has shown that the rate of change in inbreeding is

$$\Delta F = \frac{F_{t+1} - F_t}{1 - F_t}. \quad (16)$$

By substituting Equation 9 of CHESSER *et al.* (1993b) for F_{t+1} , Equation 16 becomes

$$\Delta F = \frac{\theta_t - F_t - (\theta_t - \alpha)(1 - 1/s)(d_m + d_f - d_m d_f)}{1 - F_t}, \quad (17)$$

which accounts for gene correlations within individuals (F), among individuals within groups (θ) and among individuals from different groups (α). Definitions of the F statistics (COCKERHAM 1973)

$$F_{ST(\theta)} = \frac{\theta_t - \alpha_t}{1 - \alpha_t} \quad F_{IT(\theta)} = \frac{F_t - \alpha_t}{1 - \alpha_t}. \quad (18)$$

can be substituted into Equation 17 to yield

$$\Delta F = \frac{[1 - (1 - 1/s)(d_m + d_f - d_m d_f)]F_{ST} - F_{IT}}{1 - F_{IT}}, \quad (19)$$

where the subscripts I , S and T refer to individuals, breeding groups and the entire population, respectively. Because $N_{ei} = 1/(2\Delta F)$, the instantaneous inbreeding-effective size can be expressed as

$$N_{ei} = \frac{1 - F_{IT}}{2[(1 - (1 - 1/s)(d_m + d_f - d_m d_f))F_{ST} - F_{IT}]}. \quad (20)$$

A similar representation of the intergroup-effective size can be developed substituting Equation 11 of CHESSER *et al.* (1993b) and the F statistics into $\Delta\alpha = (\alpha_{t+1} - \alpha_t)/(1 - \alpha_t)$ and solving for

$$N_{ea} = \frac{1}{2F_{ST} \left[\frac{d_m + d_f - d_m d_f}{2s} + \frac{(kn - 1)(d_m + d_f)}{4(kns - 1)} \right]} \\ \cong \frac{2s}{F_{ST}[3(d_m + d_f) - 2d_m d_f]}. \quad (21)$$

When the population size is stable ($k = 2$), then $N_{ea} =$

N_{ev} . Note that the breeding parameters and variance in progeny number are absent from Equations 20 and 21, although all are necessary for determining the values of the F statistics. Although these expressions (20 and 21) are identical to those derived in CHESSEY *et al.* (1993b), their values will not be identical when multiple paternity is evident ($\phi_w > 0$). These expressions yield exact fits to values obtained by iterating the transition matrix (T ; equations A.3 and A.4). Iteration of the transition matrix or Equations 20 and 21 has the advantage of determining effective sizes at any time t after gene correlations have begun to accrue, while the methodologies presented in Equations 13 and 14 yield only initial values ($F \cong \alpha \cong 0$).

Asymptotic effective size: As has been shown by CHESSEY *et al.* (1993b; see also CABALLERO and HILL 1992a), subsequent to several generations all effective sizes converge on the same asymptotic value. The rate at which effective sizes approach asymptotic values (denoted by a "hat") is largely dependent upon dispersal rates. Figure 2 shows two situations that differ only in dispersal rates. It is readily seen that an increase in dispersal ($D = d_m + d_f - d_m d_f$) from 0.19 (Figure 2A) to 0.285 (Figure 2B) decreases the time to asymptote by 11 generations. In general, the change in time to reach asymptote can be expressed as $\Delta T = 2/(3 - \Delta D)$, provided breeding and dispersal tactics remain constant (see also CHESSEY *et al.* 1993b).

Given the above dependence upon dispersal rate, the asymptotic effective size can be estimated by substituting D into Equation 21

$$N_{ea} \cong \frac{2s}{3DF_{ST}} \quad (22)$$

because the contribution of $d_m d_f$ is negligible for large s . At asymptote $N_{ei} \cong N_{ea}$, therefore Equations 20 and 22 should also be approximately equal

$$\frac{2s}{3D\hat{F}_{ST}} \cong \frac{1 - \hat{F}_{IT}}{2[(1 - (1 - 1/s)D)\hat{F}_{ST} - \hat{F}_{IT}]}, \quad (23)$$

and solving Equation 23 for D will yield

$$D \cong \frac{4s(\hat{F}_{ST} - \hat{F}_{IT})}{\hat{F}_{ST}(4s - 3\hat{F}_{IT} - 1)}. \quad (24)$$

The expression for dispersal can be substituted into either equation for instantaneous size (Equations 20 or 22) to solve for the asymptotic effective size

$$\hat{N}_e \cong \frac{4s - 3\hat{F}_{IT} - 1}{6(\hat{F}_{ST} - \hat{F}_{IT})}, \quad (25)$$

which is identical to the solution obtained by CHESSEY *et al.* (1993b; Equation 48). The reason that these expressions are identical is because the influence of breeding tactics, such as multiple paternity and polygyny, on gene correlations is subsumed in the fixation indices. A word of caution is needed in that the F statistics should

FIGURE 2.—Inbreeding (N_{ei} , solid lines) and intergroup (N_{ea} , dashed lines) effective sizes from the generation when gene correlations begin to accrue until asymptotic values are obtained. In both plots, values of $k = \sigma_k^2 = 2$, $n = s = 20$, $\phi_m = 0.3$, and $\phi_w = 0.5$ were used. In plot A, dispersal rate was 0.19 with $d_m = d_f = 0.1$. In plot B this rate was increased by 50% to 0.285 with all dispersal due to males ($d_f = 0$). Comparing these plots show that the change in time to asymptote is decreased by $-2/(3\Delta D)$, where $D = d_m + d_f - d_m d_f$.

be applied to the lowest levels at which gene correlations begin to accrue. Sampling regimes which combine breeding groups will incorrectly estimate θ leading to biased estimates for F_{ST} and F_{IS} . In general, the asymptotic estimate of effective size (and instantaneous effective sizes based on Equations 20 and 21) will be applicable only when $F_{IT} < F_{ST}$ and $F_{IS} < 0$ as would be expected if breeding groups are accurately defined (see also COCKERHAM 1973).

As with initial and instantaneous effective sizes, asymptotic sizes are larger with more than one sire per brood. In the case of random union of gametes (Figure 3; $\phi_m = 0$), effective sizes with multiple paternity are initially twice as large as effective sizes with only one sire per brood; however, at asymptote they are only 1.92 times as large. When the probability that random progeny within a breeding group are sired by the same male (ϕ_m) increases, then the difference in effective sizes is correspondingly decreased (Figure 3; $\phi_m = 1.0$); however

FIGURE 3.—Ratio of effective size when $\phi_w = 0$ (no progeny in a brood sharing a sire) to effective size when $\phi_w = 1$ (all progeny in a brood sharing the same sire). In each plot solid lines represent inbreeding effective sizes (N_{ei}) and dashed lines represent intergroup effective sizes (N_{ea}). Values of $k = \sigma_k^2 = 2$, $n = s = 20$, and $d_m = d_f = 0.1$ were used for each plot. Effective sizes with multiple paternity are always greater than with single sires of broods (ratios greater than 1). Although initial effective sizes start at the theoretical maximum for a given breeding system, asymptotic values are lower. In the case of all males in a breeding group mating, effective sizes are nearly double with multiple paternity. When the number of mating males decreases, the difference in effective sizes for multiple and single paternity are decreased.

the asymptotic difference is always less than the initial difference.

DISCUSSION

Traditional expressions for N_{ei} and N_{ev} (e.g., WRIGHT 1922; CROW and KIMURA 1970) have employed assumptions that restrict the application of these concepts to isolated populations that practice random mating. The expressions presented herein provide the basis for estimating the loss of genetic variation within and among breeding groups in subdivided populations exhibiting different dispersal regimes, mating tactics, and brood sizes. CHESSER *et al.* (1993b) have shown that failure to take such population level parameters into account can lead to overestimates (in the case of N_{ei}) or underestimates (in the case of N_{ev}) of the true effective sizes. Given the degree to which effective sizes are affected by polygyny, the influence of multiple paternity is of obvious importance.

It has been suggested that the number of progeny produced is a more important for the maintenance of genetic variation than the number of male mates per female (WAPLES 1987). The relative contribution of brood size (k) and the number of males mated per female (ℓ) to effective sizes can be visualized by determining the partial derivatives for equations of initial effective size with respect to ℓ and k and examining their ratios with changing values of k and ℓ . Increasing the number of males mated per female will not be more

FIGURE 4.—Three-dimensional surface plot depicting the relative importance of changing the number of surviving offspring (k) and the average number of males mated by each female (ℓ). Plot A represents the ratio $(\partial N_{ei}/\partial \ell)/(\partial N_{ei}/\partial k)$ with values less than -1 indicating that changes in ℓ results in faster changes in inbreeding effective size. Plot B represents the ratio $(\partial N_{ev}/\partial \ell)/(\partial N_{ev}/\partial k)$ with values less than -1 indicating the same outcome as for plot A. Necessary parameters for both plots were defined as $b = \sigma_b^2 = 1$, $d_m = d_f = 0.25$, $k = \sigma_k^2$, $m = n = 15$, $p = 2$, $\sigma_p^2 = 0$, and $s = 20$. These figures show that changing k always results in more rapid changes in inbreeding effective size than does changing ℓ ; however, this is not the case for variance effective size. The missing area on the surface of each plot represents impossible values for the independent variables.

important than changing the number of surviving offspring for initial N_{ei} (ratio is never less than -1 for reasonable values of k , Figure 4A). Increasing ℓ is more important than increasing k for initial variance effective size increases when brood sizes are greater than three (Figure 4B); however, this effect is asymptotic as noted by WAPLES (1987).

The relative contributions of progeny number (k) and multiple paternity (ℓ) discussed above are dependent on values for the variances of these parameters. Obviously, if the variance in k is zero, then the change of N_{ei} relative to the change in k will likewise be essentially zero, especially if n is large. Because a Poisson distribution of progeny numbers is commonly assumed (see CROW and KIMURA 1970) changes in k will result in a concomitant change in σ_k^2 . Such an assumption is not reasonable for the number of progeny in a brood sharing a sire (p) because male contributions within broods

is often a fixed tactic (*i.e.*, $\sigma_p^2 = 0$). When both variances are assumed to be zero, the relative contributions of multiple paternity to N_{ef} are always greater than those attributable to changes in progeny number; however, the relative contributions to N_{ef} remain unchanged. In situations where there are limits on increasing k , then breeding tactics that increase the number of male mates will decrease rates of loss of genetic variation.

Initial and asymptotic effective sizes differ in two regards. In the case of variance and intergroup effective sizes, the initial values are always greater than the asymptotic values. The opposite condition holds for inbreeding and coancestral effective size. Also, all effective sizes have identical values at asymptote, but they can differ considerably when gene correlations begin to accrue. The reason that initial values are dissimilar is that gene correlations are accruing at different rates within individuals, within breeding groups, and among breeding groups. With consistent breeding tactics and dispersal regimes, the rate of change in gene correlations become equivalent and WRIGHT's (1969) F statistics become asymptotic (see CHESSEY 1991a,b). The rate at which the asymptote is reached depends on the effective number of migrants, which in turn depends on proportions of males and females dispersing and their relative contributions to the variance in progeny numbers. Both initial and asymptotic effective sizes have utility in population genetics; however, the instantaneous effective sizes are likely to be most valuable when either contributions to variance in progeny numbers and dispersal rates vary.

Multiple paternity can have great consequences for both the initial and asymptotic effective sizes. Equations 11 and 12 show unequivocally that initial effective sizes are twice as large with multiple paternity, as is expected for single paternity. As gene correlations continue to accrue, this difference is reduced, and, at asymptote, only systems of mating that result in random union of gametes maintain an effective size nearly double that expected with single paternity (Figure 3). As the number of males actually mating decreases, the impact of multiple paternity decreases, as would be expected.

The results presented herein show that breeding structure can have great impacts on gene diversity in natural and captive populations. Increasing the number of males that contribute to the gene pool obviously increases all of the effective sizes, although the relationship is asymptotic. Breeding tactics that maximize the numbers of males mating preserve the maximum amounts of gene diversity at all levels, and, therefore, provide the means for greater adjustments to environmental change. The ability to double effective sizes is unrealistic for organisms that are unable to mate with more than one male during a breeding season; however, when generation times allow multiple breeding seasons, significant increases in effective sizes can be achieved. Because all effective sizes are identical at asymptote, then captive breeding programs that argue for maintenance of genetic diversity either within or among breeding groups are moot if mating tactics and dispersal regimes are held constant.

It is clear from the expressions presented herein that all aspects of the natural history of species play an important role in the fate of gene diversity within and among populations. Traditional models of effective population sizes have had limited capacity for incorporating the complexity of various breeding tactics and dispersal regimes into their formulations. The expressions presented herein demonstrate that multiple paternity, as well as other mating schemes, can be a crucial determinant of rates of change in gene diversity and inbreeding in natural populations. These parameters can now be readily incorporated into predictive models of effective sizes for the study of evolutionary biology and conservation genetics.

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APPENDIX

Transition equations for coancestry with multiple paternity: Equation A1 represents the summation of Equations 4-6 from the text, and Equation A2 expands the expression to include equations for the transition of inbreeding from Chesser *et al.* (1993b; Equation 9).

$$\theta_{t+1} = \frac{\phi_f}{4} \left\{ \frac{1+F_t}{2} + 2F_{t+1} + \frac{\phi_w(1+F_t)}{2} + (1-\phi_w) \left[\left(1 - \left(1 - \frac{kn-1}{kns-1} \right) d_m \right) \theta_t + \left(1 - \frac{kn-1}{kns-1} \right) d_m \alpha_t \right] \right\} \quad (A1)$$

$$+ \frac{(1-\phi_f)}{4} \left\{ \frac{\phi_m(1+F_t)}{2} + \left[2 - \phi_m - \left(1 - \frac{kn-1}{kns-1} \right) (d_m(1-\phi_m) + d_f) \right] \theta_t + 2F_{t+1} + \left(1 - \frac{kn-1}{kns-1} \right) (d_m(1-\phi_m) + d_f) \alpha_t \right\}$$

$$\theta_{t+1} = \frac{\phi_f(1+\phi_w) + (1-\phi_f)\phi_m}{8} (1+F_t) \quad (A2)$$

$$+ \frac{2 \left(1 - \left(1 - \frac{1}{s} \right) (d_m + d_f - d_m d_f) \right) + \phi_f(1-\phi_w) \left(1 - \left(1 - \frac{kn-1}{kns-1} \right) d_m \right) + (1-\phi_f) \left[2 - \phi_m - \left(1 - \frac{kn-1}{kns-1} \right) (d_m(1-\phi_m) + d_f) \right]}{4} \theta_t$$

$$+ \frac{2 \left(1 - \frac{1}{s} \right) (d_m + d_f - d_m d_f) + (1-\phi_w) \left(1 - \frac{kn-1}{kns-1} \right) d_m + (1-\phi_f) \left(1 - \frac{kn-1}{kns-1} \right) (d_m(1-\phi_m) + d_f)}{4} \alpha_t$$

Transition matrix used in determination of long-term effective population sizes: Exact solutions for gene correlations at any time can be obtained by iteration of the matrix **T** (Equation A.3) where $A = (kn - 1)/(kns - 1)$ and $D = d_m + d_f - d_m d_f$.

$$T = \begin{bmatrix} 0 & \frac{1 - (1 - 1/s)D}{4} & \frac{(1 - 1/s)D}{4} \\ \frac{\phi_f(1+\phi_w) + (1-\phi_f)\phi_m}{8} & \frac{2(1 - (1 - 1/s)D) + \phi_f(1-\phi_w)(1 - (1-A)d_m) + [2 - \phi_m - (1-A)(d_m(1-\phi_m) + d_f)]}{4} & \frac{2(1 - 1/s)D + \phi_f(1-\phi_w)(1-A)d_m + (1-\phi_f)(d_m(1-\phi_m) + d_f)}{4} \\ 0 & \frac{2(D/s) + A(d_m + d_f)}{4} & 1 - \frac{2(D/s) + A(d_m + d_f)}{4} \end{bmatrix} \quad (A3)$$

For the transition equations to be complete, a constant vector (Equation A.4) must be added such that

$$\{F_{t+1}, \theta_{t+1}, \alpha_{t+1}\} = \mathbf{T}\{F_t, \theta_t, \alpha_t\} + \mathbf{C}, \quad \text{with } \mathbf{C} = \begin{bmatrix} 0 \\ \frac{\phi_f(1+\phi_w) + (1-\phi_f)\phi_m}{8} \\ 0 \end{bmatrix} \quad (A4)$$