Gene Diversity and Female Philopatry

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ABSTRACT

The effect of female philopatry on the apportionment of gene diversity within a population is evaluated. Even with random mate selection, the apportionment of gene diversity within and among social lineages (groups of related females) is inherently different than in classically defined demic groups. Considerable excess heterozygosity occurs within lineages without substantial changes in total or population heterozygosity. The proportion of genetic variance among lineages within the population was dependent on the lineage size and the number of male breeders per lineage. The greatest genetic differentiation among lineages was evident when there was one polygynous male breeding within a lineage of philopatric females, a common breeding tactic in mammalian social systems. The fixation indices depicting the genetic structure of the population were found to attain constant values after the first few generations despite the continuous loss of gene diversity within the population by genetic drift. Additionally, the change of gene correlations within individuals relative to the change within the population attains a state of dynamic equilibrium, as do the changes of gene correlations within lineages relative to the total and within individuals relative to within lineages. Comparisons of coancestries and fixation indices for philopatric versus randomly dispersing females indicate that philopatry and polygyny have probably not evolved independently and that promotion of gene correlations among adults rather than offspring has been of primary importance.

BEHAVIORAL modifications of the distributions of genes and genotypes within natural populations have been well documented (BUETTNER-JANUSCH and OLIVIER 1970; SELANDER 1970; NEEL and WARD 1972; SCHWARTZ and ARMITAGE 1980; CHESSER 1983; FOLTZ and HOOGLAND 1983). Theoretically, organization of populations into identifiable breeding units results in greater genetic heterogeneity among groups and a concomitantly lower variation within groups than had random mating prevailed (WAHLUND 1928). This organization of genetic variation would promote social interactions and cooperation within breeding groups to a greater magnitude than among them (HAMILTON 1964a,b). However, several investigators (SELANDER 1970; NEEL and WARD 1972; SCHWARTZ and ARMITAGE 1980; FOLTZ and HOOGLAND 1983) have documented greater than expected heterozygosity within breeding groups, and typically have attributed this result to an active avoidance of consanguineous matings (SCHWARTZ and ARMITAGE 1980; FOLTZ and HOOGLAND 1983; MELNICK, PEARL and RICHARD 1984). These findings seemingly cast doubt on the efficacy of behaviorally segregated populations in maintaining the integrity of cooperative groups of related individuals.

Since their inception, the fixation indices (WRIGHT 1943, 1951, 1969) have been used to interpret the breeding structure of populations. The F_{ST} has been used as a measure of population divergence or the relative magnitude of progression towards fixation of alternative alleles. Likewise, divergence from random mating within (F_{IS}) and among (F_{IT}) the breeding groups has traditionally been evaluated by fixation indices. The expectations of these models have been logically derived from the predicted genetic variance within and among partially or wholly segregated demes. Given the classical components of genetic variation, subpopulations which freely exchange breeding individuals should be characterized by $F_{ST} = F_{IT} = F_{IS} = 0$, given infinitely sized populations and random breeding within groups. Deviations from these expected values in the direction of excess heterozygosity (negative F_{IT} and F_{IS} values) have led various authors to conclude a prevalence of outcrossing in socially structured populations (SCHWARTZ and ARMITAGE 1980; FOLTZ and HOOGLAND 1983).

The distribution of genotypic proportions within a single socially structured population may not be equal to those expected from the classic "demic" models for the fixation indices. One type of social structure is maintained by philopatry of one sex and high rates of exchange of the opposing sex among social lineages (GREENWOOD 1980). In social mammals females are typically philopatric whereas in birds females represent the dispersing sex. PROUT (1981) demonstrated that excess heterozygosity may be expected for pop-

ulations which are characterized by predominant dispersal of one sex. A concordant result was found by NEEL and WARD (1972) in studies of the genetic distributions of Amerindian tribes. However, the components of variance in Prout's models, as well as those classically used in the computation of the fixation indices (ROTHMAN, SING and TEMPLETON 1974; NEI 1977; WRIGHT 1978; NEI and CHESSER 1983) and kinship (MALECOT 1969; MORTON *et al.* 1971; LALOUEL and MORTON 1973), may not be directly applicable to populations which are characterized by social organization. The purpose of this paper is to determine the role of female philopatry and male polygyny in partitioning the genetic variation within populations and how such partitioning may differ from traditional demic models.

SOCIAL *VS* DEMIC STRUCTURES

There are some fundamental aspects of social structure which must be clearly understood to differentiate between demic models and those introduced herein. Demes are classically considered to be panmictically breeding subunits (MAYR 1963; DOBZHANSKY 1970; SHIELDS 1987) that are relatively isolated (MAYR 1963; HARTL 1980), in regards to breeding and dispersal tactics, from other such demes. Social units of a population for most species cannot be construed as equivalent to demes. Rather, social units may merely represent areas of a single population wherein a number of related individuals (usually of one sex) remain philopatric. Site fidelity, however, is not really necessary as long the kin remain cohesive in their breeding and dispersal characteristics; in other words, the social units may be mobile and not confined to any particular geographic area. Philopatry, in this paper will refer to absolute faithfulness to the native unit and not to a distribution of dispersal distances (see SHIELDS 1983). Breeding among natives of a social unit may seldom occur, and in fact may be actively prohibited (GREENWOOD 1980). Thus, the social units actually represent family lineages maintained by the fidelity of related individuals; therefore, I will hereafter refer to such units as social *lineages*.

A simple example is provided by a common mammalian breeding system (GREENWOOD 1980). Lineages may be comprised of philopatric females all of which are bred by a single polygynous male. All female offspring born within the lineage remain faithful to the group (are philopatric) whereas all males disperse and may be randomly selected as breeders in other, or perhaps by chance in their own, lineages. Because there is but one male breeder in each lineage, all offspring born within are at least half siblings. The social lineages can therefore be represented by predictable genealogies which are regular and repeating over generations.

There is a major difference in the effects of genetic drift for demic and socially structured populations. Drift within isolated demes results in the divergence in gene frequencies among demes. If there is a large number of demes, each undergoing random drift, then drift will not change the total amount of genetic variance for the array of demes (because drift is a random process). The proportion of the original genetic variance within isolated demes decreases with a concomitant increase in the variance among demes. Thus, the genetic variance simply is rearranged among the constituent components. However, in a single, socially structured population with genetic exchange of mates among lineages, drift will lead to a loss of genetic variance available to all social lineages. The loss of original genetic variance leads to an unavoidable correlation among lineages over successive generations. Thus, drift *within* a population causes social lineages to become more similar rather than more divergent. Obviously, gene flow among demes would counter rates of differentiation and may cause demes to approach fixation for the same gene, a scenario analogous to that for social structure.

Normally, the consanguinity of the parents becomes the inbreeding coefficient of the offspring (JACQUARD 1974); however, as will become apparent below, the parents may bestow considerable relatedness to offspring without likewise conveying inbreeding. Henceforth, the primary focus will be on the apportionment of genetic variance for neutral genes among social lineages within a single population.

PARAMETER DEFINITIONS AND FIXATION INDICES

It will be necessary to determine the gene correlation, or coancestry (COCKERHAM 1967, 1969, 1973) for parents and offspring within and among lineages within the population. I will use the following symbols to represent the coancestries:

φ = coancestry of parents of different lineages
α = coancestry of random offspring of different lineages
γ = coancestry of parents in the same lineage
θ = coancestry of random offspring in the same lineage
F = coancestry of genes within random individuals.

Additionally, I define the following constants:

n = number of females in each lineage
s = the number of lineages in the population
m = number of breeding males per lineage
b_i = the number of females in a lineage bred by the ith male.

It is assumed adult females are replaced by their female progeny within lineages each generation. Thus, females are considered as philopatric. Males, however, disperse randomly within the population.

When more than one male breeds within a lineage it will be necessary to determine the probability that pairs of females have mated with the same male. The number of unordered pairs of females within a lineage is $(n^2 - n)/2$. Thus, the probability that females have selected the same male with which to breed is

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

The parameters, variables, constants, and probabilities defined above will be used to derive the transitions of gene correlations over successive generations.

COCKERHAM (1973) defined the fixation indices as

$$F_{ST} = \frac{\theta_w - \theta_g}{1 - \theta_g}; \quad F_{IS} = \frac{F - \theta_w}{1 - \theta_w}; \quad F_{IT} = \frac{F - \theta_g}{1 - \theta_g} \qquad (2)$$

where θ_w is the correlation of genes within populations and θ_g is that among populations. COCKERHAM (1969, 1973) considered the correlation of genes among groups (θ_g) to be equal to zero, and thereby simplified the F_{ST} and F_{IT} to θ_w and F, respectively. Because of the exchange of males among lineages within a population, I will not assume that θ_g is zero. It is important to recognize that the variance components applied to social lineages pertain to a lower hierarchical level (lineages within a single population rather than a subpopulation within an array of subpopulations) than those proposed by COCKERHAM (1969, 1973); however, the F_{IS} at this level is equal to the F_{IS} of COCKERHAM because $\theta_w = \alpha$. Expression 2 is directly applicable to the solutions of the genetic variance components within socially structured populations as

$$F_{LS} = \frac{\theta - \alpha}{1 - \alpha}; \quad F_{IL} = \frac{F - \theta}{1 - \theta}; \quad F_{IS} = \frac{F - \alpha}{1 - \alpha} \qquad (3)$$

where F_{LS} is the proportion of genetic variance found among lineages within the (sub)population, F_{IL} is the correlation of genes within individuals relative to those within the lineage, and the F_{IS} is the correlation of genes within individuals relative to those within the (sub)population.

TRANSITION OF COANCESTRIES

The coancestry between any pair of individuals is the average of the coancestries of their parents (JACQUARD 1974). The average coancestry between random pairs of offspring born in different lineages in generation $t + 1$ becomes

$$\alpha_{t+1} = \frac{1}{4}[\varphi_{mm_t^*} + \varphi_{mf_t^*} + \varphi_{fm_t^*} + \varphi_{ff_t^*}] \qquad (4)$$

where the suffixes m and f refer to male and female parents and asterisks indicate individuals from different lineages. Male mates are selected randomly and without replacement. Thus, the genes of any given male are correlated to $n - 1$ males from the same lineage by θ_{mm}, and to $n(s - 1)$ males by α. Because offspring become the parents within the same generation, t,

$$\varphi_{mm_t^*} = \frac{(n - 1)\theta_{mm_t}}{ns - 1} + \frac{(ns - n)\alpha_t}{ns - 1}. \qquad (5)$$

The genes of a female are correlated to n males by θ_{mf} and to $n(s - 1)$ males by α; thus,

$$\varphi_{mf_t^*} = \varphi_{fm_t^*} = \frac{\theta_{mf_t}}{s} + \left(1 - \frac{1}{s}\right)\alpha_t \qquad (6)$$

and because females are philopatric,

$$\varphi_{ff_t^*} = \alpha_t. \qquad (7)$$

Henceforth, for ease of presentation of expressions I will substitute

$$x = \frac{n - 1}{ns - 1} \quad \text{and} \quad y = \frac{1}{s}. \qquad (8)$$

Incorporating expressions 5, 6 and 7 into expression 4,

$$\alpha_{t+1} = \frac{x\theta_{mm_t}}{4} + \frac{y\theta_{mf_t}}{2} + \frac{4 - x - 2y}{4}\alpha_t. \qquad (9)$$

Expression 9 describes the transition of gene correlations among random offspring born within different breeding lineages over successive generations.

The inbreeding coefficient, F, of offspring is equal to the coancestry of their parents (JACQUARD 1974; FALCONER 1981). In a socially structured population, the inbreeding coefficient is dependent on the probability of a male breeding within his native lineage and the probability of selecting genes identical by descent from males born in other lineages. These probabilities are

$$F_{t+1} = \gamma_{mf_t} = y\theta_{mf_t} + (1 - y)\alpha_t. \qquad (10)$$

The correlation of genes between parents within lineages (γ_{mf^*}; see expression 6) is equal to that between parents of different lineages (φ_{mft}) for any given generation as is expected with random dispersal of males among lineages.

The coancestry among male offspring born within lineages is the average of the coancestry of their parents

$$\theta_{mm_{t+1}} = \frac{1}{4}[\gamma_{mm_t} + 2\gamma_{mf_t} + \gamma_{ff_t}]. \qquad (11)$$

The correlation of gametes contributed by a single

male is $(1 + F_t)/2$. When more than one male may breed within a lineage the correlation of gametes contributed by the different males is

$$\gamma_{mm_t} = \frac{\phi(1 + F_t)}{2} + x(1 - \phi)\theta_{mm_t} + (1 - x)(1 - \phi)\alpha_t. \quad (12)$$

The value of γ_{mf_t} is given in expression 10, and because females are philopatric

$$\gamma_{ff_t} = \theta_{ff_t} = \theta_{mm_t}. \quad (13)$$

Combining these expressions,

$$\theta_{mm_{t+1}} = \frac{\phi(1 + F_t)}{8} + \frac{1 + x(1 - \phi)}{4}\theta_{mm_t} + \frac{y\theta_{mf_t}}{2} + \frac{2(1 - y) + (1 - x)(1 - \phi)}{4}\alpha_t. \quad (14)$$

The coancestry of male and female offspring born within lineages will be determined using the assumption that mothers produce equal numbers of male and female offspring. Thus, prior to dispersal of males there are n litters of equal numbers of male and female offspring. The frequency of full siblings within a lineage is $1/n$, and their coancestry is

$$\theta_{mf_{t+1}}(\text{full sibs}) = \frac{1}{n}\frac{1}{4}\left[\frac{1 + F_t}{2} + 2\gamma_{mf_t} + \frac{1 + F_t}{2}\right] = \frac{1}{4n}[1 + F_t + 2F_{t+1}]. \quad (15)$$

The coancestry of the remainder of offspring born within a lineage is determined by the coancestry of their parents as

$$\theta_{mf_{t+1}}(\text{non-sibs}) = \frac{n - 1}{n}\frac{1}{4}[\gamma_{mm_t} + 2\gamma_{mf_t} + \theta_{ff_t}] = \frac{n - 1}{4n}[\gamma_{mm_t} + 2F_{t+1} + \theta_{mm_t}]. \quad (16)$$

Combining expressions 15 and 16 and including expression 12 for γ_{mmt}, the coancestry of male and female offspring born within lineages becomes

$$\theta_{mf_{t+1}} = \frac{1 + F_t}{4n} + \frac{y\theta_{mf_t}}{2} + \frac{(1 - y)}{2}\alpha_t + \frac{(n - 1)\phi(1 + F_t)}{8n} + \frac{x(1 - \phi)(n - 1)}{4n}\theta_{mm_t} + \frac{(n - 1)(1 - x)(1 - \phi)}{4n}\alpha_t \quad (17)$$

and, collecting terms,

$$\theta_{mf_{t+1}} = \frac{2n(1 - y) + (n - 1)(1 - x)(1 - \phi)}{4n}\alpha_t + \frac{(n - 1)(1 + x(1 - \phi))\theta_{mm_t}}{4n} + \frac{y\theta_{mf_t}}{2} + \frac{(1 + F_t)(\phi(n - 1) + 2)}{8n}. \quad (18)$$

Using expressions 9, 10, 14, and 18, the transition matrix for coancestry within and among lineages can be presented. Note that only four of the original variables, α, F, θ_{mm}, and θ_{mf}, are necessary to determine the gene correlations. A column vector, **S**, of variable values at generation t is

$$\mathbf{S}_t = \begin{pmatrix} \alpha_t \\ F_t \\ \theta_{mm_t} \\ \theta_{mf_t} \end{pmatrix} \quad (19)$$

The transition matrix **T** defining the probabilistic changes of the vector of variables is

$$\mathbf{T} = \begin{pmatrix} \frac{4 - x - 2y}{4} & 0 & \frac{x}{4} & \frac{y}{2} \\ 1 - y & 0 & 0 & y \\ \frac{2(1 - y) + (1 - x)(1 - \phi)}{4} & \frac{\phi}{8} & \frac{1 + x(1 - \phi)}{4} & \frac{y}{2} \\ \frac{2n(1 - y) + (n - 1)(1 - x)(1 - \phi)}{4n} & \frac{\phi(n - 1) + 2}{8n} & \frac{(n - 1)(1 + x(1 - \phi))}{4n} & \frac{y}{2} \end{pmatrix}. \quad (20)$$

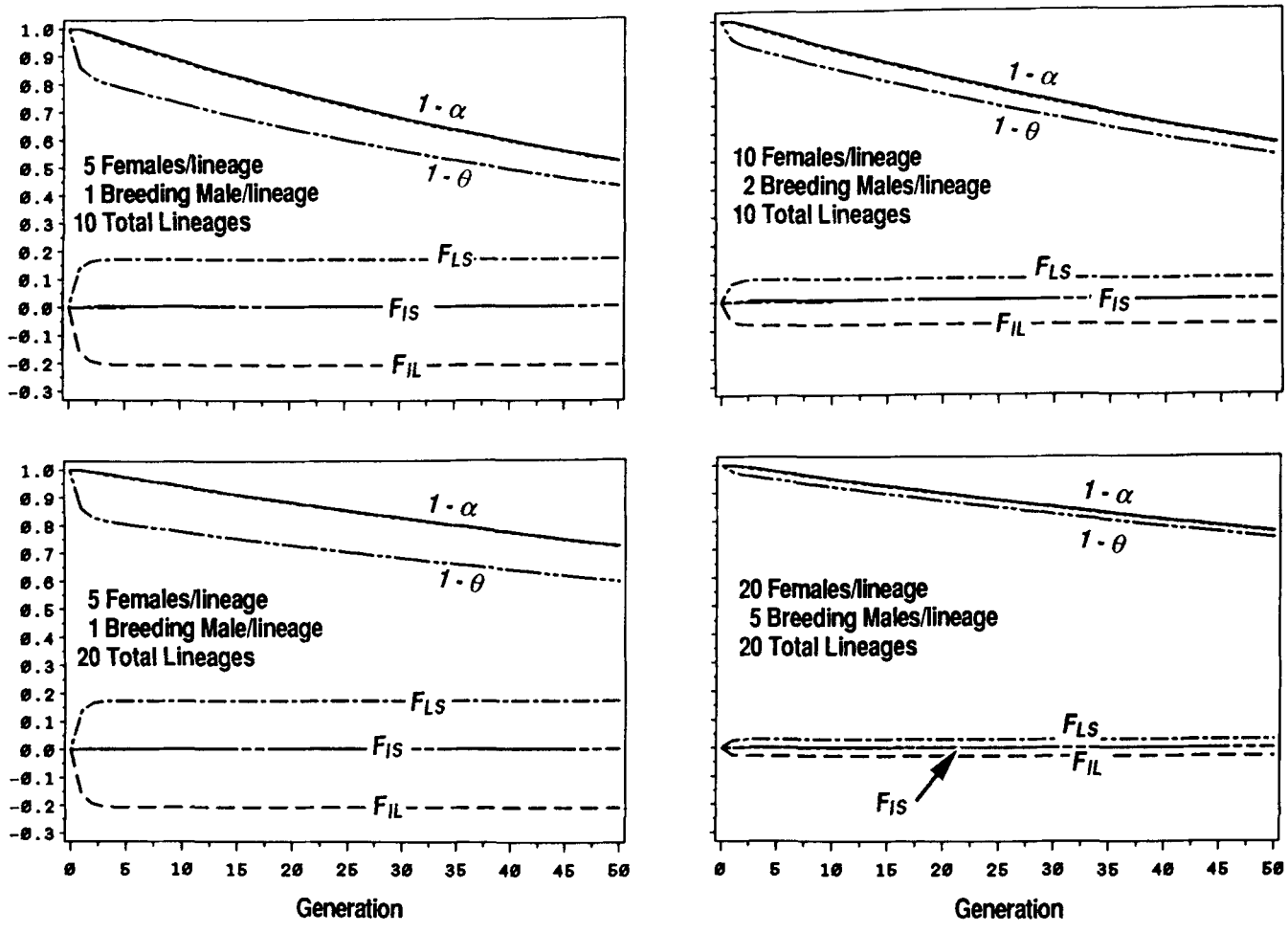

FIGURE 1.—Graphical depictions of the changes in genetic variance components and fixation indices over generations for some breeding scenarios. The values presented are: $1 - \alpha$ is the proportion of the original genetic variance remaining in the population; $1 - \theta$ is the proportion of the original genetic variance remaining within lineages; F_{LS} is the proportion of the remaining genetic variance found among lineages; F_{IL} is the correlation of genes within individuals relative to that within lineages; and the F_{IS} is the correlation of genes within individuals relative to that within the (sub)population.

It should be obvious from the expressions that the matrix **T** does not fully describe the transitions; some of the transitions are not products of variables. Therefore, a constant column vector C

$$C = \begin{pmatrix} 0 \\ 0 \\ \frac{\phi}{8} \\ \frac{\phi(n-1)+2}{8n} \end{pmatrix} \qquad (21)$$

must also be included such that the variable states at generation $t + 1$ are

$$S_{t+1} = TS_t + C \qquad (22)$$

The fixation indices for any generation may be determined using expression 3, where θ is the average coancestry of lineage members, or $(\theta_{mm} + \theta_{mf})/2$. The development leading to the matrix equations is exact and is easily programmed to provide numerical solutions for particular sets of parameters. Analytical expressions for equilibrium values do not appear to be tractable, and so approximate values have been derived in the next section. These do allow the effects of the various parameters to be seen more easily.

ASYMPTOTIC VALUES FOR FIXATION INDICES

I performed numerical solutions of the coancestries within socially structured populations exhibiting female philopatry. Matrix multiplication was performed as in expression 22 and fixation indices (via expression 3) were determined for each generation (up to 500 generations). The initial values of all gene correlations were zero, and subsequent values were retained in quadruple precision.

A graphical representation of the gene correlations for some typical breeding scenarios is presented as Figure 1. Results applicable to all breeding scenarios were: (a) despite the steady loss of genetic variation within the population, the fixation indices quickly

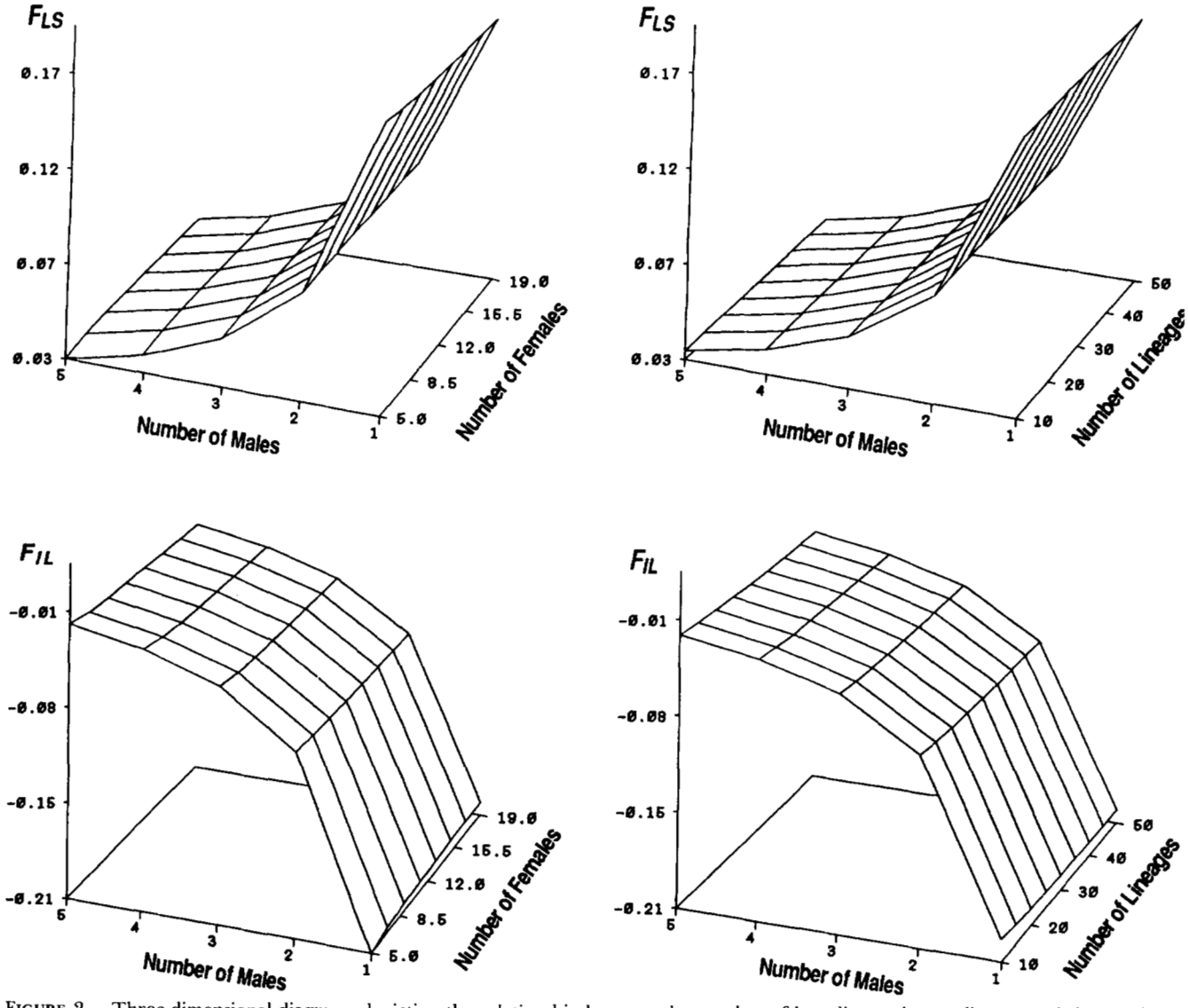

FIGURE 2.—Three-dimensional diagrams depicting the relationship between the number of breeding males per lineage and the number of females per lineage or the number of lineages in the population on the asymptotic F_{LS} and the F_{IL} values. All F_{IS} values were very close to zero and are not depicted here.

(≈10 generations) attained asymptotic values; (b) the F_{IL} values were negative indicating excess heterozygosity within lineages; and (c) the asymptotic value of the F_{LS} was inversely proportional to the number of male breeders per lineage and, to a lesser extent, the number of females per lineage.

It is obvious that with a finite number of lineages the values of F and α are continuously accumulating, thereby eroding the genetic variance within the population. Inspection of expressions 9 and 10 indicate that the accumulation of individual inbreeding (F) and inter-lineage coancestry (α) is dependent only on the values of θ_{mm} and θ_{mf}. Therefore, I should be able approximate the asymptotic solutions to the fixation indices by solving for the variables independent of prior accumulation of F and α. By this approach, I assume that the asymptotic values of θ_{mm} and θ_{mf}, if they exist, represent the initial conditions ($t = 0$) and that F_0 and α_0 are zero. Coancestries will be determined for the subsequent generation ($t = 1$). Using these criteria (from expression 14)

$$\hat{\theta}_{mm_{t+1}} = \frac{\phi}{8} + \frac{1 + x(1 - \phi)}{4} \hat{\theta}_{mm_t} \qquad (23)$$

where the "hat" indicates a partial coancestry which is free of *prior* effects of F and α. Thus, the coancestry values are asymptotic only with respect to the most distantly related genes within the population (*e.g.*, COCKERHAM 1973). In other words, the gene correlations relative to the genetic variation that *remains* within the population become asymptotic. Because of this stipulation the asymptotic approximations can not be readily derived from the numerical solutions. Resultant fixation indices, however, should be compa-

rable to those of the numerical methods because they are always relative to the remaining genetic variation (COCKERHAM 1973). Note that the term $y\theta_{mf_t}/2$ was not included in expression 23 because it was derived from the inbreeding coefficient in generation $t + 1$ (see expressions 6–9). However, because this term does not involve prior effects of inbreeding, but rather inbreeding in the subsequent generation, its value will be added later. Expression 23 is a first order difference equation with a solution

$$\hat{\theta}_{mm_t} = \frac{\phi}{8}\left[\frac{1 - \left(\frac{1 + x(1 - \phi)}{4}\right)^t}{1 - \left(\frac{1 + x(1 - \phi)}{4}\right)}\right] \tag{24}$$

(GOLDBERG 1958). The numerator in the brackets quickly approaches unity over successive generations. Thus, an asymptotic value is attained as

$$\hat{\theta}_{mm} = \frac{\phi}{6 - 2x(1 - \phi)} \tag{25}$$

Using the result of expression 25 the asymptotic value of the within-lineage coancestry of male and female offspring becomes

$$\hat{\theta}_{mf} = \frac{(n - 1)\hat{\theta}_{mm}}{n} + \frac{1}{4n} \tag{26}$$

Note that the solution of θ_{mf} also has temporarily omitted the term $y\theta_{mf}/2$ due to inbreeding in the subsequent generation. Expression 26 indicates that the asymptotic value of θ_{mf}, via this manipulation, becomes dependent solely on the variable θ_{mm}. Finally, substituting the coancestries above into the expressions for F and α,

$$\hat{F} = y\hat{\theta}_{mf};\ \hat{\alpha} = \frac{x\hat{\theta}_{mm} + 2y\hat{\theta}_{mf}}{4}. \tag{27}$$

Now all of the terms for the asymptotic generation may be gathered to derive the asymptotic average coancestry within lineages as

$$\hat{\theta} = \frac{\hat{\theta}_{mm} + \frac{\hat{F}}{2} + \hat{\theta}_{mf} + \frac{\hat{F}}{2}}{2} = \frac{\hat{\theta}_{mm} + \hat{\theta}_{mf} + \hat{F}}{2}. \tag{28}$$

The asymptotic coancestries are used to derive the asymptotic fixation indices

$$\hat{F}_{LS} \approx \frac{\hat{\theta} - \hat{\alpha}}{1 - \hat{\alpha}},\quad \hat{F}_{IL} \approx \frac{\hat{F} - \hat{\theta}}{1 - \hat{\theta}},\quad \hat{F}_{IS} \approx \frac{\hat{F} - \hat{\alpha}}{1 - \hat{\alpha}}. \tag{29}$$

Although the fixation indices above are approximations of the matrix solutions, none deviated from the actual value by more than 10^{-3} and most were accurate to the fourth decimal. Fixation indices are differentially affected by the number of females per lineage (n), the number of lineages (s), and the number of males breeding per lineage (m) (Figure 2).

Clearly, female philopatry can produce high coancestry values for offspring born within social lineages, particularly when few males breed within lineages. To understand the importance of female philopatry to genetic differentiation it is necessary to compare such breeding tactics to traditional models including female dispersal. To achieve this objective, I will assume that females born within social groups now disperse randomly with respect to lineages before breeding. In prior models, because females were philopatric, the coancestry of females from different lineages was α_t (Equation 7). With female dispersal, however,

$$\varphi_{ff_t^*} = x\theta_{mm_t} + (1 - x)\alpha_t \tag{30}$$

($\theta_{ff} = \theta_{mm}$) which is identical to Equation 5. With this change, the correlation of genes of offspring of different lineages becomes (compare with Equation 9)

$$\alpha_{t+1} = \frac{x\theta_{mm_t}}{2} + \frac{y\theta_{mf_t}}{2} + \frac{2 - x - y}{2}\alpha_t. \tag{31}$$

The coancestry of female parents within lineages (Equation 13) also changes with female dispersal, becoming equivalent to that among lineages (Equation 30). The expression for inbreeding accumulation (F) is the same as Equation 10. Using the expressions above, the coancestry of male progeny born within lineages now becomes

$$\theta_{mm_{t+1}} = \frac{\phi(1 + F_t)}{8} + \frac{x(2 - \phi)}{4}\theta_{mm_t} + \frac{y\theta_{mf_t}}{2} + \frac{2(1 - y) + (1 - x)(2 - \phi)}{4}\alpha_t. \tag{32}$$

Inspection of Equations 15 and 16 will show that the expression for $\theta_{mf(t+1)}$ does not change with female dispersal. The transition matrix, T_2, for coancestries with random male and female dispersal is

$$T_2 = \begin{pmatrix} \frac{2 - x - y}{2} & 0 & \frac{x}{2} & \frac{y}{2} \\ 1 - y & 0 & 0 & y \\ \frac{2(1 - y) + (1 - x)(2 - \phi)}{4} & \frac{\phi}{8} & \frac{x(2 - \phi)}{4} & \frac{y}{2} \\ \frac{2n(1 - y) + (n - 1)(1 - x)(1 - \phi)}{4n} & \frac{\phi(n - 1) + 2}{8n} & \frac{(n - 1)(1 + x(1 - \phi))}{4n} & \frac{y}{2} \end{pmatrix} \tag{33}$$

Note that when $\phi = 0$, $\theta_{mm} = \alpha$ as would be expected with random movement of both sexes. The column vector, C, is unchanged from Equation 21, and the variable states at generation $t + 1$ are calculated as before.

Approximation of asymptotic coancestries can be made as before. For progeny of the same sex born within lineages

$$\hat{\theta}_{mm_{t+1}} = \frac{\phi}{8} + \frac{x(2 - \phi)}{4}\,\hat{\theta}_{mm_t} \tag{34}$$

which is a first order difference equation, with a solution of

$$\hat{\theta}_{mm} = \frac{\phi}{8}\left[\frac{1 - \left[\frac{x(2 - \phi)}{4}\right]^t}{1 - \frac{x(2 - \phi)}{4}}\right] \tag{35}$$

which, after a few generations becomes

$$\hat{\theta}_{mm} = \frac{\phi}{8 - 2x(2 - \phi)}. \tag{36}$$

Asymptotic approximations for θ_{mf}, F, α, and the fixation indices are determined as in Equations 26–29 using the asymptotic value for θ_{mm} above.

The transition matrices for female philopatry (Equation 20) and random female dispersal are quite similar. The resultant fixation indices for offspring born within lineages are also similar, and are identical when there are n breeding males per lineage ($\phi = 0$). Female philopatry does increase the coancestry of progeny born within lineages when there is some degree of polygyny, and the F_{LS} for female dispersal is about 75–80% of that for philopatry when $\phi > 0.4$. The coancestry of adults within lineages, just prior to breeding, can be substantially higher with female philopatry. The coancestry of adults within lineages with philopatry is

$$\gamma_t = \frac{n - 1}{n}\,\theta_{mm_t} + \frac{y\theta_{mf_t}}{n} + \frac{(1 - y)\alpha_t}{n} \tag{37}$$

whereas that for adults with random dispersal by both sexes is

$$\gamma_t = x\theta_{mm_t} + (1 - x)\alpha_t. \tag{38}$$

Figure 3 compares the F_{LS} values for the two dispersal scenarios for adults and progeny over the range of potential breeding tactics. Clearly, for a given breeding tactic, female philopatry may be much more effective for increasing gene correlations among adults than among progeny.

It is interesting to note that at equilibrium the fixation indices are not indicative of the accumulation of gene correlations since the initial generation. At

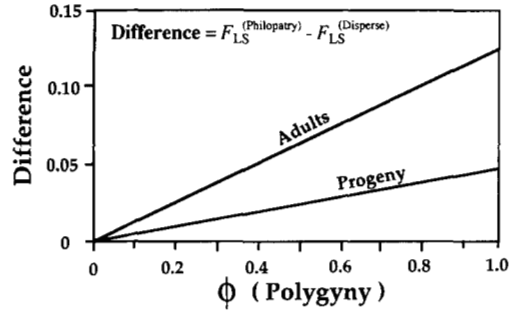

FIGURE 3.—The difference between the F_{LS} values for dispersal tactics where the females are philopatric and where females disperse randomly within a subdivided population. Difference values for progeny born within social lineages and for breeding adults within lineages are shown over the range of possible male mating schemes (ϕ). Low values of ϕ indicate greater numbers of males breeding within lineages and when $\phi = 1$ only one male mates within each lineage (see expression 1).

equilibrium, assuming that $\alpha_t \neq \alpha_{t+1}$

$$\frac{\theta_t - \alpha_t}{1 - \alpha_t} = \frac{\theta_{t+1} - \alpha_{t+1}}{1 - \alpha_{t+1}} = \frac{\theta_t + \Delta\theta - \alpha_t - \Delta\alpha}{1 - \alpha_t - \Delta\alpha} \tag{39}$$

which is reduced to

$$\hat{F}_{LS} = 1 - \frac{\Delta\theta}{\Delta\alpha}. \tag{40}$$

By the same process it can be shown that

$$\hat{F}_{IL} = 1 - \frac{\Delta F}{\Delta\theta},\ \hat{F}_{IS} = 1 - \frac{\Delta F}{\Delta\alpha}. \tag{41}$$

In reality, the equilibrium condition is never attained but only approached. Thus, Equations 40 and 41 are approximations. For socially structured populations changes of gene correlations within individuals and within lineages approach a dynamic equilibrium and the fixation indices are measures of the incremental change in gene correlations. That is, the F_{IS} measures the inbreeding coefficient relative to the genetic variability that still remains in the population at a given time, rather than that relative to the initial conditions of the population (COCKERHAM 1973; ALLEN 1965). Similar statements apply to the F_{LS} and F_{IL}. This is in contrast to a scenario of a very large number of isolated or semi-isolated demes, wherein $\alpha \approx 0$ and the F_{ST} and F_{IT} may measure total gene correlations relative to the initial conditions.

DISCUSSION

The social organization and concomitant dispersal and breeding patterns of a population have important consequences for the apportionment of genetic variance and distribution of genotypic proportions within and among lineages. Inbreeding need not be invoked to effectively decrease variance within and increase variance among lineages. Likewise, substantial excess

heterozygosity may be evident within lineages even with random selection of breeding males. The proportion of the total genetic variance attributable to differences between lineages will remain constant given no major perturbations to breeding and dispersal schemes. Knowledge of the breeding and dispersal tactics will, hence, permit direct calculations of gene correlations and fixation indices.

The maximum effect on genetic differentiation among lineages in the absence of inbreeding is evident when a single, randomly selected male breeds with philopatric females. The importance of female nondispersal has been shown in models by CHESSER and RYMAN (1986) who demonstrated that considerable site tenacity by females would be of positive selective value and that female dispersal solely for the purpose of inbreeding avoidance is not likely. The models and expressions in this paper document that female philopatry plays an important role in the disparity of variance within lineages relative to random individuals within the population, an important aspect of social behavior (HAMILTON 1964a,b).

Three-dimensional wire diagrams and plots of asymptotic fixation indices (Figures 1 and 2) illustrate three important relationships. First, the most important parameter determining the asymptotic values of F_{LS} and F_{IL} is the number of breeding males per lineage. The proportion of genetic variance among lineages (F_{LS}) and the disparity of genotypic proportions from Hardy-Weinberg expectations within lineages (F_{IL}), in favor of excess heterozygotes, are increased when few males breed within lineages. It must be pointed out, however, that the diagrams were constructed on the basis that breeding males contributed equally to the resultant offspring within lineages. Variance in male contributions within lineages decreases the effective number of males. Second, for a given number of male breeders within lineages the asymptotic values of F_{LS} and F_{IL} are strongly influenced by the number of females per lineage but are relatively insensitive to the number of lineages in the population, whereas the reverse is apparent for the F_{IS}. Finally, the value of the F_{IS} is most strongly influenced by the number of lineages within the population and secondarily by the number of males breeding per lineage. Because F_{IS} measures the increment of inbreeding these results may seem surprising at first. Traditionally, it would appear that increasing the number of males breeding within the population would increase the effective population size and thereby decrease the inbreeding increment. Increasing the number of breeding males per lineage does increase the effective population size and the rate of loss of genetic variation within the population is slowed (compare the plots for $1 - \alpha$ in Figure 1). However, as expressions 26–29 demonstrate, the asymptotic values of the fixation indices are dependent on the differential rates of change of the coancestry variables and not their total value. Increasing the number of breeding males per lineage concomitantly increases the probability of inbreeding (selection of a native male) relative to the probability of distributing males to other lineages.

The F_{IL} can not be construed as a measure of individual inbreeding at this level of analysis, although some have made such interpretations (CHESSER 1983; FOLTZ and HOOGLAND 1983; RALLS, HARVEY and LYLES 1987). CHESSER (1983) and others (SVOBODA, CHOATE and CHESSER 1985; MCCULLOUGH and CHESSER 1987; HAMILTON, CHESSER and BEST 1987) recognized the difficulties in interpreting inbreeding on such a scale. His explanations, however, were heuristic, not fully definitive of the interpretative problems, and were applied to the incorrect hierarchical scale. Negative values for the F_{IL}, indicative of excess heterozygosity within lineages, are expected for socially structured populations or any other population in which the breeding groups have been accurately defined (COCKERHAM 1969, 1973). Negative F_{IL} values have usually been concluded as demonstrative of inbreeding avoidance (SCHWARTZ and ARMITAGE 1980; FOLTZ and HOOGLAND 1983; RALLS, HARVEY and LYLES 1987; MELNICK 1987). Such conclusions of avoidance of consanguineous matings and highly outcrossed nature of social species are semantic at best. Although the magnitude of excess heterozygosity within lineages is promulgated by exchange of breeders among genetically divergent lineages, nothing more than random selection of mates is required (SADE 1972; SMITH 1982). Investigators should be aware that relatively large excesses in heterozygosity may, in some instances, be indicative of a complicated substructure and dispersal regime of the population rather than avoidance of inbreeding or heterosis (see RALLS, HARVEY and LYLES 1987). If the breeding groups have been correctly identified the expected value of the F_{IL} is negative (COCKERHAM 1969) regardless of the number of male and female mates.

Female philopatry does increase the coancestry of progeny born within social lineages over that for random female movement. The F_{LS} value with random adult dispersal is about 75% of that for philopatric females when there is only one breeding male per lineage. Female philopatry, however, can promote much higher coancestries among adults within social lineages than does random female dispersal. These results suggest that female philopatry has evolved primarily to enhance cooperative potential among breeding individuals within social groups and to eliminate the cost of dispersal for females (CHESSER and RYMAN 1986). Enhanced coancestry of offspring has probably been of secondary value for the evolution of

such breeding and dispersal tactics. The results also demonstrate that the evolution of philopatry and polygyny were not independent of one another. Philopatry concomitant with multiple male matings per lineage bestows little or no increase in intralineage coancestry. Polygyny together with female philopatry, however, produces consistently high gene correlations among progeny and adults within social groups.

Finally, I must emphasize that the values derived herein are intended only for the regular genealogies produced by social lineages within populations and may not apply to other types of breeding structures. Empirically, however, the differences between social and demic structures are primarily interpretive rather than statistical. Strategies for approximation of variables applicable to any hierarchical level have previously been documented (COCKERHAM 1969, 1973; WEIR and COCKERHAM 1984). It is important to note that the models presented pertained to discrete generations of breeding adults which are in turn replaced by offspring born within lineages. Empirically, separate analyses of fixation indices for adults and offspring have seldom been performed. SPIELMAN *et al.* (1977) discussed the value of separating generations for proper interpretation of breeding structure. Inclusion of adults and their offspring as well as nonbreeding, nonresident lineage members will usually serve to dilute the magnitude of the fixation indices. Parametric values for such samples are readily derived using the expressions presented herein. Whereas the resultant values will depict the extant genetic structure of the population, the underlying breeding structure may be obscured (see LONG 1986). Hence, it will be more informative to treat the genetic and breeding structure within populations as separate, but related, analyses.

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