Influence of Gene Flow and Breeding Tactics on Gene Diversity Within Populations

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ABSTRACT

Expressions describing the accumulation of gene correlations within and among lineages and individuals of a population are derived. The model permits different migration rates by males and females and accounts for various breeding tactics within lineages. The resultant equations enable calculation of the probabilistic quantities for the fixation indices, rates of loss of genetic variation, accumulation of inbreeding, and coefficients of relationship for the population at any generation. All fixation indices were found to attain asymptotic values rapidly despite the consistent loss of genetic variation and accumulation of inbreeding within the population. The time required to attain asymptotic values, however, was prolonged when gene flow among lineages was relatively low (<20%). The degree of genetic differentiation among breeding groups, inbreeding coefficients, and gene correlations within lineages were found to be primarily functions of breeding tactics within groups rather than gene flow among groups. Thus, the asymptotic value of S. Wright's island model is not appropriate for describing genetic differences among groups within populations. An alternative solution is provided that under limited conditions will reduce to the original island model. The evolution of polygynous breeding tactics appears to be more favorable for promoting intragroup gene correlations than modification of migration rates. Inbreeding and variance effective sizes are derived for populations that are structured by different migration and breeding tactics. Processes that reduce the inbreeding effective population size result in a concomitant increase in variance effective population size.

MIGRATION and breeding tactics are primary factors governing the differentiation of gene frequencies among, and distributions of genotypes within, populations. Gene flow promulgated by dispersing individuals will serve to ameliorate the genetic divergence, via random loss of genetic variation, of populations. Various breeding tactics such as polygyny and inbreeding may affect the rates of loss of genetic variation and alter the genotypic proportions from those expected with panmixia. Realization of the importance of migration and breeding regimes served as the impetus for the derivation of the fixation indices (WRIGHT 1943, 1951, 1969, 1978). These indices (often referenced as F statistics) describe the proportion of genetic variance among (sub)populations (overall differentiation; F_{ST}), inbreeding relative to the population (F_{IS}), and inbreeding relative to the total array of populations (F_{IT}). Given the classical components of genetic variation, infinitely sized, randomly mating, subpopulations which freely exchange breeding individuals should be characterized by $F_{ST} = F_{IS} = F_{IT} = 0$. Deviations from expected values not only provide investigators with estimates of population divergence, but also with aspects nonrandom mating within populations. WRIGHT's (1951, 1969) introduction of the island model also enabled approximation of the number of migrants among populations.

The utility of the fixation indices and island model for describing gene flow and breeding biology of populations is made obvious by their extensive use in the published literature and by the attention to proper interpretation and estimation of the coefficients (COCKERHAM 1973; ROTHMAN, SING and TEMPLETON 1974; NEI 1977 WRIGHT 1978; NEI and CHESSER 1983; WEIR and COCKERHAM 1984; LONG 1986; WEIR 1990). Initially, implementation focused on the assessment of geographically separated populations (EANES and KOHEN 1978; WRIGHT 1978; AVISE and FELLEY 1979; RYMAN *et al.* 1980). More recently, extensive analyses have been applied to intrapopulational scales, particularly for socially structured populations (SCHWARTZ and ARMITAGE 1980; CHESSER, REUTERWALL and RYMAN 1982; CHESSER 1983a, FOLTZ and HOOGLAND 1983; MCCULLOUGH and CHESSER 1987; MELNICK 1987). Interpretations of the gene flow and breeding structure at the population level were usually extrapolated from those for geographically separated populations. CHESSER (1991), however, demonstrated that substantial differentiation among social lineages and excess heterozygosity within lineages may be expected even when males disperse randomly. Thus, lack of gene flow was not the sole factor responsible

for genetic differentiation among breeding groups and inbreeding avoidance was unnecessary to promote substantial excess heterozygosity within lineages.

CHESSER's (1991) models compared the expected gene correlations resultant from complete female philopatry with random male migration and random migration by both sexes for a range of polygyny values. He found that although the population may be constantly loosing genetic variation the fixation indices attain steady state values. The greatest differentiation among and highest excess heterozygosity within breeding groups was found when a single male mated with all philopatric females within a lineage. Although female philopatry, male-biased migration, and polygyny are common tactics in mammals (GREENWOOD 1980), such conditions are certainly not ubiquitous for any taxon.

Although CHESSER's (1991) models showed that traditional predictions of demic models may not be extended to intrapopulational structures, they have limited applicability to the variety of migration and breeding schemes that exist in natural populations. The purpose of this paper is to expand previous models to include migration rates among lineages for either sex as well as permit different breeding tactics for the determination of gene correlations and fixation indices. I will examine the efficacy of WRIGHT's (1951) island model as it pertains to intrapopulational structure and provide predictive models for differentiation of gene frequencies and genotypic distributions.

INTRAPOPULATIONAL STRUCTURE

CHESSER (1991) was careful to differentiate between social and demic structures. Demes have been classically considered as panmictically breeding units that are relatively isolated from other demes (MAYR 1963; DOBZHANSKY 1970; HARTL 1980; SHIELDS 1987). Social lineages, on the other hand, represent areas of a single population wherein related individuals may remain philopatric and/or within which mate choice may not be independent. Philopatry is usually practiced by only one sex, typically females for mammals and males in bird species (GREENWOOD 1980). The nonindependence of mate choice within lineages is the probability that pairs of females have mated with the same male. The number of unordered pairs of females within a lineage is $(n^2 - n)/2$ and the probability that females have selected the same male with which to breed is (CHESSER 1991)

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

where m represents the number of breeding males per lineage, b_i is the average number of females bred by the ith male, and n is the number of breeding females per lineage. The variable ϕ, therefore, represents the proportion of females that share the same sire, and its value may range from zero (independent mate choice when $n = m$ and $b_i = n/m$) to one (all females within a lineage mate with the same male).

The delineation of lineages within populations by the above criteria was unambiguous in CHESSER's (1991) models because females were considered to be philopatric. As will become clear below, however, when migration rates for both sexes and nonindependence of mate choice are allowed to vary, the distinction between lineage and demic structures becomes difficult. Thus, the models derived will permit the investigation of a continuous distribution of lineage integrity.

Gene correlations, or coancestry (COCKERHAM 1967, 1969, 1973), for parents and offspring within and among lineages will be represented by the following variables: 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; and F = coancestry of genes within random individuals (inbreeding). The fixation indices are determined as

$$F_{LS} = \frac{\theta - \alpha}{1 - \alpha}; \qquad F_{IL} = \frac{F - \theta}{1 - \theta}; \qquad F_{IS} = \frac{F - \alpha}{1 - \alpha} \qquad (2)$$

where the subscript L, S and I reference lineages, (sub)populations, and individuals respectively (CHESSER 1991; *cf.* COCKERHAM 1973). These subscripts were chosen to distinguish the fixation indices from those of higher hierarchical levels involving an array of populations (COCKERHAM 1973; WRIGHT 1978). Thus, F_{LS} will represent the proportion of the genetic variance found among lineages within the population, F_{IL} is the correlation of genes within individuals relative to those within lineages, and F_{IS} denotes the correlation of genes within individuals relative to those within the population. Also, $1 - \alpha$ is the proportion of the original genetic variation that still remains in the population, whereas $1 - \theta$ is the proportion of the original variance remaining within lineages. Obviously, any of the coancestry variables may change through generations (t) as inbreeding and loss of genetic variation accrue. It is necessary, therefore, to derive the expected transitions of the gene correlations over time (CHESSER 1991). In so doing, it will be assumed that male and female progeny are produced in equal proportions, generations are nonoverlapping, and that migration (if any) transpires prior to mating.

TRANSITION MODELS OF GENE CORRELATIONS

Consider a single population comprising s lineages. Any migration shall be assumed to be random with

respect to lineages; such an assumption is not unrealistic as we are not concerned with geographically separated populations (CHESSER 1983a). Male and female migration rates will be represented by d_m and d_f, respectively. For ease of presentation, and to maintain conformity of expressions with CHESSER (1991), I will assign $y = 1/s$. The probability that matings occur between individuals from the same lineage is

$$(1 - d_f)(1 - d_m) + (1 - d_m)yd_f + (1 - d_f)yd_m + yd_md_f \quad (3)$$

which is reduced to

$$1 - (1 - y)(d_m + d_f - d_md_f). \quad (4)$$

The transitions of gene correlations within and among lineages are similar to those presented by CHESSER (1991) and are presented in APPENDIX I. The expressions (A.1–A.14) presented are equal to those of CHESSER (1991) if there is no female migration ($d_f = 0$) and all males disperse ($d_m = 1$). They also equal the expressions for complete migration by both sexes ($d_m = d_f = 1$; CHESSER 1991). Thus, the equations describe the transitions of gene correlations for variable migration rates by either or both sexes.

A transition matrix (T) for the coancestry within and among lineages can now be presented. Only four of the original variables, namely α, F, θ_{mm} and θ_{mf}, are necessary to determine the gene correlations for the fixation indices. The state of these variables at generation t is represented by the column vector $\mathbf{S}_t = \{\alpha_t, F_t, \theta_{mmt}, \theta_{mft}\}$. Initial values of all gene correlations (S_0) were zero. Using expressions (A.1, A.6, A.10) and (A.14) and defining $A = (d_m + d_f - d_md_f)$, and $B = (1 - x)(d_m(1 - \phi) + d_f)$, the transition matrix for these variables is

$$\mathbf{T} = \begin{bmatrix} \frac{4 - 2yA - x(d_m + d_f)}{4} & 0 & \frac{x(d_m + d_f)}{4} & \frac{yA}{2} \\ (1 - y)A & 0 & 0 & 1 - (1 - y)A \\ \frac{2(1 - y)A + B}{4} & \frac{\phi}{8} & \frac{2 - \phi - B}{4} & \frac{1 - (1 - y)A}{2} \\ \frac{2n(1 - y)A + (n - 1)B}{4n} & \frac{\phi(n - 1) + 2}{8n} & \frac{(n - 1)(2 - \phi - B)}{4n} & \frac{1 - (1 - y)A}{2} \end{bmatrix} \quad (5)$$

A column vector, $C = \{0, 0, \phi/8, [\phi(n - 1) + 2]/8n\}$, must be included such that the transition of the variable states becomes $S_{t+1} = TS_t + C$. The fixation indices for any generation can be derived from the variables as in equation 2 where θ is the average coancestry within lineages, and $\theta = (\theta_{mmt} + \theta_{mft})/2$.

As shown in CHESSER (1991) all fixation indices rapidly approach asymptotic values despite the constant loss of genetic variation within the population (Figure 1). The asymptotic value of the F_{LS} was inversely proportional to the migration rate (of either sex) and the number of breeding males per lineage. The F_{IL} values were always negative indicating excess heterozygosity within lineages even when substantial inbreeding coefficients were accruing. Values of the F_{IS} were largely dependent on the rate of migration, with low rates promoting high levels of inbreeding. The time required to attain the asymptote was usually rapid, but was inversely related to the migration rate of both sexes.

To provide a relative comparison of the importance of migration and breeding tactics on the apportionment of genetic variation within populations the asymptotic fixation indices were determined for a range of values for ϕ, d_m, and d_f. For simplification of the relationships into three dimensions, I assigned $d_m = d_f$. Three-dimensional wire diagrams (Figure 2, A–C) where constructed to demonstrate the relationships of breeding and migration tactics on the fixation indices. Figure 2A shows that nonindependence of breeding males (ϕ) is much more important to the resultant F_{LS} than was the migration rate (gene flow), unless migration rates were very low (<0.2). Influence of migration rate on the F_{IS} was relatively more pronounced (Figure 2B) but breeding tactics still were of greater importance. Migration rate had almost no influence at all on the asymptotic values for the F_{IL} (Figure 2C). The results were similar when comparisons were made for male-only and female-only migration.

APPROXIMATION OF ASYMPTOTIC VALUES

The disproportional influence of breeding tactics rather than migration on the ultimate F_{LS} values document that WRIGHT's (1951) island model is not applicable to models of intrapopulational differentiation. Close scrutiny of the asymptotic value for the island model

$$\hat{F}_t = \frac{(1 - d)^2}{2N - [2N - 1](1 - d)^2} \quad (6)$$

(d = migration rate by both sexes; N = population size) shows that Wright did not intend for the island

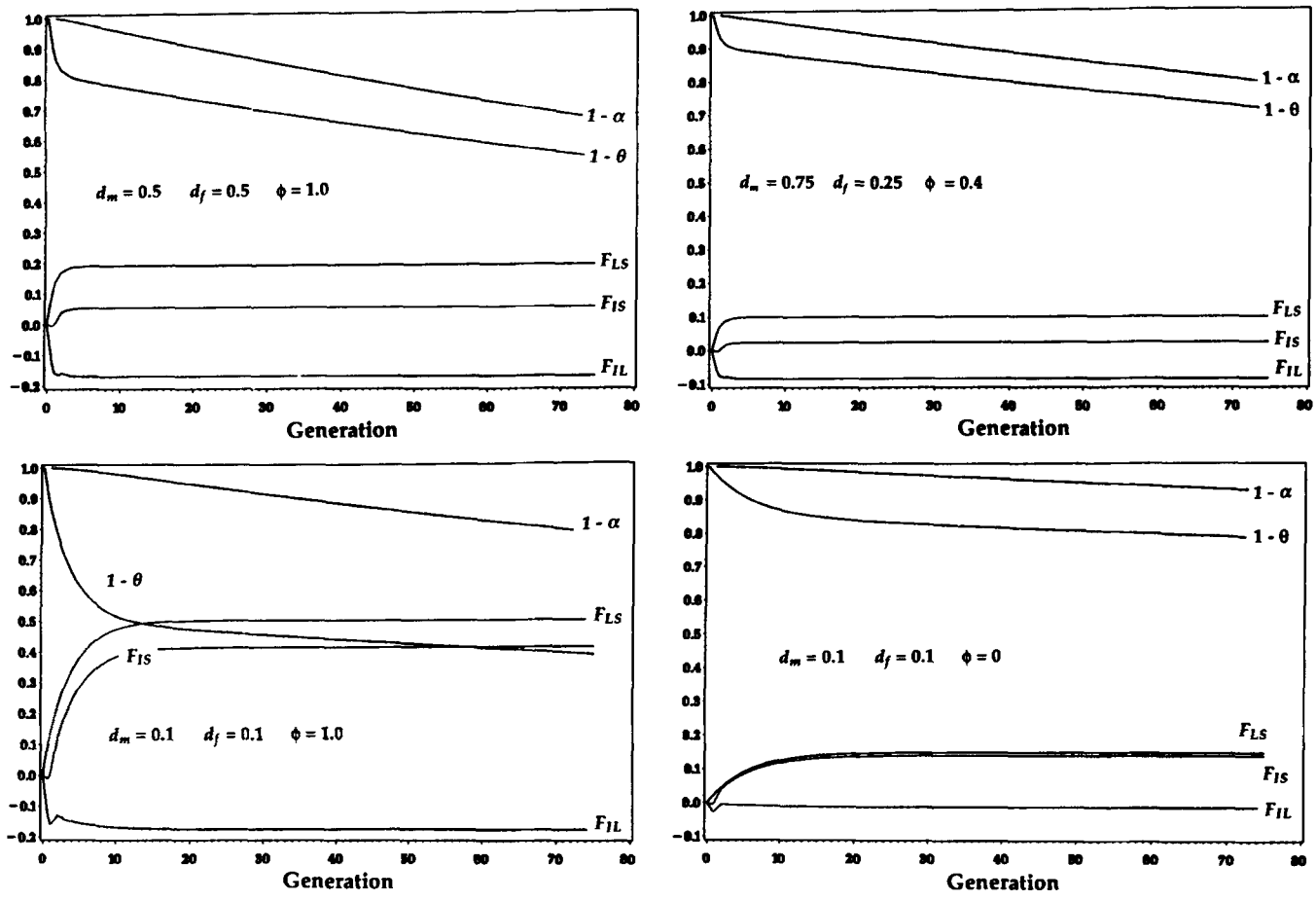

FIGURE 1.—Fixation indices and gene correlations resultant from different migration rates of males (d_m) and females (d_f) and nonindependence of male mates (ϕ): $1 - \alpha$ is the proportion of the initial genetic variation remaining in the population and $1 - \theta$ is that remaining within lineages; F_{LS} is the proportion of the gene diversity at any generation that is found among lineages, F_{IS} is the correlation of genes within individuals (inbreeding), and F_{IL} is the correlation of genes within individuals relative to those available within lineages. All graphs were generated from matrix iterations using five females per lineage and by a total of 20 lineages in the population.

model to account for a variety of breeding tactics. In fact, a large number of panmictically breeding populations was assumed. Equation 6 is actually a model of inbreeding and does not account for other sources of gene correlations. Because $F_{IS} = 0$, due to panmixia within populations, the F_{ST} is equal to the F_{IT}. Clearly, such assumptions will not suffice for depicting intrapopulational structure. Figure 3 demonstrates that the F_{LS} is not a simple function of migration rate and that a particular migration value can generate a variety of F_{LS} values depending on the breeding tactics within lineages.

Derivations of exact analytical expressions for the equilibrium values from the transition matrix are not feasible. CHESSER (1991) approximated the asymptotic values for the fixation indices by assuming that equilibrial values were immediately attained prior to the accumulation of inbreeding (F) or intergroup correlation (α). Whereas his approximations were very accurate, they do not apply when migration rates for males are less than unity. When emigration rates are less than one, the assumption that initial inbreeding coefficients are negligible is not applicable. In fact, in the extreme scenario where there is no dispersal from the native lineage, asymptotic inbreeding coefficients will not be attained until $F = 1$. Therefore, the asymptotic value for inbreeding within lineages must be derived prior to derivation of intralineal coancestry.

From expression (A.1) it can be seen that accumulation of inbreeding is a function of the coancestry among male and female progeny within lineages (θ_{mf}) and the intergroup coancestry (α). Using expressions (A.1) and (A.14), the accumulation of inbreeding can be approximated by the first-order difference equation

$$F_{t+1} = (1 - (1 - y)(d_m + d_f - d_m d_f)) \cdot \left[\frac{\phi(n-1)+2}{8n} + \left(1 - \frac{\phi(n-1)+2}{8n}\right) F_t\right]. \quad (7)$$

This expression incorporates variables which account for a finite number of lineages ($y = 1/s$), differential migration by males and females (d_m and d_f), and for nonindependent mate choice by females within lineages (ϕ). When there are an infinite number of lineages ($y \approx 0$), males and females migrate equally ($d_m = d_f$), and independent mate choice ($\phi = 0$), Equation 7

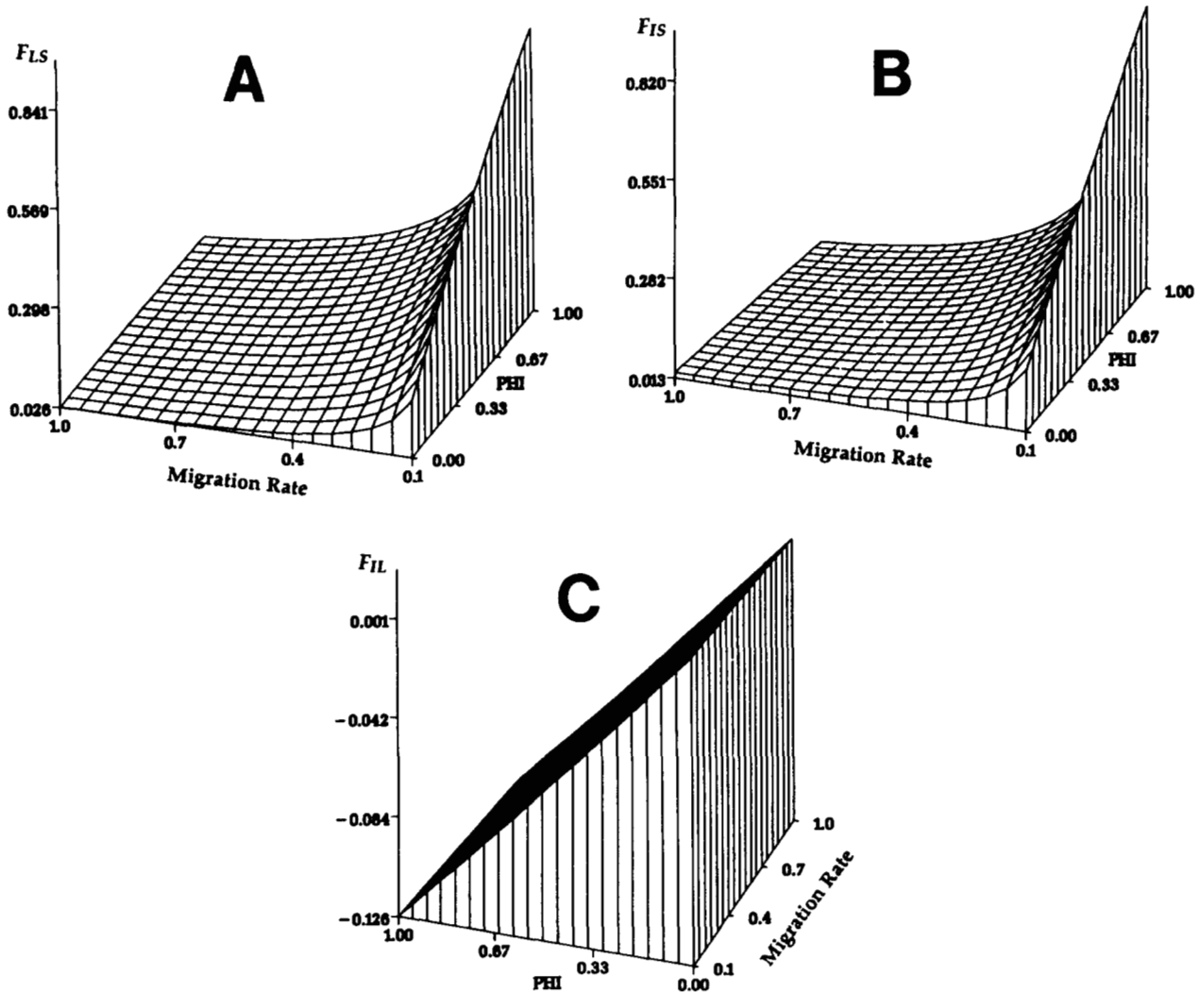

FIGURE 2.—Three-dimensional wire diagrams depicting the relationship of migration rates, nonindependence of male mates (ϕ; PHI), and the asymptotic fixation indices. All graphs were generated for five females per lineage and a total of 20 lineages in the population.

is identical to the unreduced form of WRIGHT's (1951, p. 331) island model (note that $2n = N$). Although PROUT (1981) derived the island models accounting for sex-biased migration, his expressions did not include deviations from random mating and finite population size. The solution to the difference equation is determined as

$$\hat{F}_t = \frac{(1-(1-y)(d_m+d_f-d_md_f))(\phi(n-1)+2)}{8n-[8n-\phi(n-1)-2][1-(1-y)(d_m+d_f-d_md_f)]} \tag{8}$$

where the "hat" refers to the asymptotic value. With the stipulations made above, it can be seen that expressions (6) and (8) would be identical. In reality, because there are a finite number of lineages within a population, the inbreeding coefficient is never truly asymptotic and will continue to accrue until complete ($F = 1$). Genetic variation within the population is being lost due to the correlation among individuals from different lineages (α). Equation 8 is the value of the inbreeding coefficient relative to the genetic variation that still remains within the population, and it is this value that is attained at equilibrium. CHESSER (1991) described this relationship and determined that the asymptotic value satisfies the expression $F = 1 - \Delta F/\Delta\alpha$. The asymptotic values described herein shall therefore refer to "asymptotic relative to the genetic variation that remains" or in COCKERHAM's (1973) terms "relative to the most distantly related genes."

Asymptotic values of coancestry within lineages (θ) can only be attained after the asymptotic inbreeding coefficient is attained. The asymptotic value for coancestry among like-sexed progeny ($\theta_{mm} = \theta_{ff}$) is determined by

$$\theta_{mm_{t+1}} = \frac{\phi}{8} + \frac{2-\phi-(1-x)(d_m(1-\phi)+d_f)}{4}\,\theta_{mm_t} \tag{9}$$

which is, after a few generations, resolved as

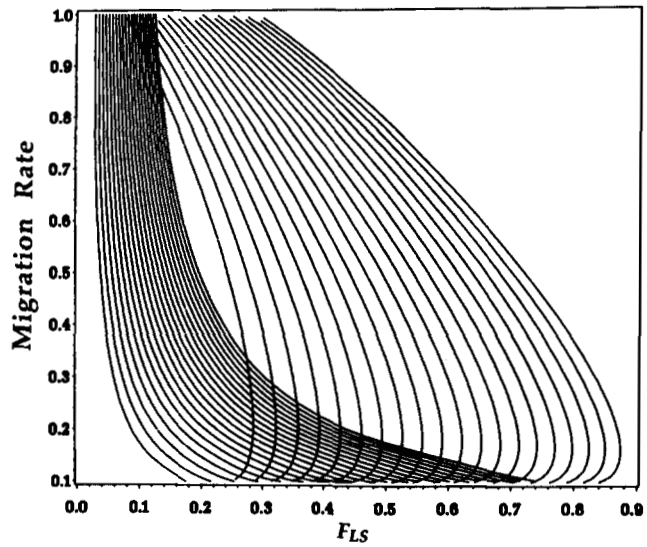

FIGURE 3.—The relationship of migration rate and the differentiation among lineages within populations (F_{LS}) for a range of breeding tactics [$\phi = 0$ (left) to 1 (right)]. The graph was generated using five females per lineage and a total of 20 lineages in the population.

$$\hat{\theta}_{mm} = \frac{\phi}{4 + 2\phi + 2(1 - x)(d_m(1 - \phi) + d_f)}. \quad (10)$$

Assuming, for the moment, that $F = 0$, from expression (A.13)

$$\hat{\theta}_{mf} = \frac{n - 1}{n}\hat{\theta}_{mm} + \frac{1}{4n}. \quad (11)$$

With the inbreeding accumulation expressions (10) and (11) are modified to become

$$\hat{\theta}_{mm} = \hat{\theta}_{mm}(1 - \hat{F}) + \hat{F}$$

and (12)

$$\hat{\theta}_{mf} = \hat{\theta}_{mf}(1 - \hat{F}) + \hat{F}$$

(*e.g.*, WRIGHT 1952; JACQUARD 1974, p. 223). The average coancestry within lineages is, therefore, approximated by

$$\hat{\theta} = \frac{[\hat{\theta}_{mm} + \hat{\theta}_{mf}](1 - \hat{F})}{2} + \hat{F} \quad (13)$$

Asymptotic inbreeding is now incremented to the subsequent generation (because equilibrium coancestry values occur subsequent to that of F) to become

$$\hat{F} = (1 - (1 - y)(d_m + d_f - d_m d_f))\hat{\theta}_{mf} \quad (14)$$

and the correlation of genes among lineages becomes

$$\hat{\alpha} = \frac{x(d_m + d_f)}{4}\hat{\theta}_{mm} + \frac{y(d_m + d_f - d_m d_f)}{2}\hat{\theta}_{mf}. \quad (15)$$

The approximate fixation indices are determined from expression (2) using the asymptotic values derived above. The approximations do not represent exact solutions to the matrix iterations but were always accurate to within 5×10^{-3}. Again, WRIGHT's (1951) island model, now for intrapopulational inbreeding, is subsumed in Equation 8 for the F_{IS} rather than the F_{LS}. Unfortunately, no simplifying assumptions can be applied to estimate the number of migrating individuals among groups as did WRIGHT when he derived his familiar approximation $F \approx 1/[4Nd + 1]$.

DISCUSSION

Solutions to the transitions of gene correlations within structured populations document that the apportionment of extant genetic variation within and among lineages, within individuals relative to their lineage, and within individuals relative to the population attain steady state values despite the progressive loss of gene diversity. The attainment of asymptotic fixation indices apply to any regular genealogy of breeding and migration scenarios and are not specific to the cases of female philopatry and complete male migration models described by CHESSER (1991). Thus, the fixation indices are not measures of the total gene correlations accumulated since the initial generations, but rather can be expressed as rate functions (CHESSER 1991); at equilibrium these functions are ($\alpha_t \neq \alpha_{t+1}$)

$$\hat{F}_{LS} = 1 - \frac{\Delta\theta}{\Delta\alpha}; \qquad \hat{F}_{IL} = 1 - \frac{\Delta F}{\Delta\theta};$$
$$\hat{F}_{IS} = 1 - \frac{\Delta F}{\Delta\alpha}. \quad (16)$$

WRIGHT (1951, 1969) determined that the island model described the equilibrium F_{ST} when loss of gene diversity within a population was equally countered by supplementation of genetic variation via gene flow. Wright however assumed an infinite number of populations, and genetic variation was not lost. Expression 16 demonstrates that within structured populations the increases of gene correlations within lineages become proportional to the loss of gene diversity from the population (for the F_{LS}). Thus, a counterbalance of drift and gene flow may not be the sole factors determining differentiation among groups. COCKERHAM (1973) also showed that maintenance of initial genetic variance ($\alpha = 0$) was not necessary for the determination of the ultimate fixation indices among populations.

The magnitude of the asymptotic values attained is a function of the breeding tactics within lineages and the migration rate for each sex. Breeding tactics (nonindependence of female mate choice; ϕ) was of much greater importance to the differentiation among lineages (F_{LS}) than was migration rate of either or both sexes except when migration rates were very low (<0.2). A particular migration rate for males or females or both can result in a variety of F_{LS} values depending on the mating schemes within lineages. A similar, yet less pronounced, difference of effects was evident for the inbreeding coefficient (F_{IS}). The F_{IL}, however, was relatively unaffected by gene flow when compared to the F_{LS} and F_{IS} and as such is a rather robust indicator of breeding tactics.

The effects of male-biased and female-biased migration are somewhat asymmetrical in their influence on the differentiation among lineages. Male-biased migration always resulted in higher F_{LS} values than did female predominated movement for a particular breeding tactic (ϕ). However, if one sex exhibited complete migration, then the rate of migration by the alternate sex made relatively little impact on the resultant fixation indices for progeny. However, the coancestry of parents is more positively influenced by female philopatry than that for the progeny (CHESSER 1991). Thus, the evolution of altruism (HAMILTON 1964a,b) may be promoted among adults to a greater extent than among progeny by female philopatry.

CHESSER (1991) concluded that polygyny and philopatry probably evolved in concert with one another in order to promote greater coancestry among lineage members. Female philopatry ($d_f = 0$) with random selection of male mates by each female ($\phi = 0$) will not promote intragroup gene correlations beyond that of panmixia if male migration is random. Inbreeding within the group, however, could generate similar gene correlations to those for the conditions of polygyny and random male movement. Altruism within groups is a function of the coefficient of relationship (HAMILTON 1964a,b; CHESSER and RYMAN 1986)

$$r_{xy} = \frac{2\theta}{1 + F} \tag{17}$$

(WRIGHT 1922). Using this expression and equations (8) and (10–13) the migration rate of progeny sired by different males ($\phi = 0$) necessary to result in the same asymptotic r_{xy} as that with complete male polygyny ($\phi = 1$) and random migration ($d_m = 1$) can be approximated for female philopatric systems. For independent (random) male selection (noting that $\phi = 0$, $d_f = 0$)

$$F^{(\text{random})} = \frac{1 - (1 - y)d_m}{4n - (4n - 1)(1 - (1 - y)d_m)} \tag{18}$$

$$\theta_{mm}^{(\text{random})} = 0, \qquad \theta_{mf}^{(\text{random})} = \frac{1}{4n} \tag{19}$$

$$\theta^{(\text{random})} = \frac{1 - F^{(\text{random})}}{8n} + F^{(\text{random})} \tag{20}$$

and the coefficient of relationship is reduced to

$$r_{xy}^{(\text{random})} = \frac{d_m(1 - y) - 2}{2d_m(1 - 2n - y + 2ny) - 2}. \tag{21}$$

Likewise, for complete polygyny ($\phi = 1$) and random male movement ($d_m = 1$),

$$F^{(\text{polygyny})} = y \tag{22}$$

$$\theta_{mm}^{(\text{polygyny})} = \frac{1}{6}; \qquad \theta_{mf}^{(\text{polygyny})} = \frac{2n + 1}{12n} \tag{23}$$

$$\theta^{(\text{polygyny})} = \frac{(4n + 1)(1 - y)}{24n} + y \tag{24}$$

and

$$r_{xy}^{(\text{polygyny})} = \frac{(4n + 1)(1 - y) + 12ny}{12n(1 + y)}. \tag{25}$$

By setting

$$r_{xy}^{(\text{random})} - r_{xy}^{(\text{polygyny})} = 0 \tag{26}$$

and solving for d_m, the migration rate for randomly mating males from their native lineage that is necessary to produce the same relationship within lineages as that for complete polygyny with random male movement is determined as

$$d_m = \frac{4n(2 + y) + y - 1}{(1 - y)[(4n - 1)(1 - y) + 8n^2(1 + y)]} \tag{27}$$

If the number of lineages in the population is sufficiently large such that $y \approx 0$, then the male migration rate necessary for equivalence of r_{xy} is approximately

$$d_m \approx \frac{8n - 1}{8n^2 + 4n - 1} \approx \frac{1}{n} \tag{28}$$

and the resultant asymptotic inbreeding coefficient within lineages would be

$$\hat{F}^{(\text{random})} \approx \frac{2n - 1}{10n - 2} \approx \frac{1}{5} \tag{29}$$

Clearly, substantial inbreeding (about 20%) would be necessary for independent mate choice to produce relationships with lineages equal to that acquired by polygyny and random male movement. Inbreeding of this magnitude would probably not be advantageous for maintaining fitnesses of progeny (CHESSER and RYMAN 1986; NOBLE, CHESSER and RYDER 1990). The rate of attainment of asymptotic relationship values is also much more rapid with polygyny than for inbreeding scenarios. Thus, it appears that evolution may favor the development of different breeding tactics rather than limited migration by both sexes for enhancing intragroup gene correlations.

The loss of genetic variation within the population (α) and the loss within individuals (F) are predictable from the models (see Figure 1). In the models of female philopatry and random migration by both sexes (CHESSER 1991) these values were very similar. For models involving variable migration and breeding tactics, the values may differ appreciably. The rates of change for these two variables are functions of the variance effective population size (N_{ev}) and inbreeding effective size (N_{ef}), respectively (CROW and KIMURA 1970). Because inbreeding progresses as

$$F_t = \frac{1}{2N_{ef}} + \left[1 - \frac{1}{2N_{ef}}\right]F_{t-1} \tag{30}$$

the inbreeding effective size can be approximated from expression (7) as

$$N_{ef} \approx \frac{4n}{(\phi(n - 1) + 2)[1 - (1 - y)(d_m + d_f - d_m d_f)]}. \tag{31}$$

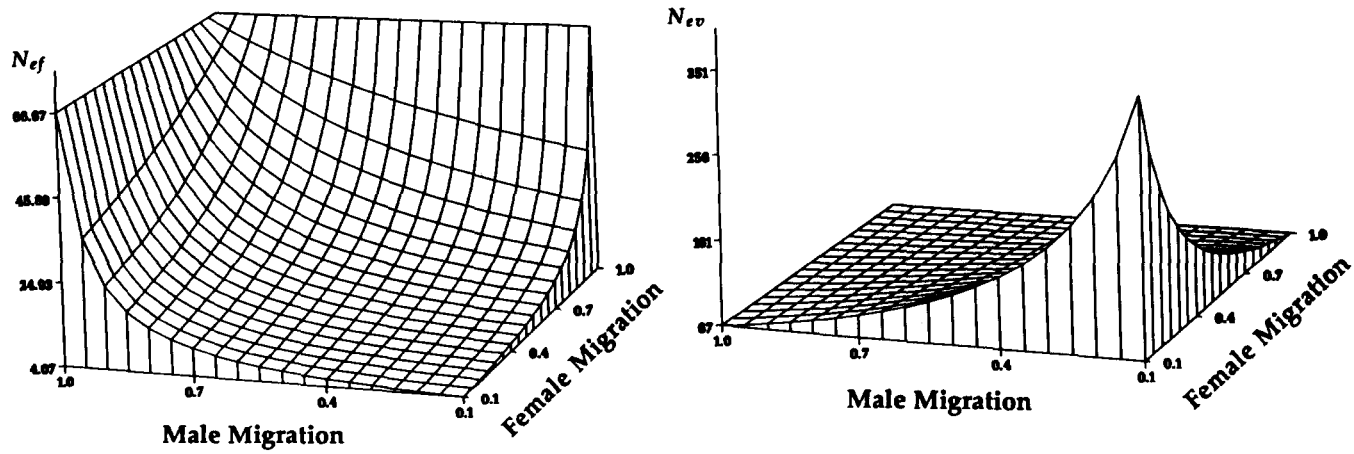

FIGURE 4.—Three-dimensional wire diagrams depicting the influence of migration rates by males (d_m) and females (d_f) on the inbreeding and variance effective sizes (N_{ef} and N_{ev}, respectively). The graphs were generated using five females per lineage, 20 lineages in the population, and complete male polygyny ($\phi = 1.0$).

By a similar procedure, the variance effective population size can be approximated as

$$N_{ev} \approx \frac{4n}{y(\phi(n-1)+2)(d_m + d_f - d_m d_f)}. \quad (32)$$

When migration by males, females, or both is complete then the variance and inbreeding effective sizes will be approximately equal. However, as migration rates are decreased, the N_{ef} will be reduced with a concomitant increase in N_{ev} (Figure 4). Contrasting effects of migration on inbreeding and genetic variance have been previously recognized CROW and KIMURA 1970; CHESSER, SMITH and BRISBIN 1980; CHESSER 1983b) but formulas for approximating effective sizes for such scenarios have not been previously presented. Whereas previous approximations of effective population sizes have focused on single populations and sex ratios of breeding individuals, the relative isolation of groups by incomplete migration has not been addressed. The expressions above provide estimates of effective sizes for an array of potentially interacting population units. Breeding tactics, as measured by the nonindependence of female mate choice (ϕ), also affect changes in both N_{ef} and N_{ev}, but increasing polygyny serves to decrease both measures in an equal manner (Figure 4). Obviously, if there are an infinite number of lineages ($y = 0$), then

$$N_{ev} = \infty$$
$$N_{ef} = \frac{4n}{\{\phi(n-1)+2\}(1-d_m)(1-d_f)} \quad (33)$$

The asymptotic values of the fixation indices appear to be robust in regard to periodic perturbations as they quickly return to their previous values. Because the fixation indices are based on gene correlations the gene frequencies for the hypothetical loci involved are inconsequential; this, of course, would not be the case in estimating the values empirically. The time required for attainment of the equilibrium indices, however, is altered by some rate limiting functions. As is seen in Figure 1, inbreeding promulgated by incomplete migration by both sexes will require a longer period of time for the asymptotic fixation indices to be reached. This is because the asymptotic inbreeding must be achieved before the other coancestry values will become asymptotic. Hence, inbreeding affects both the time required to attain an equilibrium and the ultimate value for the equilibrium. Other rate limiting functions may not affect the values of the fixation indices. In the models presented the population was initiated with s lineages and the number of lineages remained constant. The number of lineages, however, can be used as a variable rather than a parameter. Assume the population was initiated with only a single lineage and permitted to add new lineages in a logistic fashion to a maximum number of lineages (s_{max}). If λ is the intrinsic growth rate of the population, then the number of lineages in the population will progress as

$$s_{t+1} = \lambda \frac{s_{max} - s_t}{s_{max} - 1}. \quad (34)$$

When this function for population growth was implemented in the numerical iterations for the models it was found that it had no effect on the asymptotic fixation indices previously described (Figure 5); it did however extend the time necessary to attain the asymptotic values. The choice of the logistic growth model was arbitrary and served only as an example. Regardless of the mode of population growth, the population must approach a stable size before the equilibrial genetic distributions can be manifested. Slower growth rates result in increased times for asymptotic fixation indices to be reached. Even though the population may loose considerable amounts of genetic variation by small numbers of founding individuals and slow growth rates (CHESSER, WILLIS and MATHEWS 1991), the gene diversity re-

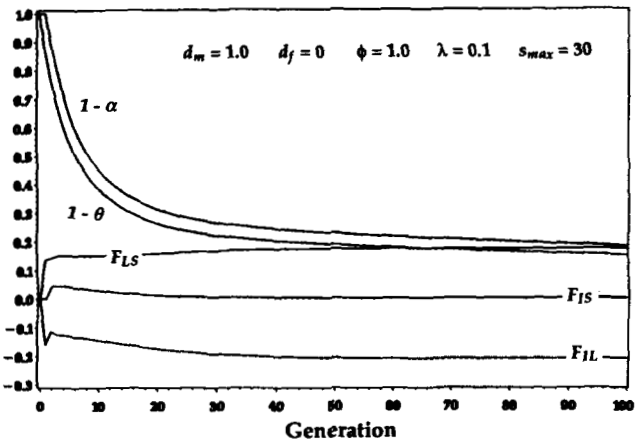

FIGURE 5.—Fixation indices and gene correlations resultant from logistic population growth from one to 30 (s_{max}) lineages. The graph was generated using five females per lineage, complete polygyny within lineages ($\phi = 1.0$), complete female philopatry ($d_f = 0$), and random male migration ($d_m = 1$). The intrinsic growth rate (λ) of the population was 0.1.

maining will ultimately be distributed solely in accordance to the migration and breeding tactics.

It is interesting to note that the predictions for the apportionment of gene diversity provided by the models herein cannot be reconciled with hypothesized breeding structure for some species. Positive values for levels analogous to the F_{IL} (usually reported as F_{IS} but within populations) have been found in many studies (CHESSER 1983a; HAMILTON, CHESSER and BEST 1987; MCCULLOUGH and CHESSER 1987). Inspection of expression (2) clearly will show that such values are possible only when coancestry within the lineage is less than the average inbreeding coefficient for individuals. Because the coancestry within the lineage represents the potential inbreeding coefficient that would result in the subsequent generation should lineage members interbreed, a positive F_{IL} could only transpire if the inbreeding coefficient would be potentially decreasing. A simple explanation of overdispersion will not suffice because both the coancestry and inbreeding coefficient would approach α, and the F_{IL} would approach zero. Some extended period of inbreeding within lineages followed by an episode of dispersal would result in positive values of F_{IL} at least for adults because F would be high and the coancestry subsequent to migration would be low (α). Such a scenario, however, would not apply to the resultant progeny and sampling a population at the appropriate time to evidence this pattern would be serendipitous. It is more likely that the breeding groups were not correctly defined (CHESSER 1991). Inadvertent inclusion of individuals from several breeding groups into a defined unit will serve to decrease the estimated coancestry within lineages. In order for this procedure to create positive F_{IL} values, however, inbreeding must be greater than α, indicative of incomplete dispersal from the native groups. Thus, correct delineation of breeding groups is necessary for accurate approximation of breeding structure. It is not known to what extent such problems have played in analysis of social structures.

CHESSER (1983a) and FOLTZ and HOOGLAND (1983) reported very different fixation indices within populations of the black-tailed prairie dog. Although there has been considerable speculation regarding the disparity of reported values (*cf.* RALLS, HARVEY and LYLES 1987), investigators have failed to notice that the studies were performed on very different scales and by very different methods. CHESSER (1983a) reported traditional (WRIGHT 1978; NEI 1977) fixation indices among regions (in New Mexico), among populations within regions, within and among wards of a single population, and among coteries (breeding units) of a population. FOLTZ and HOOGLAND (1983) only reported the F_{ST} between two populations (10 km apart) and F_{IS} within a single population. FOLTZ and HOOGLAND (1983, p. 274) also instigated interative procedures to remove the bias of sibling clusters (RASMUSSEN 1979) in producing excess heterozygosity. However, they failed to account for the potential genetic relationship among breeding females within coteries as a similar bias. CHESSER's positive estimates of F_{IS} (reported as F_{IT}) within a population would indicate considerable inbreeding. Positive values for F_{IL} (reported as F_{IS}) may indicate inaccurate delineation of breeding groups, as discussed above. FOLTZ and HOOGLAND found negative values for the F_{IS} but their fixation indices were not significantly different from zero (random mate selection). Estimates of F_{LS} and F_{IL} are not possible from their data. Thus, CHESSER's results are inconsistent with those that should result given the hypothesized female philopatry and male polygyny (HOOGLAND 1977) but probably suffer from inaccurate identification of breeding groups. FOLTZ and HOOGLAND did not attempt to identify breeding groups and therefore their data are not useful in determination of breeding structure; however, their data do not provide any evidence for outbreeding or incest avoidance.

The models presented permit precise examination of the probabilistic results for accumulation of gene correlations for a continuum of population structures manifested by various migration and breeding tactics. The intent of the models is to derive the various gene correlations from known or hypothesized behaviors of organisms in natural environments. Inference of such behaviors from empirical data may prove difficult unless sampling regimes are carefully and accurately designed. The models document the importance of breeding and migration tactics on the apportionment of gene diversity within populations and provide a mechanism for examining the evolution of complex behaviors.

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APPENDIX I: TRANSITION EQUATIONS FOR GENE CORRELATIONS

Symbol definitions are provided in the text. The transition of inbreeding from one generation to the next is

$$F_{t+1} = \gamma_{mf_t} = [1 - (1 - y)(d_m + d_f - d_m d_f)]\theta_{mf_t} + (1 - y)(d_m + df - d_m d_f)\alpha_t. \quad (A.1)$$

The average coancestry between random pairs of offspring born in different lineages in generation $t + 1$ is

$$\alpha_{t+} = \tfrac{1}{4}\,[\varphi_{mm_{*_t}} + \varphi_{mf_{*_t}} + \varphi_{fm_{*_t}} + \varphi_{ff_{*_t}}] \quad (A.2)$$

where suffixes m and f refer to male and female parents and asterisks indicate individuals from different lineages. 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_t. Assigning $x = (n - 1)/(ns - 1)$ and because offspring become the parents within the same generation, t,

$$\varphi_{mm*_t} = xd_m\theta_{mm_t} + (1 - xd_m)\alpha_t. \tag{A.3}$$

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

$$\begin{aligned}\varphi_{mf*_t} = \varphi_{fm*_t} &= y(d_m + d_f - d_md_f)\theta_{mf_t} \\ &+ (1 - y(d_m + d_f - d_md_f))\alpha_t.\end{aligned} \tag{A.4}$$

The coancestry of female parents from different lineages is similar to expression A.3 because $\theta_{ff} = \theta_{mm}$

$$\varphi_{ff*_t} = xd_f\theta_{mm_t} + (1 - xd_f)\alpha_t. \tag{A.5}$$

Finally, combining Equations A.3–A.5,

$$\begin{aligned}\alpha_{t+1} = \frac{x(d_m + d_f)}{4}\theta_{mm_t} + \frac{y(d_m + d_f - d_md_f)}{2}\theta_{mf_t} \\ + \frac{4 - 2y(d_m + d_f - d_md_f) - x(d_m + d_f)}{4}\alpha_t.\end{aligned} \tag{A.6}$$

The coancestry among male offspring born within lineages is

$$\theta_{mm_{t+1}} = \tfrac{1}{4}[\gamma_{mm_t} + 2\gamma_{mf_t} + \gamma_{ff_t}]. \tag{A.7}$$

The gene correlation of male parents within lineages is

$$\begin{aligned}\gamma_{mm_t} = \frac{\phi(1 + F_t)}{2} + (1 - \phi)(1 - (1 - x)d_m)\theta_{mm_t} \\ + (1 - x)d_m(1 - \phi)\alpha_t.\end{aligned} \tag{A.8}$$

The value of γ_{mf_t} has already been defined in expression A.1 ($\gamma_{mf_t} = F_{t+1}$). The coancestry among female parents within lineages is determined as

$$\gamma_{ff_t} = (1 - (1 - x)d_f)\theta_{mm_t} + (1 - x)d_f\alpha_t. \tag{A.9}$$

Combining expressions,

$$\begin{aligned}\theta_{mm_{t+1}} &= \frac{\phi(1 + F_t)}{8} \\ &+ \frac{2 - \phi - (1 - x)(d_m(1 - \phi) + d_f)}{4}\theta_{mm_t} \\ &+ \frac{1 - (1 - y)(d_m + d_f - d_md_f)}{2}\theta_{mf_t} \\ &+ \frac{2(1 - y)(d_m + d_f - d_md_f) + (1 - x)(d_m(1 - \phi) + d_f)}{4}\alpha_t.\end{aligned} \tag{A.10}$$

Correlations of genes among male and female progeny within lineages will be determined assuming that 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 contribution to the coancestry within lineages is

$$\theta_{mf_{t+1}} = \frac{1}{4n}[1 + F_t + 2F_{t+1}]. \tag{A.11}$$

The remainder of the offspring within a lineage likewise contribute

$$\theta_{mf_{t+1}} = \frac{n - 1}{4n}[\gamma_{mm_t} + 2\gamma_{mf_t} + \gamma_{ff_t}]. \tag{A.12}$$

Summing, the coancestry of male and female progeny within lineages is

$$\theta_{mf_{t+1}} = \frac{1 + F_t}{4n} + \frac{\gamma_{mf_t}}{2n} + \frac{n - 1}{n}\theta_{mm_{t+1}} \tag{A.13}$$

which, when expanded becomes

$$\begin{aligned}\theta_{mf_{t+1}} &= \frac{(1 + F_t)(\phi(n - 1) + 2)}{8n} \\ &+ \frac{(n - 1)(2 - \phi - (1 - x)(d_m(1 - \phi) + d_f))}{4n}\theta_{mm_t} \\ &+ \frac{1 - (1 - y)(d_m + d_f - d_md_f)}{2}\theta_{mf_t} \\ &+ \frac{2n(1 - y)(d_m + d_f - d_md_f) + (n - 1)(1 - x)(d_m(1 - \phi) + d_f)}{4n}\alpha_t.\end{aligned} \tag{A.14}$$