

Adaptive Topography in Fertility–Viability Selection Models: An Alternative to Inclusive Fitness in Kin Selection Models

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In this paper, we propose an alternative to inclusive fitness in kin selection models. The key point is to show that kin selection in family-structured models can be put into a context of fertility selection. First, we extend T. Nagylaki's (1987, *Genetics* 115, 367–375) result on approximate adaptive topographies in two-sex populations under weak selection by considering sex-differentiated fertilities of matings. The result is that the change in the geometric average and in the arithmetic average of the mean fertilities in male and female offspring is approximately equal to the additive genetic variance in fertility. Then we show that fertility–viability selection models and kin selection models with sex differences are special cases if appropriate fitness parameters are introduced and if genotype frequencies are considered at an appropriate time of the life cycle. Kin selection models with partial adoption of offspring giving rise to frequency-dependent selection are also studied. © 1993 Academic Press, Inc.

INTRODUCTION

In a recent paper, Nagylaki (1987) studied evolution at a single multi-allelic locus under arbitrary weak selection on fertility and viability. In the case of constant fertilities of matings and constant viabilities of male and female offspring determined at an autosomal locus in random mating dioecious diploid populations undergoing discrete nonoverlapping generations, he proved that after enough generations the change in the geometric average of the mean fitnesses of males and females is approximately given by the additive genetic variance in fitness, the mean fitnesses of males and females being defined as the product of the mean viabilities of males and

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females, respectively, with the square root of the mean fertility. One of the main steps in the proof is to show that in the long run deviations of genotypic frequencies from Hardy–Weinberg proportions are small and vary slowly compared to the order of magnitude of viability and fertility differences.

Nagylaki's analysis confirmed and extended a result of Abugov (1985) for the case of a diallelic locus and a result of Wright (1942) for the case of sex-differentiated viability. The result can be viewed as an extension of the "*Fundamental Theorem of Natural Selection*" of Fisher (1930) for the case of viability selection with no sex differences, which asserts that the increase in the mean viability is (approximately) equal to the additive genetic variance of viability differences. In Wright's (1932, 1969) interpretation of the Fundamental Theorem of Natural Selection, the mean viability is an adaptive topography on which the population tends to move upward until it reaches a peak. In other words, "*the mean viability is maximized.*"

On the other hand, Michod and Abugov (1980) studied evolution at a single diallelic locus under the effects of kin selection with no sex differences in family-structured populations. Assuming Hardy–Weinberg proportions, they showed that evolution does proceed along an adaptive topography in Wright's sense determined by the mean "*inclusive fitness*" as proposed by Hamilton (1964). In other words, "*the mean inclusive fitness is maximized.*" The main idea behind an inclusive fitness formulation of kin selection is to transfer fitness benefits of altruistic acts, weighted by coefficients of relatedness and reproductive values of the sexes when applicable, from beneficiaries to actors. In diploid populations with no inbreeding, the coefficient of relatedness of a donor to a recipient at an autosomal locus undergoing weak selection is given by the expected fraction of genes identical by descent in the recipient to one or more genes in the donor at the given locus. Such a coefficient can be computed from the pedigrees of the donor and the recipient and is strictly positive only for relatives. Moreover, it is usually assumed that benefits to recipients and costs to donors incurred by altruistic acts are combined additively as increments and decrements of fitness. This assumption of additivity seems to be crucial for an inclusive fitness formulation to be valid at least near allele fixation states to predict invasion or extinction of mutant alleles (see, e.g., Cavalli–Sforza and Feldman, 1978).

For exact one-locus two-allele sib-to-sib altruism selection models with sex differences, Uyenoyama and Feldman (1981) constructed *ad hoc* adaptive topographies based on inclusive fitnesses and Hardy–Weinberg proportions. They used the regression coefficient of the recipient's additive genotypic value for altruism propensity on that of the donor to measure relatedness as proposed meanwhile by Hamilton (1970, 1972). In several cases, the stationary points of the *ad hoc* adaptive topographies turned out

to correspond to the equilibria and the local maxima to the stable equilibria. But in some cases as sister-to-brother altruism and sister-to-sib altruism, the authors had to assume no genetic dominance (actually, semi-dominance) in the propensity of performing altruism in order to make correct descriptions of the equilibrium structures from the *ad hoc* adaptive topographies. It was proposed that the exceptions might represent limits within which Hamilton's theory on the maximization of the mean inclusive fitness applies.

With multiple alleles at one locus, Uyenoyama *et al.* (1981) developed a covariance formula of Li (1967) and Price (1970) for the change of gene frequencies which led to necessary conditions for polymorphic equilibrium and necessary and sufficient conditions (ignoring degeneracies in linear approximations) for an initial increase in the frequency of mutant alleles which were consistent with Hamilton's theory. One of the advantages of the covariance approach is to yield general definitions for the coefficient of relatedness (see also Michod and Hamilton, 1980; Seger, 1981; Uyenoyama, 1984; and references therein) to be used in kin selection theory, even in cases of inbreeding and strong selection which do not justify the use of Hardy-Weinberg proportions, such that conditions for the invasion of mutant alleles and conditions for polymorphic equilibrium can be obtained from an inclusive fitness formulation.

With costs and benefits being defined from fitness functions instead of being defined as intrinsic constants, even the initial increase in frequency of mutant alleles cannot be predicted in general from an inclusive fitness formulation unless penetrance, that is, the propensity of performing altruism, is small (Karlín and Matessi, 1983). As with the assumptions of additivity and Hardy-Weinberg proportions, this is "*tantamount to the validity of Hamilton's theory under conditions of very weak selection.*"

In this paper, we propose an alternative to inclusive fitness in kin selection models. The key point is to show that kin selection in family-structured models can be put into a context of fertility selection. First, we extend Nagylaki's (1987) result on approximate adaptive topographies in two-sex populations under weak selection by considering sex-differentiated fertilities of matings. The result is that *the change in the geometric average and in the arithmetic average of the mean fertilities in male and female offspring is approximately equal to the additive genetic variance in fertility.* Then we show that fertility-viability selection models and kin selection models with sex differences are special cases if appropriate fitness parameters are introduced and if genotype frequencies are considered at an appropriate time of the life cycle. Kin selection models with partial adoption of offspring giving rise to frequency-dependent selection are also studied.

1. GENERAL TWO-SEX FERTILITY SELECTION MODELS

Consider a diploid random mating population with sex-differentiated fertility differences determined at an autosomal locus with multiple alleles A_1, \dots, A_n . More specifically, let the parameters f_{ikjl} and m_{ikjl} be the *fertilities in female and male offspring*, respectively (that is the expected numbers of female and male offspring, respectively), of a mating between a female of genotype $A_i A_k$ and a male of genotype $A_j A_l$ ($i, k, j, l = 1, \dots, n$). The quantities f_{ikjl} and m_{ikjl} represent the female and male fitnesses, respectively, of a mating between an $A_i A_k$ female and an $A_j A_l$ male ($i, k, j, l = 1, \dots, n$).

The fitness parameters satisfy the *symmetry conditions*

$$\begin{aligned} f_{ikjl} &= f_{kijl} = f_{klij} = f_{iklj}, \\ m_{ikjl} &= m_{kijl} = m_{kili} = m_{iklj}, \end{aligned} \quad (1)$$

for $i, k, j, l = 1, \dots, n$, which correspond to the assumption that the genes in the parent genotypes are not ordered. But in general, we may have

$$\begin{aligned} f_{ikjl} &\neq f_{jlik}, \\ m_{ikjl} &\neq m_{jlik}, \end{aligned}$$

whenever $\{j, l\}$ is different from $\{i, k\}$, which means that male and female parents may have distinct roles in fertility determination. We posit *weak selection* by assuming

$$\begin{aligned} f_{ikjl} &= 1 + 0(s), \\ m_{ikjl} &= 1 + 0(s), \end{aligned} \quad (2)$$

where s is small and $0(s)$ denotes any function of s such that $|0(s)/s|$ is bounded as s goes to $0(s \rightarrow 0)$. We say that $0(s)$ is a function of order s . A simple example of a function $0(s)$ is cs where c is a constant.

Assuming an infinite population with nonoverlapping generations and denoting the *frequency of genotype $A_i A_j$ in females* by $2P_{ij}$ if $j \neq i$ and P_{ii} if $j = i$, and *in males* by $2Q_{ij}$ if $j \neq i$ and Q_{ii} if $j = i$ ($i, j = 1, \dots, n$), we have from one generation to the next one

$$\begin{aligned} P'_{ij} &= \frac{\sum_{kl} P_{ik} Q_{jl} f_{ikjl} + \sum_{kl} P_{jl} Q_{ik} f_{jlik}}{2\bar{f}}, \\ Q'_{ij} &= \frac{\sum_{kl} P_{ik} Q_{jl} m_{ikjl} + \sum_{kl} P_{jl} Q_{ik} m_{jlik}}{2\bar{m}}, \end{aligned} \quad (3)$$

for $i, j = 1, \dots, n$, where \bar{f} and \bar{m} represent the mean fertilities in female and male offspring, namely,

$$\begin{aligned}\bar{f} &= \sum_{ikjl} P_{ik} Q_{jl} f_{ikjl}, \\ \bar{m} &= \sum_{ikjl} P_{ik} Q_{jl} m_{ikjl}.\end{aligned}\tag{4}$$

In what follows we show that, after enough generations and with an error of order at most s^3 , we have the approximations

$$\Delta(\frac{1}{2}\bar{f} + \frac{1}{2}\bar{m}) \cong V_x$$

and

$$\Delta(\bar{f}^{1/2} \times \bar{m}^{1/2}) \cong V_x,$$

where Δ denotes the change from one generation to the next one and V_x represents the additive genetic variance in fertility. Since V_x is always non-negative, we conclude at once that the arithmetic average and the geometric average of the mean fertilities in female and male offspring increase as long as V_x is not too small compared to s^3 , that is, as long as there is enough genetic variability. This is the case when the population is not near an equilibrium and selection is weak enough, which means that s is small enough. The fact that the arithmetic average and the geometric average have a similar behavior is also due to weak selection. Finally, the same weight 1/2 given to the mean fertilities in female and male offspring can be explained by symmetry between the sexes in diploid autosomal one-locus models.

The first step in the proof of the approximations is to show that the allelic frequencies are approximately the same in males and females and the genotypic frequencies approximately given by Hardy-Weinberg proportions after sufficient generations have passed. The next step is to note that the rate of change in the allelic frequencies over successive generations are given, with an error of order at most s^2 , by the additive allelic effects on fertility. Finally, the changes in the averages of the mean fertilities over successive generations are deduced from the corresponding changes in the genotypic frequencies.

Let us proceed. Introducing the allelic frequencies in female and male parents

$$\begin{aligned}P_i &= \sum_j P_{ij}, \\ Q_i &= \sum_j Q_{ij},\end{aligned}\tag{5}$$

for $i = 1, \dots, n$, we have in the next generation

$$\begin{aligned} P'_i &= \frac{\sum_k P_{ik} f_{ik..} + \sum_k Q_{ik} f_{..ik}}{2\bar{f}}, \\ Q'_i &= \frac{\sum_k P_{ik} m_{ik..} + \sum_k Q_{ik} m_{..ik}}{2\bar{m}}, \end{aligned} \quad (6)$$

for $i = 1, \dots, n$, where

$$\begin{aligned} f_{ik..} &= \sum_{jl} Q_{jl} f_{ikjl}, \\ f_{..ik} &= \sum_{jl} P_{jl} f_{jlik}, \\ m_{ik..} &= \sum_{jl} Q_{jl} m_{ikjl}, \\ m_{..ik} &= \sum_{jl} P_{jl} m_{jlik}, \end{aligned} \quad (7)$$

for $i, k = 1, \dots, n$. These quantities represent the *marginal fertilities in female and male offspring*, respectively, of a female and male parent, respectively, whose genotype is $A_i A_k$ ($i, k = 1, \dots, n$).

The *allelic frequencies in all parents* are

$$x_i = \frac{P_i + Q_i}{2}, \quad (8)$$

for $i = 1, \dots, n$. Under the assumption of weak selection (2), we have

$$\begin{aligned} \bar{f} &= 1 + 0(s), & \bar{m} &= 1 + 0(s), \\ f_{ik..} &= 1 + 0(s), & m_{ik..} &= 1 + 0(s), \\ f_{..ik} &= 1 + 0(s), & m_{..ik} &= 1 + 0(s), \end{aligned} \quad (9)$$

for $i, k = 1, \dots, n$ and the following lemma ensues:

LEMMA 1. *After enough generations, we have for the allelic and genotypic frequencies in females and males*

$$\begin{aligned} P_i &= x_i + 0(s), & Q_i &= x_i + 0(s), & \Delta P_i &= \Delta x_i + 0(s^2), \\ \Delta Q_i &= \Delta x_i + 0(s^2), & P_{ij} &= x_i x_j + 0(s), & Q_{ij} &= x_i x_j + 0(s), \\ \Delta P_{ij} &= \Delta(x_i x_j) + 0(s^2), & \Delta Q_{ij} &= \Delta(x_i x_j) + 0(s^2), \end{aligned} \quad (10)$$

for $i, j = 1, \dots, n$, where

$$\Delta x_i = 0(s), \quad \Delta(x_i x_j) = 0(s),$$

for $i, j = 1, \dots, n$, and Δ denotes the change from one generation to the next one.

Lemma 1 states that, with an error of order s , Hardy-Weinberg proportions for genotypes in males and females with the same allelic frequencies in both sexes given in (8) are established after enough generations and then, with an error of order s^2 , the changes in the exact allelic and genotypic frequencies are given by the changes in the corresponding approximate frequencies after enough generations. In practice, this means that, to a first approximation, the allelic frequencies in males and females can be assumed equal and the genotypic frequencies given by Hardy-Weinberg proportions. The proof of Lemma 1, presented in the Appendix, follows Nagylaki (1987).

From now on, it will be assumed that *enough generations* have elapsed such that (10) holds.

Then, using (6) and (8), the changes in the allelic frequencies from one generation to the next one take the form

$$\Delta x_i = \frac{\sum_k P_{ik}(f_{ik..} - \bar{f}) + \sum_k Q_{ik}(f_{..ik} - \bar{f})}{4\bar{f}} + \frac{\sum_k P_{ik}(m_{ik..} - \bar{m}) + \sum_k Q_{ik}(m_{..ik} - \bar{m})}{4\bar{m}},$$

for $i = 1, \dots, n$. Therefore, an appeal to (9) and (10) yields

$$\Delta x_i = x_i \alpha_i + 0(s^2), \quad (11)$$

for $i = 1, \dots, n$, where

$$\alpha_i = \frac{\sum_k x_k(f_{ik..} - \bar{f}) + \sum_k x_k(f_{..ik} - \bar{f}) + \sum_k x_k(m_{ik..} - \bar{m}) + \sum_k x_k(m_{..ik} - \bar{m})}{4}, \quad (12)$$

for $i = 1, \dots, n$. The quantities α_i for $i = 1, \dots, n$ are of order s (that is, $0(s)$) and give the rates of change in the allelic frequencies with an error of order s^2 (that is, $0(s^2)$). Moreover, they satisfy

$$\sum_i x_i \alpha_i = 0(s^2) \quad (13a)$$

and, with an error of order s^2 , they minimize the sum of squares

$$SSQ = \frac{\sum_{ikjl} P_{ik} Q_{jl} (f_{ikjl} - \bar{f} - \alpha_i - \alpha_k - \alpha_j - \alpha_l)^2}{4\bar{f}} + \frac{\sum_{ikjl} P_{ik} Q_{jl} (m_{ikjl} - \bar{m} - \alpha_i - \alpha_k - \alpha_j - \alpha_l)^2}{4\bar{m}}. \quad (13b)$$

In order to prove these properties, note first that the minimum of SSQ must be achieved at a critical point. But the derivatives of SSQ with respect to α_i for $i = 1, \dots, n$ vanish if and only if

$$\begin{aligned}
 0 = & \frac{\sum_{kjl} P_{ik} Q_{jl} (f_{ikjl} - \bar{f} - \alpha_i - \alpha_k - \alpha_j - \alpha_l)}{\bar{f}} \\
 & + \frac{\sum_{kjl} P_{jl} Q_{ik} (f_{jlik} - \bar{f} - \alpha_j - \alpha_l - \alpha_i - \alpha_k)}{\bar{f}} \\
 & + \frac{\sum_{kjl} P_{ik} Q_{jl} (m_{ikjl} - \bar{m} - \alpha_i - \alpha_k - \alpha_j - \alpha_l)}{\bar{m}} \\
 & + \frac{\sum_{kjl} P_{jl} Q_{ik} (m_{jlik} - \bar{m} - \alpha_j - \alpha_l - \alpha_i - \alpha_k)}{\bar{m}}, \quad (14)
 \end{aligned}$$

for $i = 1, \dots, n$. Summing over i in (14) yields (13a) and then (14) reduces to (12) by using (9) and (10) and noting that α_i for $i = 1, \dots, n$ is of order s . The properties (13a, b) show that, with an error of order s^2 , the quantities α_i for $i = 1, \dots, n$ are the *additive allelic effects on fertility, or fitness*. Therefore, we have:

LEMMA 2. *The change in the frequency of allele A_i from one generation to the next one but after enough generations is given by*

$$\Delta x_i = x_i \alpha_i + 0(s^2)$$

where α_i is the additive allelic effect on fertility, or fitness, of A_i for $i = 1, \dots, n$.

Note also that (11) implies

$$\begin{aligned}
 \Delta(x_i x_j) &= (\Delta x_i) x_j + x_i (\Delta x_j) + (\Delta x_i)(\Delta x_j) \\
 &= x_i x_j \alpha_i + x_i x_j \alpha_j + 0(s^2) \\
 &= x_i x_j (\alpha_i + \alpha_j) + 0(s^2),
 \end{aligned}$$

for $i, j = 1, \dots, n$. Therefore, from Lemma 1, we have also

$$\begin{aligned}
 \Delta P_{ij} &= x_i x_j (\alpha_i + \alpha_j) + 0(s^2), \\
 \Delta Q_{ij} &= x_i x_j (\alpha_i + \alpha_j) + 0(s^2), \quad (15)
 \end{aligned}$$

for $i, j = 1, \dots, n$.

Owing to (4), (10), and (15), the change in the mean fertility in female offspring from one generation to the next one is

$$\begin{aligned}
 \Delta \bar{f} &= \sum_{ikjl} [\Delta(P_{ik} Q_{jl})] f_{ikjl} \\
 &= \sum_{ikjl} [\Delta(P_{ik} Q_{jl})] (f_{ikjl} - \bar{f}) \\
 &= \sum_{ikjl} [(\Delta P_{ik}) Q_{jl} + P_{ik} (\Delta Q_{jl}) + (\Delta P_{ik})(\Delta Q_{jl})] (f_{ikjl} - \bar{f}) \\
 &= \sum_{ikjl} x_i x_k x_j x_l (\alpha_i + \alpha_k + \alpha_j + \alpha_l) (f_{ikjl} - \bar{f}) + 0(s^3) \\
 &= 2 \sum_i x_i \alpha_i \left[\sum_k x_k (f_{ik..} - \bar{f}) + \sum_k x_k (f_{..ik} - \bar{f}) \right] + 0(s^3).
 \end{aligned}$$

Similarly, the change in the mean fertility in male offspring from one generation to the next one is

$$\Delta \bar{m} = 2 \sum_i x_i \alpha_i \left[\sum_k x_k (m_{ik..} - \bar{m}) + \sum_k x_k (m_{..ik} - \bar{m}) \right] + 0(s^3).$$

Therefore, we have

$$\frac{1}{2} \Delta \bar{f} + \frac{1}{2} \Delta \bar{m} = 4 \sum_i x_i \alpha_i^2 + 0(s^3). \tag{16}$$

Using (10) and (13a), the above equation can be written in the form

$$\Delta(\frac{1}{2} \bar{f} + \frac{1}{2} \bar{m}) = V_\alpha + 0(s^3), \tag{17}$$

where $\bar{f}/2 + \bar{m}/2$ represents the *arithmetic average of the mean fertilities in female and male offspring* and V_α is the *additive genetic variance in fertility, or fitness*, that is,

$$V_\alpha = \sum_{ikjl} P_{ik} Q_{jl} (\alpha_i + \alpha_k + \alpha_j + \alpha_l)^2. \tag{18}$$

Note also that $\Delta \bar{f}$ and $\Delta \bar{m}$ are of order s^2 and then, by Taylor expansions of $\bar{f}^{1/2}$ and $\bar{m}^{1/2}$ as functions of \bar{f} and \bar{m} , respectively, we have

$$\begin{aligned}
 \Delta \bar{f}^{1/2} &= \frac{1}{2\bar{f}^{1/2}} \Delta \bar{f} + 0((\Delta \bar{f})^2) = \frac{1}{2} \Delta \bar{f} + 0(s^3), \\
 \Delta \bar{m}^{1/2} &= \frac{1}{2\bar{m}^{1/2}} \Delta \bar{m} + 0((\Delta \bar{m})^2) = \frac{1}{2} \Delta \bar{m} + 0(s^3),
 \end{aligned} \tag{19}$$

where $\Delta \bar{f}^{1/2}$ and $\Delta \bar{m}^{1/2}$ stand for $\Delta(\bar{f}^{1/2})$ and $\Delta(\bar{m}^{1/2})$, respectively. Hence, we have

$$\begin{aligned}
 \Delta(\bar{f}^{1/2} \times \bar{m}^{1/2}) &= (\Delta \bar{f}^{1/2}) \bar{m}^{1/2} + \bar{f}^{1/2} (\Delta \bar{m}^{1/2}) + (\Delta \bar{f}^{1/2})(\Delta \bar{m}^{1/2}) \\
 &= \frac{1}{2} \Delta \bar{f} + \frac{1}{2} \Delta \bar{m} + 0(s^3),
 \end{aligned} \tag{20}$$

where $\bar{f}^{1/2} \times \bar{m}^{1/2}$ represents the geometric average of the mean fertilities in female and male offspring.

Let us summarize:

RESULT 1. After enough generations, we have for the geometric and arithmetic averages of the mean fertilities in female and male offspring

$$\Delta(\bar{f}^{1/2} \times \bar{m}^{1/2}) = \Delta(\frac{1}{2}\bar{f} + \frac{1}{2}\bar{m}) + O(s^3)$$

and

$$\Delta(\frac{1}{2}\bar{f} + \frac{1}{2}\bar{m}) = V_x + O(s^3),$$

where V_x is the additive genetic variance in fertility, or fitness, given in (18).

2. TWO-SEX FERTILITY-VIABILITY SELECTION MODELS

We want to generalize model (3) by introducing viability differences. Consider that model with

$$\begin{aligned} f_{ikjl} &= u_{ik} v_{jl} \phi_{ikjl}, \\ m_{ikjl} &= u_{ik} v_{jl} \psi_{ikjl}, \end{aligned} \quad (21)$$

for $i, k, j, l = 1, \dots, n$, as parameters and

$$\begin{aligned} u_{ik} &= u_{ki}, \\ v_{jl} &= v_{lj}, \\ \phi_{ikjl} &= \phi_{kijl} = \phi_{kilj} = \phi_{iklj}, \\ \psi_{ikjl} &= \psi_{kijl} = \psi_{kilj} = \psi_{iklj}, \end{aligned}$$

for $i, k, j, l = 1, \dots, n$, as symmetry conditions. Then, we have the recurrence equations

$$\begin{aligned} P'_{ij} &= \frac{\sum_{kl} P_{ik}^* Q_{jl}^* \phi_{ikjl} + \sum_{kl} P_{jl}^* Q_{ik}^* \phi_{jlik}}{2\bar{\phi}^*}, \\ Q'_{ij} &= \frac{\sum_{kl} P_{ik}^* Q_{jl}^* \psi_{ikjl} + \sum_{kl} P_{jl}^* Q_{ik}^* \psi_{jlik}}{2\bar{\psi}^*}, \end{aligned} \quad (22)$$

for $i, j = 1, \dots, n$, where

$$\begin{aligned} \bar{\phi}^* &= \sum_{ikjl} P_{ik}^* Q_{jl}^* \phi_{ikjl}, \\ \bar{\psi}^* &= \sum_{ikjl} P_{ik}^* Q_{jl}^* \psi_{ikjl}, \end{aligned} \quad (23)$$

and

$$P_{ik}^* = \frac{P_{ik} u_{ik}}{\bar{u}}, \quad (24)$$

$$Q_{jl}^* = \frac{Q_{jl} v_{jl}}{\bar{v}},$$

for $i, k, j, l = 1, \dots, n$, with

$$\bar{u} = \sum_{ik} P_{ik} u_{ik}, \quad (25)$$

$$\bar{v} = \sum_{jl} Q_{jl} v_{jl}.$$

The quantities u_{ik} and v_{jl} are interpreted as *viabilities* (that is, probabilities of survival from conception to maturity) of $A_i A_k$ females and $A_j A_l$ males, respectively, while ϕ_{ikjl} and ψ_{ikjl} stand for *fertilities* in female and male offspring, respectively, of a mating between a mature $A_i A_k$ female and a mature $A_j A_l$ male for $i, k, j, l = 1, \dots, n$. Note that, in model (22), viability differences are followed by random mating and reproduction while, in the corresponding model (3) with parameters (21), random mating precedes viability differences and reproduction. But both models are formally equivalent.

The quantities P_{ik} and Q_{jl} represent the frequencies of $A_i A_k$ females and $A_j A_l$ males, respectively, before viability differences take place, while P_{ik}^* and Q_{jl}^* represent the corresponding frequencies after the effects of viability differences for $i, k, j, l = 1, \dots, n$. (See Fig. 1.) Therefore, the first are *genotypic frequencies in immature (young) females and males* while the second are *genotypic frequencies in mature (adult) females and males*. Moreover, we have

$$\bar{f} = \bar{u} \bar{v} \bar{\phi}^*, \quad (26)$$

$$\bar{m} = \bar{u} \bar{v} \bar{\psi}^*,$$

where \bar{u} and \bar{v} are the *mean viabilities* of females and males, respectively, and $\bar{\phi}^*$ and $\bar{\psi}^*$ the *mean fertilities* of mated couples in female and male offspring, respectively.

Our purpose in this section is to show that, if selection is weak, the quantities

$$\bar{u} + \bar{v} + \frac{1}{2} \bar{\phi}^* + \frac{1}{2} \bar{\psi}^* \quad \text{and} \quad \bar{u} \times \bar{v} \times \bar{\phi}^{*1/2} \times \bar{\psi}^{*1/2}$$

increase from one generation to the next one after enough generations have passed and as long as the population is not near an equilibrium. This result will follow from Result 1. Moreover, the result will still be valid if the mean

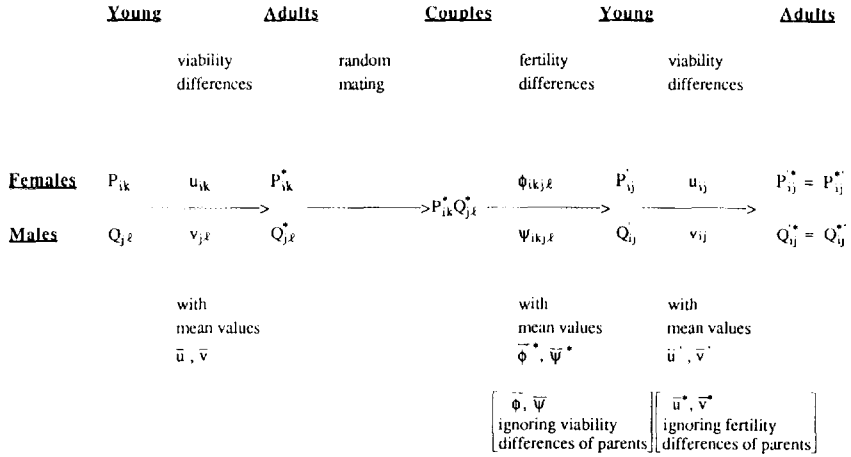


FIG. 1. Schematization of the life cycle and notation.

viabilities \bar{u} and \bar{v} are computed in the next generation, ignoring or not the fertility differences between the parents for that generation.

The same weight given to the mean viabilities of females and males as the same weight given to the mean fertilities in female and male offspring can be explained by symmetry between the sexes. The weight 1 given to the mean viability of one sex compared to the weight 1/2 given to the mean fertility in offspring of one sex can be explained by the fact that parents of one sex contribute for a half the offspring of each sex.

Note that there is another way of writing the recurrence equations (22). Introducing the fitness parameters

$$\begin{aligned} f_{ikjl}^* &= u_{ij} \phi_{ikjl}, \\ m_{ikjl}^* &= v_{ij} \psi_{ikjl}, \end{aligned} \tag{27}$$

for $i, k, j, l = 1, \dots, n$, the recurrence equations for P_{ik}^* and $Q_{j\ell}^*$ for $i, k, j, l = 1, \dots, n$ from one generation to the next one take the form

$$\begin{aligned} P_{ij}^{*'} &= \frac{\sum_{kl} P_{ik}^* Q_{j\ell}^* f_{ikjl}^* + \sum_{kl} P_{jl}^* Q_{ik}^* f_{jlik}^*}{2\bar{f}^*}, \\ Q_{ij}^{*'} &= \frac{\sum_{kl} P_{ik}^* Q_{j\ell}^* m_{ikjl}^* + \sum_{kl} P_{jl}^* Q_{ik}^* m_{jlik}^*}{2\bar{m}^*}, \end{aligned} \tag{28}$$

where

$$\begin{aligned} \bar{f}^* &= \sum_{ikjl} P_{ik}^* Q_{j\ell}^* f_{ikjl}^*, \\ \bar{m}^* &= \sum_{ikjl} P_{ik}^* Q_{j\ell}^* m_{ikjl}^*, \end{aligned}$$

which is the form of the recurrence equations (3). The quantities f_{ikjl}^* and m_{ikjl}^* represent *fitnesses* of females and males, respectively, of genotype $A_i A_j$ whose mother's genotype is $A_i A_k$ and father's genotype $A_j A_l$ for $i, k, j, l = 1, \dots, n$. In general, the symmetry conditions (1) *do not hold* for these quantities whenever $i \neq k$ and $j \neq l$. This is the difference between the equations (28) and the equations (3). The equations (28) will be useful to model kin selection regimes in family-structured populations.

Note also that the *mean fitnesses* satisfy

$$\bar{f}^* = \bar{\phi}^* \bar{u}' \quad \text{and} \quad \bar{m}^* = \bar{\psi}^* \bar{v}',$$

where \bar{u}' and \bar{v}' stand for the mean viabilities of females and males, respectively, in the next generation, that is,

$$\bar{u}' = \sum_{ij} P'_{ij} u_{ij} \quad \text{and} \quad \bar{v}' = \sum_{ij} Q'_{ij} v_{ij}. \quad (29)$$

Assuming *weak selection* in the form

$$\begin{aligned} u_{ik} &= 1 + 0(s), & v_{jl} &= 1 + 0(s), \\ \phi_{ikjl} &= 1 + 0(s), & \psi_{ikjl} &= 1 + 0(s), \end{aligned} \quad (30)$$

for $i, k, j, l = 1, \dots, n$, we have

$$\begin{aligned} \bar{u} &= 1 + 0(s), & \bar{v} &= 1 + 0(s), \\ \bar{u}' &= 1 + 0(s), & \bar{v}' &= 1 + 0(s), \\ \bar{\phi}^* &= 1 + 0(s), & \bar{\psi}^* &= 1 + 0(s). \end{aligned} \quad (31)$$

Defining the means (see Fig. 1)

$$\begin{aligned} \bar{\phi} &= \sum_{ikjl} P_{ik} Q_{jl} \phi_{ikjl}, \\ \bar{\psi} &= \sum_{ikjl} P_{ik} Q_{jl} \psi_{ikjl}, \\ \bar{u}^* &= \sum_{ikjl} P_{ik}^* Q_{jl}^* u_{ij} = \sum_{ij} P_i^* Q_j^* u_{ij}, \\ \bar{v}^* &= \sum_{ikjl} P_{ik}^* Q_{jl}^* v_{ij} = \sum_{ij} P_i^* Q_j^* v_{ij}, \end{aligned} \quad (32)$$

where

$$P_i^* = \sum_j P_{ij}^* \quad \text{and} \quad Q_j^* = \sum_i Q_{ij}^*,$$

for $i, j=1, \dots, n$, which correspond to mean fertilities ignoring viability differences of parents and mean viabilities ignoring fertility differences of parents, and noting that after enough generations

$$\begin{aligned} P_{ij}^* &= P_{ij} + 0(s), & Q_{ij}^* &= Q_{ij} + 0(s), \\ \Delta P_{ij}^* &= \Delta P_{ij} + 0(s^2), & \Delta Q_{ij}^* &= \Delta Q_{ij} + 0(s^2), \\ \Delta P'_{ij} &= \Delta P_{ij} + 0(s^2), & \Delta Q'_{ij} &= \Delta Q_{ij} + 0(s^2), \end{aligned} \quad (33)$$

for $i, j=1, \dots, n$, we can prove the following (see the Appendix for the proof):

LEMMA 3. *After enough generations, we have for the mean fertilities and viabilities*

$$\begin{aligned} \Delta \bar{\phi}^* &= \Delta \bar{\phi} + 0(s^3), & \Delta \bar{\psi}^* &= \Delta \bar{\psi} + 0(s^3), \\ \Delta \bar{u}^* &= \Delta \bar{u} + 0(s^3), & \Delta \bar{v}^* &= \Delta \bar{v} + 0(s^3), \\ \Delta \bar{u}' &= \Delta \bar{u} + 0(s^3), & \Delta \bar{v}' &= \Delta \bar{v} + 0(s^3), \end{aligned} \quad (34)$$

where

$$\Delta \bar{u} = 0(s^2), \quad \Delta \bar{v} = 0(s^2), \quad \Delta \bar{\phi} = 0(s^2), \quad \Delta \bar{\psi} = 0(s^2).$$

Lemma 3 and (31) guarantee that

$$\begin{aligned} \Delta \bar{f} &= (\Delta \bar{u}) \bar{v} \bar{\phi}^* + \bar{u} (\Delta \bar{v}) \bar{\phi}^* + \bar{u} \bar{v} (\Delta \bar{\phi}^*) \\ &\quad + (\Delta \bar{u}) (\Delta \bar{v}) \bar{\phi}^* + (\Delta \bar{u}) \bar{v} (\Delta \bar{\phi}^*) + \bar{u} (\Delta \bar{v}) (\Delta \bar{\phi}^*) \\ &\quad + (\Delta \bar{u}) (\Delta \bar{v}) (\Delta \bar{\phi}^*) \\ &= \Delta \bar{u} + \Delta \bar{v} + \Delta \bar{\phi}^* + 0(s^3) \\ &= \Delta \bar{u}^* + \Delta \bar{v}^* + \Delta \bar{\phi}^* + 0(s^3), \end{aligned}$$

and similarly

$$\Delta \bar{m} = \Delta \bar{u}^* + \Delta \bar{v}^* + \Delta \bar{\psi}^* + 0(s^3).$$

Therefore, using the formula (19), we get

$$\begin{aligned} \frac{1}{2} \Delta \bar{f} + \frac{1}{2} \Delta \bar{m} &= \Delta \bar{u}^* + \Delta \bar{v}^* + \frac{1}{2} \Delta \bar{\phi}^* + \frac{1}{2} \Delta \bar{\psi}^* + 0(s^3) \\ &= \Delta \bar{u}^* + \Delta \bar{v}^* + \Delta \bar{\phi}^{*1/2} + \Delta \bar{\psi}^{*1/2} + 0(s^3) \\ &= (\Delta \bar{u}^*) \bar{v}^* \bar{\phi}^{*1/2} \bar{\psi}^{*1/2} + \bar{u}^* (\Delta \bar{v}^*) \bar{\phi}^{*1/2} \bar{\psi}^{*1/2} \\ &\quad + \bar{u}^* \bar{v}^* (\Delta \bar{\phi}^{*1/2}) \bar{\psi}^{*1/2} + \bar{u}^* \bar{v}^* \bar{\phi}^{*1/2} (\Delta \bar{\psi}^{*1/2}) + 0(s^3) \\ &= \Delta (\bar{u}^* \bar{v}^* \bar{\phi}^{*1/2} \bar{\psi}^{*1/2}) + 0(s^3). \end{aligned}$$

Then, Result 1 with (30) and (33) yields:

RESULT 2. *After enough generations, we have in model (28) with fitness parameters (27)*

$$\Delta(\bar{u}^* \times \bar{v}^* \times \bar{\phi}^{*1/2} \times \bar{\psi}^{*1/2}) = \Delta(\bar{u}^* + \bar{v}^* + \frac{1}{2}\bar{\phi}^* + \frac{1}{2}\bar{\psi}^*) + 0(s^3)$$

and

$$\Delta(\bar{u}^* + \bar{v}^* + \frac{1}{2}\bar{\phi}^* + \frac{1}{2}\bar{\psi}^*) = V_{z^*} + 0(s^3), \quad (35)$$

where V_{z^*} is the additive genetic variance in fitness (18) computed with the fitness parameters (21) and the genotypic frequencies (24).

Obviously, Result 2 is valid with \bar{u}^* and \bar{v}^* replaced by \bar{u} and \bar{v} , respectively. Owing to Lemma 3, it is also valid with \bar{u}^* and \bar{v}^* replaced by \bar{u}' and \bar{v}' , respectively. This case with $\phi_{ikjl} = \psi_{ikjl}$ for $i, k, j, l = 1, \dots, n$ is due to Nagylaki (1987). The main advantage of the result with \bar{u}^* and \bar{v}^* is that the mean viabilities \bar{u}^* and \bar{v}^* and the mean fertilities $\bar{\phi}^*$ and $\bar{\psi}^*$ are defined with respect to the same genotypic frequencies.

3. PARENT-TO-OFFSPRING AND SIB-TO-SIB ALTRUISM SELECTION MODELS

Classical kin selection models in family-structured populations assume that the fitness of an individual is affected by the behaviors of its parents and/or its sibs in addition to its own behavior. For instance, an altruistic behavior of a male or a female might decrease the individual's own fitness but increase the fitnesses of male and female offspring and/or sibs irrespective of their genotype.

In a one-locus genetic framework, if an individual of genotype $A_i A_j$ adopts an altruistic behavior with probability h_{ij} ($= h_{ji}$), called its *phenotype* for $i, j = 1, \dots, n$, and if such a behavior has small sex-differentiated effects on the fitnesses of kin (specifically, sibs and offspring) and if mating is at random, then we have model (28) with fitness parameters

$$\begin{aligned} f_{ikjl}^* &= 1 - \gamma_1^v sh_{ij} + \beta_M^v sh_{ik} + \beta_F^v sh_{jl} \\ &\quad + (\beta_S^v s + \beta_B^v s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \\ m_{ikjl}^* &= 1 - \gamma_1^s sh_{ij} + \beta_M^s sh_{ik} + \beta_F^s sh_{jl} \\ &\quad + (\beta_S^s s + \beta_B^s s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \end{aligned} \quad (36)$$

for $i, k, j, l = 1, \dots, n$, where $\gamma_1^i, \beta_M^i, \beta_F^i, \beta_S^i, \beta_B^i, \gamma_1^j, \beta_M^j, \beta_F^j, \beta_S^j, \beta_B^j$ are nonnegative coefficients in which I stands for individual, M for mother, F for father, S for sister, B for brother, ♀ for female and ♂ for male. The coefficients γ_1^i and γ_1^j correspond to *costs* while all other coefficients correspond to *benefits*. The presence of s positive and small which multiplies all coefficients serves to model weak selection. The above expressions for f_{ikjl}^* and m_{ikjl}^* represent Taylor expansions of smooth functions of $h_{ij}, h_{ik}, h_{jl}, h_{il}, h_{kj}, h_{kl}$ for $i, k, j, l = 1, \dots, n$. These expressions generalize the additive models of Cavalli-Sforza and Feldman (1978), Uyenoyama and Feldman (1981), and Uyenoyama *et al.* (1981), among others.

The quantities (36) can be written in the form (27) with

$$\begin{aligned} u_{ij} &= 1 - \gamma_1^i sh_{ij} + 0(s^2), \\ v_{ij} &= 1 - \gamma_1^j sh_{ij} + 0(s^2), \\ \phi_{ikjl} &= 1 + \beta_M^i sh_{ik} + \beta_F^i sh_{jl} + (\beta_S^i s + \beta_B^i s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \\ \psi_{ikjl} &= 1 + \beta_M^j sh_{ik} + \beta_F^j sh_{jl} + (\beta_S^j s + \beta_B^j s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \end{aligned} \quad (37)$$

for $i, k, j, l = 1, \dots, n$. Note from (28) and (36) that after one generation the genotypic frequencies in females and males satisfy

$$\begin{aligned} P_{ij}^* &= P_i^* Q_j^* + 0(s), \\ Q_{ij}^* &= P_i^* Q_j^* + 0(s), \end{aligned}$$

where P_i^* and Q_j^* are the corresponding allelic frequencies, that is,

$$P_i^* = \sum_j P_{ij}^* \quad \text{and} \quad Q_j^* = \sum_i Q_{ij}^*,$$

for $i, j = 1, \dots, n$. Then, introducing the notation

$$x_i^* = \frac{P_i^* + Q_i^*}{2},$$

for $i = 1, \dots, n$ for the *allelic frequencies in the whole population* and the quantity

$$\bar{h}^* = \sum_{ij} P_i^* Q_j^* h_{ij}, \quad (38)$$

which represents the *mean phenotype in the whole population*, Result 2 and Lemma 2 with (7), (8), (10), (21), (33), and (37) in hand yield:

RESULT 3. After enough generations in model (28) with fitness parameters (36), we have from one generation to the next one

$$\Delta x_i^* = A s x_i^* \delta_i^* + 0(s^2), \quad (39)$$

for $i = 1, \dots, n$, and

$$\Delta \bar{h}^* = A s V_{\delta^*} + 0(s^2), \quad (40)$$

where

$$A = - \left[\frac{\gamma_I^v + \gamma_I^s}{2} \right] + \left[\frac{\beta_M^v + \beta_F^v + \beta_S^v + \beta_B^v + \beta_M^s + \beta_F^s + \beta_S^s + \beta_B^s}{4} \right],$$

$$\delta_i^* = \sum_j x_j^* (h_{ij} - \bar{h}^*),$$

for $i = 1, \dots, n$, and

$$V_{\delta^*} = \sum_{ij} P_i^* Q_j^* (\delta_i^* + \delta_j^*)^2. \quad (41)$$

Actually, Result 2 yields

$$2As \Delta \bar{h}^* = 2A^2 s^2 V_{\delta^*} + 0(s^3),$$

which is equivalent to (40).

It can easily be checked that, after enough generations and with an error of order s , the quantities δ_i^* for $i = 1, \dots, n$ are such that

$$\sum_{ij} P_i^* Q_j^* (h_{ij} - \bar{h}^* - \delta_i^* - \delta_j^*)^2$$

is minimum. Thus, these quantities are the *additive allelic effects on phenotype*, and the quantity V_{δ^*} is the *additive genetic variance in phenotype*.

A more important remark is that we get exactly the same result, that is, Result 3, with an "inclusive fitness formulation" which has (21) in the form

$$\begin{aligned} f_{ikjl}^{\text{incl}} &= u_{ik}^{\text{incl}} v_{jl}^{\text{incl}}, \\ m_{ikjl}^{\text{incl}} &= u_{ik}^{\text{incl}} v_{jl}^{\text{incl}}, \end{aligned} \quad (42)$$

where

$$\begin{aligned} u_{ik}^{\text{incl}} &= 1 + \left[-\gamma_I^v + \frac{\beta_M^v + \beta_S^v + \beta_M^s + \beta_S^s}{2} \right] s h_{ik} + 0(s^2), \\ v_{jl}^{\text{incl}} &= 1 + \left[-\gamma_I^s + \frac{\beta_F^v + \beta_B^v + \beta_F^s + \beta_B^s}{2} \right] s h_{jl} + 0(s^2), \end{aligned} \quad (43)$$

for $i, k, j, l = 1, \dots, n$. The multiplicative factor $1/2$ in (43) can be viewed as the *coefficient of relatedness* of a mother (or father) to her (or his) son (or daughter) and of a sister (or brother) to her (or his) sister (or brother) compared to 1 for the coefficient of relatedness of an individual (male or female) to itself. This is in agreement with Hamilton (1964) who measured the relatedness of an individual to a relative by the expected fraction of genes identical by descent in the relative to one or more genes in the individual. Note also that reproductive values of males and females in diploid populations under weak selection are equal and therefore do not come into play in (43).

4. ALTRUISM SELECTION MODELS WITH PARTIAL ADOPTION OF OFFSPRING

As proposed by Karlin and Matessi (1983) for kin selection models, consider the case of altruism in family-structured models with partial “adoption” of offspring. More specifically, let $1 - \lambda$ be the expected proportion of offspring chosen at random in the population that are adopted by a family. Therefore, λ is the probability that an offspring stays in the family of its own parents and $1 - \lambda$ the probability that it joins a family of parents chosen at random. It is assumed that this occurs independently for all offspring. Moreover, altruistic behaviors benefit sibs and adopted offspring irrespective of their origin.

If we proceed as in Section 3 but take into account the possibility for offspring to be adopted, we obtain model (28) with fitness parameters

$$\begin{aligned} \tilde{f}_{ikjl}^* &= 1 - \gamma_1^i sh_{ij} + \lambda \left\{ (\beta_M^i sh_{ik} + \beta_F^i sh_{jl}) \right. \\ &\quad \left. + \lambda(\beta_S^i s + \beta_B^i s) \left[\frac{h_{ij} + h_{ii} + h_{kj} + h_{kl}}{4} \right] \right. \\ &\quad \left. + (1 - \lambda)(\beta_S^i s + \beta_B^i s) \bar{h}^* \right\} \\ &\quad + (1 - \lambda) \{ (\beta_M^i s + \beta_F^i s + \beta_S^i s + \beta_B^i s) \bar{h}^* \} + O(s^2), \end{aligned} \tag{44}$$

$\tilde{m}_{ikjl}^* = \text{idem with } \tilde{f},$

for $i, k, j, l = 1, \dots, n$, where $O(s^2)$ is frequency-dependent through its dependence on \bar{h}^* defined in (38). Dividing \tilde{f}_{ikjl}^* by

$$1 + [(1 - \lambda)(\beta_M^i s + \beta_F^i s) + (1 - \lambda)(1 + \lambda)(\beta_S^i s + \beta_B^i s)] \bar{h}^*$$

to get f_{ikjl}^* , and \bar{m}_{ikjl}^* by the corresponding quantity with \mathfrak{J} to get m_{ikjl}^* , for $i, k, j, l = 1, \dots, n$, we have model (28) with fitness parameters

$$\begin{aligned} f_{ikjl}^* &= 1 - \gamma_1^i sh_{ij} + \lambda(\beta_M^i sh_{ik} + \beta_F^i sh_{jl}) \\ &\quad + \lambda^2(\beta_S^i s + \beta_B^i s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \end{aligned} \quad (45)$$

$$m_{ikjl}^* = \text{idem with } \mathfrak{J},$$

for $i, k, j, l = 1, \dots, n$, which can be put into the form (27) with

$$\begin{aligned} u_{ij} &= 1 - \gamma_1^i sh_{ij} + 0(s^2), \\ v_{ij} &= 1 - \gamma_1^j sh_{ij} + 0(s^2), \\ \phi_{ikjl} &= 1 + \lambda(\beta_M^i sh_{ik} + \beta_F^i sh_{jl}) \\ &\quad + \lambda^2(\beta_S^i s + \beta_B^i s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \\ \psi_{ikjl} &= 1 + \lambda(\beta_M^j sh_{ik} + \beta_F^j sh_{jl}) \\ &\quad + \lambda^2(\beta_S^j s + \beta_B^j s) \left[\frac{h_{ij} + h_{il} + h_{kj} + h_{kl}}{4} \right] + 0(s^2), \end{aligned} \quad (46)$$

for $i, k, j, l = 1, \dots, n$, where the function $0(s^2)$ depends on \bar{h}^* . Given its relative order of magnitude, such a frequency-dependence in fitness parameters is negligible in the change of genotypic and allelic frequencies and in the computation of additive allelic effects on fitness. It is also negligible: (1) in the change of genotypic and allelic frequencies, (2) in the computation of additive allelic effects on fitness, and (3) in the change of \bar{u}^* , \bar{v}^* , $\bar{\phi}^*$, and $\bar{\psi}^*$, owing to the following ancillary result:

LEMMA 4. *After enough generations in model (28) with fitness parameters in the form (27) with (46), we have from one generation to the next one*

$$\begin{aligned} \Delta u_{ij} &= 0(s^3), & \Delta v_{ij} &= 0(s^3), \\ \Delta \phi_{ikjl} &= 0(s^3), & \Delta \psi_{ikjl} &= 0(s^3), \end{aligned} \quad (47)$$

for $i, k, j, l = 1, \dots, n$.

Therefore, a comparison of (46) with (37) yields:

RESULT 4. *After enough generations in model (28) with the fitness parameters (45), Result 3 holds with*

$$A = - \left[\frac{\gamma_1^i + \gamma_1^j}{2} \right] + \left[\frac{\lambda\beta_M^i + \lambda\beta_F^i + \lambda^2\beta_S^i + \lambda^2\beta_B^i + \lambda\beta_M^j + \lambda\beta_F^j + \lambda^2\beta_S^j + \lambda^2\beta_B^j}{4} \right].$$

An equivalent inclusive fitness formulation in the form (42) has

$$u_{ik}^{\text{incl}} = 1 + \left[-\gamma_i^i + \frac{\lambda\beta_M^i + \lambda^2\beta_S^i + \lambda\beta_M^j + \lambda^2\beta_S^j}{2} \right] sh_{ik} + O(s^2),$$

$$v_{jl}^{\text{incl}} = 1 + \left[-\gamma_i^j + \frac{\lambda\beta_F^i + \lambda^2\beta_B^i + \lambda\beta_F^j + \lambda^2\beta_B^j}{2} \right] sh_{jl} + O(s^2),$$

for $i, k, j, l = 1, \dots, n$. This suggests $\lambda/2$ as the coefficient of relatedness of a mother (or father) to an offspring (male or female) and $\lambda^2/2$ as the coefficient of relatedness of an offspring (male or female) to another offspring (male or female). This again is in agreement with Hamilton's definition for the coefficient of relatedness to be used in kin selection theory since λ is the probability for an offspring not to be adopted and λ^2 is the probability for two sibs not to be adopted.

5. DISCUSSION

In this paper, we have first generalized a result of Nagylaki (1987) for fertility–viability selection models to include sex-differentiated fertilities of matings. Nagylaki had previously shown that for a single, multiallelic, autosomal locus subject to weak fertility and viability selection in random mating dioecious diploid populations undergoing nonoverlapping generations, the change in the geometric average of the mean fitnesses of males and females from one generation to the next one is approximately equal to the additive genetic variance in fitness, under the restriction that enough generations have passed and the population is not near equilibrium. The mean fitnesses of males and females were defined as the mean viabilities of males and females, respectively, times the square root of the mean fertility. Introducing fertilities of mated pairs according to the sex of offspring, we have shown that fertility–viability selection models can be cast as two-sex fertility selection models in which the change in the arithmetic average, as well as the change in the geometric average, of the mean fertilities in male and female offspring is approximately given by the additive genetic variance in fertility, if selection is weak enough and under the same restrictions as previously (Result 1). With the inclusion of viability differences, the fertilities of mated pairs in male and female offspring have both to be multiplied by the viabilities of the male and female parents to give the new fertilities in male and female offspring. The same is true for the means. As a consequence, the mean viabilities of males and females have twice the weight of the mean fertilities of mated pairs in male and female offspring in the expression of the corresponding arithmetic and geometric averages in

agreement with Nagylaki (Result 2). But it must be stressed that Results 1 and 2 do not guarantee the increase of the averages over successive generations even if selection is weak since (1) the results are based on Hardy-Weinberg approximations for the genotypic frequencies in males and females, which are valid if enough generations have passed (Lemma 1), and (2) the additive genetic variances can become negligible compared to the errors made on the approximations for the changes in the averages, which occurs near equilibrium with additive allelic effects on fertility becoming very small.

In two-sex viability selection models with no fertility differences, the geometric average in Result 2 becomes the product of the mean viabilities in females and males. Exact one-locus multiallele models of this kind have been previously analysed (see, e.g., Karlin and Lessard, 1986; Lessard, 1989). In this case, it is known that, although rare and small, a decrease of the product of the mean viabilities from one equilibrium to the next one following the invasion of a mutant allele is possible. This confirms that weak selection is an essential feature to predict the increase of the averages of the mean fertilities in general two-sex fertility selection models from Results 1 and 2.

The changes in the allelic frequencies from one generation to the next one in two-sex fertility selection models can be approximated by means of the additive allelic effects on fertility if selection is weak. Note that Eq. (11) for those changes can be put into Wright's (1942, 1969) form. As a matter of fact, Lemma 1 with the assumption of weak selection (2) entails for the arithmetic average of the mean fertilities in female and male offspring, after enough generations have passed,

$$\begin{aligned}
 \frac{\bar{f} + \bar{m}}{2} &= \sum_{ikjl} P_{ik} Q_{jl} \left[\frac{f_{ikjl} + m_{ikjl}}{2} \right] \\
 &= \sum_{ikjl} x_i x_k x_j x_l \left[\frac{f_{ikjl} + m_{ikjl}}{2} \right] \\
 &\quad + \sum_{ikjl} (P_{ik} Q_{jl} - x_i x_k x_j x_l) \left[\frac{f_{ikjl} + m_{ikjl}}{2} \right] \\
 &= \sum_{ikjl} x_i x_k x_j x_l \left[\frac{f_{ikjl} + m_{ikjl}}{2} \right] + 0(s^2), \tag{48}
 \end{aligned}$$

from which

$$\frac{d}{dx_i} \left[\frac{\bar{f} + \bar{m}}{2} \right] = \frac{4\alpha_i}{1 - x_i} + 0(s^2),$$

for $i = 1, \dots, n$, where x_i is the frequency of allele A_i for $i = 1, \dots, n$, d/dx_i denotes the formal derivative with respect to x_i with $x_j/(1-x_i)$ kept constant for all $j \neq i$ ($i = 1, \dots, n$) and α_i is the additive allelic effect on fertility of allele A_i for $i = 1, \dots, n$. Therefore, Eq. (11) becomes

$$\Delta x_i = \frac{x_i(1-x_i)}{4} \frac{d}{dx_i} \left[\frac{\bar{f} + \bar{m}}{2} \right] + 0(s^2), \quad (49)$$

for $i = 1, \dots, n$, and the arithmetic average $(\bar{f} + \bar{m})/2$ is indeed an approximate *adaptive* topography in Wright's sense. The geometric average $(\bar{f} \times \bar{m})^{1/2}$ satisfies the same property.

Another important remark concerning Eq. (11) is that

$$4x_i \alpha_i = x_i \left\{ \frac{\partial}{\partial x_i} \left[\frac{\bar{f} + \bar{m}}{2} \right] - \sum_j x_j \frac{\partial}{\partial x_j} \left[\frac{\bar{f} + \bar{m}}{2} \right] \right\} + 0(s^2), \quad (50)$$

for $i = 1, \dots, n$, where $\partial/\partial x_i$ denotes the partial derivative with respect to x_i without any constraint. The first term of the right hand member in Eq. (50) is, with an error of order s^2 , the i th component of the projection of the Shahshahani gradient of $(\bar{f} + \bar{m})/2$ into the simplex of frequency vectors (see, e.g., Akin, 1979). With this interpretation, Eq. (11) with (50) in hand can be viewed as an extension of Kimura's (1958) *maximum principle*.

These results on two-sex fertility selection models can be applied to fertility–viability selection models by adding or multiplying the mean viabilities of females and males to both the mean fertilities in female and male offspring. The corresponding adaptive topographies are given in Result 2.

It is interesting that fertility–viability selection models can be put into the framework of general fertility selection models. Even more interesting is the fact that selection models in which the fitness of an individual depends on its genotype and the genotypes of its parents and sibs can be viewed as fertility–viability selection models. In particular, this makes possible the analysis of kin selection models in family-structured populations when selection is weak. Under this assumption, the kin selection models which have been analysed in Sections 3 and 4 are similar to the additive models considered by Cavalli-Sforza and Feldman (1978), except allowing for sex differences in costs and benefits of altruistic acts and possibilities of adoption of offspring. The assumption of weak selection (which corresponds to small costs and benefits associated with altruistic acts) is used to write the fitness of individuals according to their genotypes and their parents' genotypes in an appropriate form (Eq. (27)). This is crucial for the correspondance between the kin selection models and the

fertility–viability selection models to hold. That correspondence is important since it allows an alternative to the approach of Cavalli–Sforza and Feldman, who modeled kin selection as a kind of frequency-dependent selection. Moreover, since the fertility–viability selection models were shown to follow approximate adaptive topographies, inspection of these topographies reveals when altruistic traits should evolve (Results 3 and 4).

Our results on kin selection models are in agreement with Hamilton's (1964) principle on the maximization of the mean inclusive fitness. This was to be expected since weak selection makes the models practically additive and, in additive models, the conditions for equilibrium and initial increase in frequency of mutant alleles are known to agree with Hamilton's principle (see, e.g., Cavalli–Sforza and Feldman, 1978; Uyenoyama *et al.*, 1981). Our results apply to evolution away from equilibria, however, and therefore complement the results previously obtained.

Our approach also allows an interpretation for the coefficients of relatedness introduced by Hamilton to define inclusive fitness. These appear as the results of weights given to mean viabilities and mean fertilities in adaptive topographies for fertility–viability selection models.

One of the main theoretical interests in introducing inclusive fitnesses was to transform frequency-dependent fitnesses (neighbor-modulated fitnesses in Hamilton's (1964) terminology) into frequency-independent fitnesses to which the Fundamental Theorem of Natural Selection, that is, the maximization of the mean fitness, applies. We have shown that, in family-structured populations, kin selection models can be cast as fertility–viability selection models to which extensions of the Fundamental Theorem hold without any recourse to inclusive fitnesses. Our approach also clearly support the necessity of the assumption of weak selection to have at least approximate adaptive topographies given by appropriate mean fitnesses in family-structured populations under kin selection.

Note that several familial selection models (Haldane, 1924) could be treated in a similar way as fertility–viability selection models. More generally, our approach might have applications to a wide variety of models and selection regimes other than those examined in this paper. In this respect, the approach might play a unifying role in our understanding of selection models.

More general population structures for kin selection models as those considered in Hamilton (1970) and Taylor (1989) remain to be studied. Other interpretations for the evolution of altruism based on conflicts between individual selection and group selection (see, e.g., Wade, 1980, Aoki, 1982; Uyenoyama, 1984) which come into play following a decomposition of fitness within and between groups or families are also of interest.

Finally, as suggested in Nagylaki (1987) and illustrated in Section 4, the

fitness parameters considered in this paper could be frequency-dependent without affecting the results as long as their change over two successive generations is of order s^3 (that is, $0(s^3)$) after enough generations.

APPENDIX

Proof of Lemma 1. From (5), (6), (8), and (9), we have in the next generation

$$P'_i = x_i (1 + 0(s)),$$

and similarly for Q'_i , $i = 1, \dots, n$, in such a way that

$$x'_i = \frac{P'_i + Q'_i}{2} = x_i (1 + 0(s)), \quad (\text{A1})$$

for $i = 1, \dots, n$. Therefore

$$P''_i = x'_i (1 + 0(s)) = x'_i + 0(s), \quad (\text{A2})$$

and similarly for Q''_i , $i = 1, \dots, n$.

From (3), (A1), and (A2), we have after one more generation

$$\begin{aligned} P''_{ij} &= \left[\frac{P'_i Q'_j + P'_j Q'_i}{2} \right] (1 + 0(s)) \\ &= x'_i x'_j (1 + 0(s)) \\ &= x''_i x''_j (1 + 0(s)) \\ &= x''_i x''_j + 0(s), \end{aligned} \quad (\text{A3})$$

and similarly for Q''_{ij} , $i, j = 1, \dots, n$. Note that the last function $0(s)$ in (A3) is a function of $\mathbb{P} = \|P_{ij}\|_{i,j=1}^n$ and $\mathbb{Q} = \|Q_{ij}\|_{i,j=1}^n$ which can be written in the form

$$sg_{ij}(s, \mathbb{P}, \mathbb{Q}), \quad (\text{A4})$$

where g_{ij} is bounded as $s \rightarrow 0$.

Using (A3) and (A4) after one more generation, we find

$$P'''_{ij} - P''_{ij} = x''_i x''_j - x''_i x''_j + s [g_{ij}(s, \mathbb{P}', \mathbb{Q}') - g_{ij}(s, \mathbb{P}, \mathbb{Q})], \quad (\text{A5})$$

for $i, j = 1, \dots, n$, where $\mathbb{P}' = \|P'_{ij}\|_{i,j=1}^n$ and $\mathbb{Q}' = \|Q'_{ij}\|_{i,j=1}^n$. But (A1) implies

$$x'''_i x'''_j - x''_i x''_j = x''_i x''_j (1 + 0(s)) - x''_i x''_j = 0(s). \quad (\text{A6})$$

Therefore, Eq. (A5) yields that ΔP_{ij} is $0(s)$ after two generations and similarly for ΔQ_{ij} , $i, j = 1, \dots, n$. Then, after two generations, a Taylor expansion of $g_{ij}(s, \mathbb{P}', \mathbb{Q}')$ around \mathbb{P} and \mathbb{Q} gives

$$g_{ij}(s, \mathbb{P}', \mathbb{Q}') - g_{ij}(s, \mathbb{P}, \mathbb{Q}) = 0(s), \quad (\text{A7})$$

for $i, j = 1, \dots, n$. We conclude from (A5) and (A7) that after four generations

$$\Delta P_{ij} = \Delta(x_i x_j) + 0(s^2), \quad (\text{A8})$$

and similarly for ΔQ_{ij} , $i, j = 1, \dots, n$. Summing over j in (A8) yields

$$\Delta P_i = \Delta x_i + 0(s^2), \quad (\text{A9})$$

and similarly for ΔQ_i , $i = 1, \dots, n$. Finally, (A1) and (A6) imply that Δx_i and $\Delta(x_i x_j)$ are $0(s)$ for $i, j = 1, \dots, n$.

Proof of Lemma 3. Note first that (10), (25), (30), and (31) yield

$$\Delta \bar{u} = \sum_{ik} (\Delta P_{ik}) u_{ik} = \sum_{ik} (\Delta P_{ik})(u_{ik} - \bar{u}) = 0(s^2), \quad (\text{A10})$$

and similarly for $\Delta \bar{v}$. From (24), we have

$$P_{ik}^* \bar{u} = P_{ik} u_{ik}, \quad (\text{A11})$$

which implies that

$$P_{ik}^* = P_{ik} + 0(s), \quad (\text{A12})$$

for $i, k = 1, \dots, n$. Similarly, we have

$$Q_{jl}^* = Q_{jl} + 0(s), \quad (\text{A13})$$

for $j, l = 1, \dots, n$. Moreover, (A11) gives

$$(\Delta P_{ik}^*) \bar{u} + P_{ik}^* (\Delta \bar{u}) + (\Delta P_{ik}^*) (\Delta \bar{u}) = (\Delta P_{ik}^*) u_{ik},$$

which leads to

$$\Delta P_{ik}^* = \Delta P_{ik} + 0(s^2), \quad (\text{A14})$$

for $i, k = 1, \dots, n$, by appeal to (A10). Similarly, we have

$$\Delta Q_{jl}^* = \Delta Q_{jl} + 0(s^2), \quad (\text{A15})$$

for $j, l = 1, \dots, n$. With (A12), (A13), (A14), (A15), and Lemma 1 in hand, we have after enough generations

$$\begin{aligned} \Delta(P_{ik}^* Q_{jl}^*) &= (\Delta P_{ik}^*) Q_{jl}^* + P_{ik}^* (\Delta Q_{jl}^*) + (\Delta P_{ik}^*)(\Delta Q_{jl}^*) \\ &= (\Delta P_{ik}) Q_{jl} + P_{ik} (\Delta Q_{jl}) + (\Delta P_{ik})(\Delta Q_{jl}) + 0(s^2) \\ &= \Delta(P_{ik} Q_{jl}) + 0(s^2), \end{aligned} \quad (\text{A16})$$

for $i, k, j, l = 1, \dots, n$, where

$$\Delta(P_{ik} Q_{jl}) = 0(s),$$

for $i, k, j, l = 1, \dots, n$. Therefore, the conditions of weak selection (30) guarantee

$$\begin{aligned} \Delta \bar{\phi}^* &= \sum_{ikjl} [\Delta(P_{ik}^* Q_{jl}^*)] \phi_{ikjl} \\ &= \sum_{ikjl} [\Delta(P_{ik}^* Q_{jl}^*)] (\phi_{ikjl} - \bar{\phi}) \\ &= \sum_{ikjl} [\Delta(P_{ik} Q_{jl})] (\phi_{ikjl} - \bar{\phi}) + 0(s^3), \\ &= \Delta \bar{\phi} + 0(s^3), \end{aligned}$$

where

$$\Delta \bar{\phi} = 0(s^2),$$

from which

$$\Delta \left(\frac{1}{\bar{\phi}^*} \right) = -\frac{1}{\bar{\phi}^{*2}} \Delta \bar{\phi}^* + 0((\Delta \bar{\phi}^*)^2) = 0(s^2). \quad (\text{A17})$$

Similarly, we have

$$\Delta \bar{\psi}^* = \Delta \bar{\psi} + 0(s^3), \quad \Delta \bar{u}^* = \Delta \bar{u} + 0(s^3), \quad \Delta \bar{v}^* = \Delta \bar{v} + 0(s^3),$$

where

$$\Delta \bar{\psi} = 0(s^2), \quad \Delta \bar{u} = 0(s^2), \quad \Delta \bar{v} = 0(s^2),$$

from which in particular

$$\Delta \left(\frac{1}{\bar{\psi}^*} \right) = 0(s^2). \quad (\text{A18})$$

Owing to (31), (A16), and (A17), the system of equations (22) and Lemma 1 yield

$$\begin{aligned}
\Delta P'_{ij} &= \frac{1}{2\bar{\phi}^*} \left\{ \sum_{kl} [\Delta(P_{ik}^* Q_{jl}^*)] \phi_{ikjl} + \sum_{kl} [\Delta(P_{jl}^* Q_{ik}^*)] \phi_{jilk} \right\} + 0 \left(\Delta \left(\frac{1}{\bar{\phi}^*} \right) \right) \\
&= \frac{1}{2} \left\{ \sum_{kl} [\Delta(P_{ik} Q_{jl})] + \sum_{kl} [\Delta(P_{jl} Q_{ik})] \right\} + 0(s^2) \\
&= \frac{1}{2} \left\{ \sum_{kl} [(\Delta P_{ik}) Q_{jl} + P_{ik} (\Delta Q_{jl}) + (\Delta P_{ik})(\Delta Q_{jl})] \right. \\
&\quad \left. + \sum_{kl} [(\Delta P_{jl}) Q_{ik} + P_{jl} (\Delta Q_{ik}) + (\Delta P_{jl})(\Delta Q_{ik})] \right\} + 0(s^2) \\
&= (\Delta x_i) x_j + x_i (\Delta x_j) + (\Delta x_i)(\Delta x_j) + 0(s^2) \\
&= \Delta(x_i x_j) + 0(s^2) \\
&= \Delta P_{ij} + 0(s^2), \tag{A19}
\end{aligned}$$

for $i, j = 1, \dots, n$. Similarly, we have

$$\Delta Q'_{ij} = \Delta Q_{ij} + 0(s^2), \tag{A20}$$

for $i, j = 1, \dots, n$. Therefore, we have

$$\begin{aligned}
\Delta \bar{u}' &= \sum_{ij} (\Delta P'_{ij}) u_{ij} \\
&= \sum_{ij} (\Delta P'_{ij})(u_{ij} - \bar{u}) \\
&= \sum_{ij} (\Delta P_{ij})(u_{ij} - \bar{u}) + 0(s^3) \\
&= \Delta \bar{u} + 0(s^3), \tag{A21}
\end{aligned}$$

and similarly

$$\Delta \bar{v}' = \Delta \bar{v} + 0(s^3), \tag{A22}$$

which completes the proof.

Proof of Lemma 4. Any function $0(s^2)$ in (46) can be written in the form

$$s^2 \mathcal{F}(s, \bar{h}^*),$$

where \mathcal{F} is a bounded function as $s \rightarrow 0$. On the other hand, (A16) is still valid with (46) and implies after enough generations

$$\begin{aligned}\Delta \bar{h}^* &= \sum_{ij} [\Delta(P_i^* Q_j^*)] h_{ij} \\ &= \sum_{ijkl} [\Delta(P_{ik}^* Q_{jl}^*)] h_{ij} \\ &= 0(s).\end{aligned}$$

Then, a Taylor expansion of \mathcal{F} around \bar{h}^* yields

$$\Delta \mathcal{F}(s, \bar{h}^*) = 0(s\bar{h}^*) = 0(s),$$

from which

$$\Delta[s^2 \mathcal{F}(s, \bar{h}^*)] = s^2 0(s) = 0(s^3).$$

This is the order of magnitude for the change of u_{ij} , v_{ij} , ϕ_{ijkl} , and ψ_{ijkl} in (46) for $i, k, j, l = 1, \dots, n$, after enough generations.

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