

Adaptive Topography in Fertility–Viability Selection Models: The Haplodiploid Case

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Received August 6, 1993

A linear combination of partial changes of mean fitnesses from one generation to the next one is shown to be approximately equal to the additive genetic variance in fitness after enough generations and away from equilibrium in random mating haplodiploid populations under arbitrary weak frequency-dependent selection on sex-differentiated viability of individuals and sex-differentiated fertility of matings controlled at a single multiallelic locus. The result can be applied to *X*-linked locus models in diploid populations. The result is used to deduce approximate adaptive topographies for frequency-independent selection models in the cases of nonsex-differentiated fertilities and multiplicative sex-differentiated fertilities and for kin selection models in family-structured populations under the assumptions of single insemination and multiple insemination of females. Multiple insemination creates frequency-dependent selection regimes. © 1994 Academic Press, Inc.

INTRODUCTION

Evolution at a single multiallelic autosomal locus under arbitrary weak selection on fertility and viability has been studied in a previous paper (Lessard, 1993). Considering sex-differentiated viabilities of zygotes and sex-differentiated fertilities of mated females in random mating diploid populations undergoing discrete nonoverlapping generations and assuming that these fitness parameters are close enough to 1, it has been shown that after enough generations have passed the change in a weighted sum of the mean viabilities of females and males and the mean fertilities in female and male offspring is approximately equal to the additive genetic variance in fitness. In the weighted sum, the mean viabilities have weight 1 and the mean fertilities weight $\frac{1}{2}$. These weights can be explained by the facts that, in diploid models, all males and all females of a given generation participate equally to reproduction and each group contributes half the genes of all males and all females of the next generation.

* Supported in part by Natural Sciences and Engineering Research Council of Canada Grant OGP0008833.

Therefore, in the above model, the sum of the mean viabilities of females and males and half the mean fertilities in female and male offspring defines an *approximate adaptive topography* in the sense that it increases in the long run as long as the additive genetic variance in fitness dominates all other terms of higher order with respect to fitness differences. If fitness differences are small enough, that will be the case at least away from equilibrium where the additive genetic variance is far enough from 0. This result confirmed and extended many previous results (Wright, 1942; Abugov, 1985; Nagylaki, 1987). Moreover, it was noticed that the result applies to weak frequency-dependent selection but only when the fitness changes from one generation to the next one are much smaller than the fitness differences.

In this paper, the corresponding result for one-locus multiallele models in haplodiploid populations is presented in the general case of *arbitrary weak frequency-dependent selection*. The result is also valid for *X-linked locus models* in diploid populations. The result is used to study kin selection models in family-structured populations under the hypotheses of single insemination and multiple insemination of females. Multiple insemination leads naturally to frequency-dependent selection regimes.

1. FERTILITY-VIABILITY SELECTION MODEL

The following assumptions on the population are made: size is infinite, generations are discrete and nonoverlapping, females are diploid and males haploid, segregation in females is Mendelian, mating is random. There are n possible alleles A_1, \dots, A_n at a single locus such that females of genotype $A_i A_k$ have viability u_{ik} , males of genotype A_j have viability v_j , and matings between $A_i A_k$ females and A_j males have fertilities ϕ_{ikj} in female offspring and ψ_{ikj} in male offspring for $i, k, j = 1, \dots, n$. In this model, sex-differentiated viability differences reflecting the relative abilities for the alternative genotypes in females and males to survive from conception to maturity take place first. Then there is random mating between mature females and mature males. Finally, sex-differentiated fertility differences measure the relative contributions of mated couples to the next generation in female offspring and male offspring separately. *Both viabilities and fertilities may depend on the composition of the population.*

The genes in the genotypes of females are assumed to be interchangeable so that the *viability and fertility parameters* satisfy the *symmetry conditions*

$$\begin{aligned} u_{ik} &= u_{ki}, \\ \phi_{ikj} &= \phi_{kij}, \\ \psi_{ikj} &= \psi_{kij}, \end{aligned} \tag{1}$$

for $i, k, j = 1, \dots, n$. But males and females are distinguished in mated couples and in general the fertility parameters ϕ_{ikj} and ψ_{ikj} may not be the same if the index j is permuted with one of the indexes i or k , for $i, k, j = 1, \dots, n$.

Introducing the *fitness parameters*

$$f_{ikj} = u_{ik} v_j \phi_{ikj}, \quad (2)$$

$$m_{ikj} = u_{ik} v_j \psi_{ikj},$$

for $i, k, j = 1, \dots, n$, and denoting the frequency of $A_i A_j$ females by $2P_{ij}$ if $j \neq i$ and P_{ii} if $j = i$ and the frequency of A_i males by Q_i , for $i, j = 1, \dots, n$, the recurrence equations from one generation to the next one are

$$P'_{ij} = \frac{\sum_k P_{ik} Q_j f_{ikj} + \sum_k P_{jk} Q_i f_{jki}}{2\bar{f}}, \quad (3)$$

$$Q'_i = \frac{\sum_{kj} P_{ik} Q_j m_{ikj}}{\bar{m}},$$

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

$$\bar{f} = \sum_{ikj} P_{ik} Q_j f_{ikj},$$

$$\bar{m} = \sum_{ikj} P_{ik} Q_j m_{ikj}.$$

These are *mean fitnesses* in the population.

Note that the fitness parameters (2) can be interpreted as *generalized fertility parameters* which incorporate the viabilities of the parents. The product form of these parameters is in agreement with the equivalence of multiplicative fertility selection models with fertility parameters being expressed as products of factors attributable to the parents and viability selection models having those factors as viability parameters. (See, e.g., Ewens, 1979; Karlin, 1978; and references therein.) Moreover, the fitness parameters (2) are allowed to be *frequency dependent*.

In order to model *weak selection* it is assumed that all the selection parameters (viability parameters, fertility parameters, fitness parameters) can be written in the form $1 + O(s)$ where $O(s)$ designates a function of order s , that is, a function such that $|O(s)/s|$ remains bounded as s becomes small.

In general, a function $O(s)$ can be written in the form gs where g is a bounded function for s in a vicinity of 0. In the case of a frequency-dependent function $O(s)$, the function g is assumed to be uniformly bounded for s in a vicinity of 0. In particular, this is the case for a mean of a finite number of functions $O(s)$.

Under the above assumptions, it can be shown as in Nagylaki (1987) that, after enough generations and with an error of order s , the allelic frequencies in males and females are approximately equal, that is,

$$Q_i \cong P_i = \sum_k P_{ik},$$

for $i = 1, \dots, n$, while the genotypic frequencies in females are approximately in Hardy-Weinberg proportions, that is,

$$P_{ik} \cong x_i x_k,$$

for $i, k = 1, \dots, n$, where x_1, \dots, x_n are the allelic frequencies in the whole population, that is,

$$x_i = \frac{1}{3}Q_i + \frac{2}{3}P_i,$$

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

Moreover, with an error of order s^2 , the differences between the allelic frequencies in males and females and the deviations of the genotypic frequencies in females from Hardy-Weinberg proportions can be ignored in the changes of allelic and genotypic frequencies over two successive generations. In practice, this means that, to a first approximation, the allelic frequencies in males and females can be considered equal and the genotypic frequencies in females in Hardy-Weinberg proportions.

Throughout the paper, it will be assumed that enough generations have passed and selection is weak enough, that is, s is small enough, for the approximations (indicated by \cong) to be valid. Then, with an error of order s^2 , we have the following approximation for the allelic frequencies in the whole population from one generation to the next one:

LEMMA 1.

$$\Delta x_i \cong x_i \alpha_i, \tag{4}$$

where

$$\alpha_i = \frac{1}{3} \sum_k x_k (m_{ik\bullet} - \bar{m}) + \frac{1}{3} \sum_k x_k (f_{ik\bullet} - \bar{f}) + \frac{1}{3} (f_{\bullet\bullet i} - \bar{f}),$$

for $i = 1, \dots, n$, with the marginal fitness parameters

$$m_{ik\bullet} = \sum_j Q_j m_{ikj},$$

$$f_{ik\bullet} = \sum_j Q_j f_{ikj},$$

$$f_{\bullet\bullet i} = \sum_{jk} P_{jk} f_{jki},$$

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

With an error of order s^2 , the quantities $\alpha_1, \dots, \alpha_n$ represent *average allelic effects on fitness* (Fisher, 1930) in the long run and satisfy

$$\sum_i x_i \alpha_i \cong 0.$$

Let us introduce *partial changes of the mean fitnesses* caused by changes in the genotypic frequencies in females and males from one generation to the next one as follows:

$$\begin{aligned} \Delta_P \bar{f} &= \sum_{ikj} (\Delta P_{ik}) Q_j f_{ikj}, \\ \Delta_Q \bar{f} &= \sum_{ikj} P_{ik} (\Delta Q_j) f_{ikj}, \\ \Delta_P \bar{m} &= \sum_{ikj} (\Delta P_{ik}) Q_j m_{ikj}, \\ \Delta_Q \bar{m} &= \sum_{ikj} P_{ik} (\Delta Q_j) m_{ikj}, \end{aligned} \tag{5}$$

where

$$\Delta P_{ik} = P'_{ik} - P_{ik} \quad \text{and} \quad \Delta Q_j = Q'_j - Q_j,$$

for $i, k, j = 1, \dots, n$. Note that the fitness parameters, although they may be frequency dependent, are kept constant in the above partial changes of the mean fitnesses. Moreover, the effects of the changes in the genotypic frequencies in females and males on the mean fitnesses are considered separately. Then, after enough generations and with an error of order s^3 , we have:

RESULT 1.

$$\frac{1}{2} \Delta_P \bar{m} + \frac{1}{2} \Delta_P \bar{f} + \Delta_Q \bar{f} \cong V_\alpha, \tag{6}$$

where V_x is the additive genetic variance in fitness, that is,

$$V_x = 3 \sum_i x_i \alpha_i^2.$$

A factor 3 appears in the expression of V_x because the fitness parameters are controlled by triplets of genes in the mated couples. Result 1 guarantees that, if selection is weak enough, a weighted sum of partial changes of mean fitnesses is positive in the long run as long as the additive genetic variance in fitness is not too small, which is expected to occur as long as the population is not too close to equilibrium. With fitness parameters in the form (2), we have

$$\bar{f} = \bar{u}\bar{v}\bar{\phi} \quad \text{and} \quad \bar{m} = \bar{u}\bar{v}\bar{\psi}, \quad (7)$$

where \bar{u} and \bar{v} are the mean viabilities of females and males respectively, while $\bar{\phi}$ and $\bar{\psi}$ are the mean fertilities in female and male offspring, respectively, that is,

$$\bar{u} = \sum_{ik} P_{ik} u_{ik},$$

$$\bar{v} = \sum_j Q_j v_j,$$

$$\bar{\phi} = \sum_{ikj} P_{ik}^* Q_j^* \phi_{ikj},$$

$$\bar{\psi} = \sum_{ikj} P_{ik}^* Q_j^* \psi_{ikj},$$

with

$$P_{ik}^* = \frac{P_{ik} u_{ik}}{\bar{u}} \quad \text{and} \quad Q_j^* = \frac{Q_j v_j}{\bar{v}},$$

for $i, k, j = 1, \dots, n$. These quantities represent *genotypic frequencies in mature individuals* after the effects of viability differences. After enough generations and with an error of order s^3 , the partial changes of the mean fitnesses are approximated as follows:

LEMMA 2.

$$\begin{aligned} \Delta_P \bar{f} &\cong \Delta_P \bar{u} + \Delta_P \bar{\phi}, \\ \Delta_Q \bar{f} &\cong \Delta_Q \bar{v} + \Delta_Q \bar{\phi}, \\ \Delta_P \bar{m} &\cong \Delta_P \bar{u} + \Delta_P \bar{\psi}, \\ \Delta_Q \bar{m} &\cong \Delta_Q \bar{v} + \Delta_Q \bar{\psi}, \end{aligned} \quad (8)$$

where

$$\Delta_P \bar{u} = \sum_{ik} (\Delta P_{ik}) u_{ik},$$

$$\Delta_Q \bar{v} = \sum_j (\Delta Q_j) v_j,$$

$$\Delta_P \bar{\phi} \cong \sum_{ikj} (\Delta P_{ik}) Q_j \phi_{ikj},$$

$$\Delta_Q \bar{\phi} \cong \sum_{ikj} P_{ik} (\Delta Q_j) \phi_{ikj},$$

$$\Delta_P \bar{\psi} \cong \sum_{ikj} (\Delta P_{ik}) Q_j \psi_{ikj},$$

$$\Delta_Q \bar{\psi} \cong \sum_{ikj} P_{ik} (\Delta Q_j) \psi_{ikj}.$$

Note that

$$\Delta_Q \bar{u} = 0 \quad \text{and} \quad \Delta_P \bar{v} = 0.$$

Note also the use of the genotypic frequencies in immature individuals, P_{ik} and Q_j , instead of the genotypic frequencies in mature individuals, P_{ik}^* and Q_j^* , in the expressions for $\Delta_P \bar{\phi}$, $\Delta_Q \bar{\phi}$ and $\Delta_P \bar{\psi}$, $\Delta_Q \bar{\psi}$. This does not affect the validity of the approximations in (8) and has the advantage of simplifying the notation since then all partial changes are expressed with respect to the same genotypic frequencies.

With the approximations of Lemma 2 in hand, Result 1 yields:

COROLLARY 1.

$$\Delta_P \bar{u} + \Delta_Q \bar{v} + \Delta_Q \bar{\phi} + \frac{1}{2} \Delta_P \bar{\phi} + \frac{1}{2} \Delta_P \bar{\psi} \cong V_x. \quad (9)$$

In order to interpret this result, we will consider two special cases. But before we proceed, let us introduce the following definition:

DEFINITION 1. A mean function \bar{F} defines an *approximate adaptive topography* if \bar{F} increases at least in the long run and away from equilibrium.

Owing to Corollary 1, if we can find a function \bar{F} such that, after enough generations, the total change of \bar{F} from one generation to the next one is approximately given by

$$\Delta \bar{F} \cong (\Delta_P \bar{u} + \Delta_Q \bar{v} + \Delta_Q \bar{\phi} + \frac{1}{2} \Delta_P \bar{\phi} + \frac{1}{2} \Delta_P \bar{\psi}) G, \quad (10)$$

where G is a positive function, then \bar{F} will define an approximate adaptive topography.

Case 1. Frequency-independent selection with

$$\psi_{ikj} = \phi_{ikj} \quad \text{for } i, k, j = 1, \dots, n.$$

This is a case of nonsex-differentiated fertilities. In such a case, we have

$$\Delta_Q \bar{\phi} + \frac{1}{2} \Delta_P \bar{\phi} + \frac{1}{2} \Delta_P \bar{\psi} = \Delta_Q \bar{\phi} + \Delta_P \bar{\phi} \cong \Delta \bar{\phi},$$

where

$$\Delta \bar{\phi} = \sum_{ikj} \Delta(P_{ik} Q_j) \phi_{ikj}.$$

This is the expression for the *total change of the mean fertility* from one generation to the next one since all fertility parameters are frequency independent. Moreover we have

$$\Delta_P \bar{u} = \Delta \bar{u} \quad \text{and} \quad \Delta_Q \bar{v} = \Delta \bar{v},$$

where $\Delta \bar{u}$ and $\Delta \bar{v}$ represent the *total changes of the mean viabilities in females and males*, respectively, from one generation to the next one, since all viability parameters for females and males are frequency independent. Owing to Corollary 1, we conclude that

$$\bar{F} = \bar{u} + \bar{v} + \bar{\phi}$$

defines an adaptive topography in case 1. Therefore, the sum of the mean viabilities in females and males and the mean fertility increases at least in the long run and away from equilibrium.

Case 2. Frequency-independent selection with fertility parameters in the form

$$\phi_{ikj} = \beta_{ik} \delta_j \quad \text{and} \quad \psi_{ikj} = \gamma_{ik} \varepsilon_j \quad \text{for } i, k, j = 1, \dots, n.$$

This is the multiplicative case for sex-differentiated fertilities that are products of factors attributable to the female and male parents. All factors are assumed to be in the form $1 + O(s)$. It is easy to check that

$$\Delta_P \bar{\phi} \cong \Delta \bar{\beta} \quad \text{where} \quad \bar{\beta} = \sum_{ik} P_{ik} \beta_{ik},$$

$$\Delta_Q \bar{\phi} \cong \Delta \bar{\delta} \quad \text{where} \quad \bar{\delta} = \sum_j Q_j \delta_j,$$

$$\Delta_P \bar{\psi} \cong \Delta \bar{\gamma} \quad \text{where} \quad \bar{\gamma} = \sum_{ik} P_{ik} \gamma_{ik}.$$

In this case, an approximate adaptive topography is defined by

$$\bar{F} = \bar{u} + \bar{v} + \bar{\delta} + \frac{1}{2}\bar{\beta} + \frac{1}{2}\bar{\gamma}. \quad (11)$$

The coefficients of the means in the above approximate adaptive topography can be explained as follows: male parents and female parents have the same weight in the producing of offspring, but female parents transmit half their genes to male and female offspring while male parents transmit all their genes to female offspring. The mean

$$\bar{\varepsilon} = \sum_j Q_j \varepsilon_j$$

has a coefficient 0 because male parents do not transmit any gene to male offspring.

Remark 1. As noted for previous models (Nagylaki, 1987; Lessard, 1993), our results in cases 1 and 2 are valid with frequency-dependent fitness parameters as long as the changes of these parameters from one generation to the next one and after enough generations have passed are small enough with respect to fitness differences (actually, of order s^3) in order not to affect significantly the changes in the mean fitnesses.

2. KIN SELECTION MODELS

In the preceding model, the system of recurrence equations for the genotypic frequencies in mature individuals, P_{ij}^* and Q_i^* for $i, j = 1, \dots, n$, is the same as (3) but with *fitness parameters*

$$\begin{aligned} f_{ikj}^* &= u_{ij} \phi_{ikj}, \\ m_{ikj}^* &= v_i \psi_{ikj}, \end{aligned} \quad (12)$$

for $i, k, j = 1, \dots, n$. These parameters are *not symmetric* in i, k . The quantity f_{ikj}^* can be interpreted as the fitness of an $A_i A_j$ female offspring from an $A_i A_k \times A_j$ mating and the quantity m_{ikj}^* as the corresponding fitness for an A_i male offspring. Our previous results on fertility–viability selection models make possible the analysis of this kind of models and in particular of kin selection models in family-structured populations.

Let an $A_i A_j$ female adopt an altruistic behavior with constant probability h_{ij} ($= h_{ji}$) and an A_i male with constant probability h_i , for $i, j = 1, \dots, n$. Assume that such a behavior has small sex-differentiated effects on the fitness of sibs, possibly halfsibs, and offspring, besides the individual's

own fitness. Halfsibs come into play when there is multiple insemination of females. We will consider first the case of single insemination.

Single Insemination

In this case an offspring of an $A_i A_k \times A_j$ mating has female sibs of genotypes $A_i A_j$ and $A_k A_j$ in the same expected proportion of $\frac{1}{2}$, and male sibs of genotypes A_i and A_k in the same expected proportion of $\frac{1}{2}$. Assuming that altruistic individuals (*donors*) see their own fitnesses decreased by a quantity of order s and the fitnesses of their sibs and offspring (*recipients*) increased by quantities of order s , we get fitness parameters in the form (12) with

$$\begin{aligned}
 u_{ij} &\cong 1 - \gamma_I^f s h_{ij}, \\
 v_i &\cong 1 - \gamma_I^m s h_i, \\
 \phi_{ikj} &\cong 1 + \beta_M^f s h_{ik} + \beta_F^f s h_j \\
 &\quad + \beta_S^f s \left[\frac{h_{ij} + h_{kj}}{2} \right] + \beta_B^f s \left[\frac{h_i + h_k}{2} \right], \\
 \psi_{ikj} &\cong 1 + \beta_M^m s h_{ik} + \beta_F^m s h_j \\
 &\quad + \beta_S^m s \left[\frac{h_{ij} + h_{kj}}{2} \right] + \beta_B^m s \left[\frac{h_i + h_k}{2} \right], \tag{13}
 \end{aligned}$$

for $i, k, j = 1, \dots, n$, where $\gamma_I^f, \gamma_I^m, \beta_M^f, \beta_F^f, \beta_S^f, \beta_B^f, \beta_M^m, \beta_F^m, \beta_S^m, \beta_B^m$ are nonnegative coefficients in which I stands for individual, M for mother, F for father, S for sister, B for brother, f for female and m for male. The coefficients γ_I^f and γ_I^m correspond to *costs* and all other coefficients to *benefits*. The multiplicative factor s serves to model weak selection. The fitness parameters (13), which can be viewed as approximations with errors of order s^2 , generalize previous kin selection models proposed by Cavalli-Sforza and Feldman (1978), Uyenoyama and Feldman (1981), and Uyenoyama *et al.* (1981), among others. But here, since selection is weak, there is no difference between additive models and multiplicative models: we can indifferently add (or subtract) an effect or multiply by 1 plus (or minus) the effect. The difference is of order s^2 and is negligible. But note that ϕ_{ikj} and ψ_{ikj} in (13) cannot be written as products of factors depending only on i, k and factors depending only on j because of the presence of the terms h_{ij} and h_{kj} .

Taking the means in (13), we find the following approximations for the partial changes from one generation to the next one:

LEMMA 3.

$$\begin{aligned}
 \Delta_P \bar{u} &\cong -\gamma_I^f s \Delta \bar{h}_P, \\
 \Delta_Q \bar{v} &\cong -\gamma_I^m s \Delta \bar{h}_Q, \\
 \Delta_Q \bar{\phi} &\cong \beta_F^f s \Delta \bar{h}_Q + \beta_S^f s \frac{1}{2} \Delta \bar{h}_P, \\
 \Delta_P \bar{\psi} &\cong \beta_M^f s \Delta \bar{h}_P + \beta_S^f s \frac{1}{2} \Delta \bar{h}_P + \beta_B^f s \Delta \bar{h}_Q, \\
 \Delta_P \bar{\psi} &\cong \beta_M^m s \Delta \bar{h}_P + \beta_S^m s \frac{1}{2} \Delta \bar{h}_P + \beta_B^m s \Delta \bar{h}_Q,
 \end{aligned} \tag{14}$$

where

$$\bar{h}_P = \sum_{ij} P_{ij} h_{ij} \quad \text{and} \quad \bar{h}_Q = \sum_i Q_i h_i.$$

From Corollary 1, an approximate adaptive topography for model (13) is:

RESULT 2.

$$\begin{aligned}
 \bar{F} &= [-\gamma_I^f + \frac{1}{2}\beta_M^f + \frac{1}{2}\beta_M^m + \frac{1}{4}\beta_S^m + \frac{3}{4}\beta_S^f] \bar{h}_P \\
 &\quad + [-\gamma_I^m + \beta_F^f + \frac{1}{2}\beta_B^f + \frac{1}{2}\beta_B^m] \bar{h}_Q.
 \end{aligned} \tag{15}$$

This approximate adaptive topography is a weighted average of \bar{h}_P and \bar{h}_Q . In the *additive case* for altruism propensity, that is,

$$h_{ij} = \frac{h_i + h_j}{2} \quad \text{for } i, j = 1, \dots, n,$$

we have

$$\bar{h}_P = \bar{h}_Q,$$

and the mean for altruism propensity is an approximate adaptive topography if the sum of the above coefficients is positive, that is,

$$\gamma_I^f + \gamma_I^m < \beta_F^f + \frac{1}{2}\beta_M^f + \frac{1}{2}\beta_M^m + \frac{1}{2}\beta_B^f + \frac{1}{2}\beta_B^m + \frac{1}{4}\beta_S^m + \frac{3}{4}\beta_S^f.$$

It is instructive to note that the same approximate adaptive topography (15) is obtained with fitness parameters in the form

$$\begin{aligned}
 f_{ikj} &= u_{ik}^{\text{incl}} v_j^{\text{incl}}, \\
 m_{ikj} &= u_{ik}^{\text{incl}} v_j^{\text{incl}},
 \end{aligned} \tag{16}$$

where

$$u_{ik}^{\text{incl}} \cong 1 + [-\gamma_I^f + \frac{1}{2}\beta_M^f + \frac{1}{2}\beta_M^m + \frac{1}{4}\beta_S^m + \frac{3}{4}\beta_S^f] sh_{ik},$$

$$v_j^{\text{incl}} = 1 + [-\gamma_I^m + \beta_F^f + \frac{1}{2}\beta_B^f + \frac{1}{2}\beta_B^m] sh_j.$$

This is the *inclusive fitness formulation* of (13) in the spirit of Hamilton (1964). The coefficients of the benefits in (16) are known as *coefficients of relatedness* (see Hamilton, 1972).

Multiple Insemination

With multiple insemination, it suffices to replace the following quantities in (13):

$$h_j \quad \text{by} \quad \bar{h}_Q,$$

$$\frac{h_{ij} + h_{kj}}{2} \quad \text{by} \quad \frac{h_{i\bullet} + h_{k\bullet}}{2}, \quad (17)$$

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

$$\bar{h}_Q = \sum_l Q_l h_l,$$

$$h_{i\bullet} = \sum_l Q_l h_{il},$$

for $i = 1, \dots, n$. We get again the approximations (14) but the following:

LEMMA 4.

$$\Delta_Q \bar{\phi} \cong 0. \quad (18)$$

Therefore, an approximate adaptive topography for model (17) may be defined as follows:

RESULT 3.

$$\bar{F} = [-\gamma_I^f + \frac{1}{2}\beta_M^f + \frac{1}{2}\beta_M^m + \frac{1}{4}\beta_S^m + \frac{1}{4}\beta_S^f] \bar{h}_P$$

$$+ [-\gamma_I^m + \frac{1}{2}\beta_B^f + \frac{1}{2}\beta_B^m] \bar{h}_Q. \quad (19)$$

Again, the coefficients of the benefits in the approximate adaptive topography correspond to coefficients of relatedness given by Hamilton (1972).

Remark 2. In the case of multiple insemination, the fitness parameters are frequency dependent through their dependence on \bar{h}_Q and $h_{i\bullet}$ for $i = 1, \dots, n$.

3. DISCUSSION

For a haplodiploid population under weak selection on fertility and viability controlled at a single multiallelic locus, we have shown that a linear combination of partial changes of mean fitnesses from one generation to the next one is approximately equal to the additive genetic variance in fitness if enough generations have passed but the population is still far from equilibrium (Result 1). Actually, the linear combination corresponds to a linear combination of partial changes of mean viabilities and mean fertilities, whose coefficients reflect the principle that male parents and female parents have the same weight in breeding success but female parents pass on half their genes to male and female offspring while male parents pass on all their genes to female offspring and none of their genes to male offspring (Corollary 1). The same principle is reflected in the average allelic effects on fitness, whose expressions in the long run and with an error of order s^2 are given in Lemma 1, which are such that

$$\begin{aligned} & \frac{1}{4} \sum_{ik} P_{ik} (f_{ik\bullet} - \bar{f} - \alpha_i - \alpha_k)^2 \\ & + \frac{1}{4} \sum_{ik} P_{ik} (m_{ik\bullet} - \bar{m} - \alpha_i - \alpha_k)^2 \\ & + \frac{2}{4} \sum_i Q_i (f_{\bullet\bullet i} - \bar{f} - \alpha_i)^2 \end{aligned}$$

is minimum.

In some cases of frequency-independent selection (or very weak frequency-dependent selection such that the changes of the fitness parameters from one generation to the next one are of third order compared to the fitness differences) as cases with fertilities of matings that are the same for male and female offspring or that are products of fertilities of the male and female parents, the linear combination of partial changes of mean fitnesses reduces to the total change of a linear combination of mean viabilities and mean fertilities. Then, such a combination defines an approximate adaptive topography (see Cases 1 and 2).

But, in general, partial changes of mean selective values have to be considered. These, noted Δ_P and Δ_Q , express changes with respect to changes from one generation to the next one in the genotypic frequencies in females and males separately and with the selection parameters kept constant. In this notation, the result equivalent to Corollary 1 for diploid populations would be

$$\Delta_P \bar{u} + \Delta_Q \bar{v} + \frac{1}{2} \Delta_P \bar{\phi} + \frac{1}{2} \Delta_Q \bar{\phi} + \frac{1}{2} \Delta_P \bar{\psi} + \frac{1}{2} \Delta_Q \bar{\psi} \cong V_\alpha,$$

where \bar{u} would be the mean viability of females, \bar{v} the mean viability of males, $\bar{\phi}$ the mean fertility in female offspring and $\bar{\psi}$ the mean fertility in male offspring. If selection is frequency independent or very weak, then we get

$$\Delta\bar{u} + \Delta\bar{v} + \frac{1}{2} \Delta\bar{\phi} + \frac{1}{2} \Delta\bar{\psi} \cong V_a,$$

where Δ denotes the total change from one generation to the next one (Lessard, 1993). In such a case, the function $\bar{u} + \bar{v} + \bar{\phi}/2 + \bar{\psi}/2$ defines an approximate adaptive topography. The general case with frequency-dependent selection shares some similarity with Li (1955) who constructed an adaptive topography for two-allele frequency-dependent viability models without sex differences from Wright's (1942) formula for the change of gene frequencies. One of the fundamental element of the construction is to regard the viability parameters "as constant in any particular instant." The same element is present in our results. With sex differences, we have to assume that selection is weak in order to have approximately the same allelic frequencies in males and females. The relative weights of fertility differences as compared to viability differences and the relative contributions of males and females to the next generation are reflected in the coefficients of the partial changes of the mean selective values appearing above and in Result 1 and Corollary 1.

It is interesting to compare our results with those of Ewens (1989) on the interpretation of the Fundamental Theorem of Natural Selection (Fisher, 1930). Ewens showed that a partial change of the mean fitness in diploid populations under any viability selection regime without sex differences but allowing for nonrandom mating is exactly equal to the additive genetic variance in fitness divided by the mean fitness. The partial change is obtained by replacing the fitness parameters by the corresponding additive genotypic values (or breeding values, Falconer, 1960, p. 120), which are generally frequency dependent, but keeping those values constant from one generation to the next one. The "fundamental theorem" concerns that partial change as first noted by Price (1972). In this paper, we have shown that, in two-sex viability-fertility selection models under arbitrary weak frequency-dependent selection but with the assumption of random mating, the additive genetic variance is approximately equal to a combination of partial changes of mean fitnesses which ignore any frequency dependence in the fitness parameters. In this perspective, our result can be viewed as an extension of the Fundamental Theorem of Natural Selection.

It is remarkable that kin selection models in family-structured populations can be put into the framework of viability-fertility selection models (Result 2). This is true for haplodiploid populations as for diploid populations (Lessard, 1993). It is even more remarkable that approximate

adaptive topographies can be deduced for such models even in the case of multiple insemination of females which creates a kind of frequency-dependent selection (Result 3). Finally, the adaptive topographies are in agreement with the inclusive fitness formulation of Hamilton (1964). But we have to remind ourselves that the assumption of weak selection is crucial.

APPENDIX

Proof of Lemma 1.

$$\begin{aligned}
 \Delta x_i &= \frac{1}{3} \Delta Q_i + \frac{2}{3} \Delta P_i \\
 &= \frac{1}{3} (Q'_i - Q_i) + \frac{2}{3} (P'_i - P_i) \\
 &= \frac{1}{3} (Q'_i - Q_i) + \frac{2}{3} \left(\sum_j P'_{ij} - \sum_j P_{ij} \right) \\
 &= \frac{1}{3\bar{m}} \sum_k P_{ik} \left(m_{ik\bullet} - \bar{m} \frac{Q_i}{P_i} \right) \\
 &\quad + \frac{1}{3\bar{f}} \left\{ \sum_k P_{ik} (f_{ik\bullet} - \bar{f}) + Q_i \left(f_{\bullet\bullet i} - \bar{f} \frac{P_i}{Q_i} \right) \right\} \\
 &= \frac{1}{3\bar{m}} \sum_k P_{ik} (m_{ik\bullet} - \bar{m}) \\
 &\quad + \frac{1}{3\bar{f}} \left\{ \sum_k P_{ik} (f_{ik\bullet} - \bar{f}) + Q_i (f_{\bullet\bullet i} - \bar{f}) \right\} \\
 &\cong x_i \left\{ \frac{1}{3} \sum_k x_k (m_{ik\bullet} - \bar{m}) + \frac{1}{3} \sum_k x_k (f_{ik\bullet} - \bar{f}) + \frac{1}{3} (f_{\bullet\bullet i} - \bar{f}) \right\}.
 \end{aligned}$$

Proof of Result 1.

$$\begin{aligned}
 \Delta_P \bar{m} &= \sum_{ikj} (\Delta P_{ik}) Q_j (m_{ikj} - \bar{m}) \\
 &= \sum_{ik} (\Delta P_{ik}) (m_{ik\bullet} - \bar{m}) \\
 &\cong \sum_{ik} [\Delta(x_i x_k)] (m_{ik\bullet} - \bar{m}) \\
 &\cong \sum_{ik} [(\Delta x_i) x_k + x_i (\Delta x_k)] (m_{ik\bullet} - \bar{m}) \\
 &\cong \sum_{ik} [\alpha_i x_i x_k + \alpha_k x_i x_k] (m_{ik\bullet} - \bar{m}) \\
 &= 2 \sum_{ik} \alpha_i x_i x_k (m_{ik\bullet} - \bar{m}),
 \end{aligned}$$

$$\begin{aligned}
 \Delta_P \bar{f} &\cong 2 \sum_{ik} \alpha_i x_i x_k (f_{ik\bullet} - \bar{f}), \\
 \Delta_Q \bar{f} &= \sum_{ikj} P_{ik} (\Delta Q_j) (f_{ikj} - \bar{f}) \\
 &= \sum_j (\Delta Q_j) (f_{\bullet\bullet j} - \bar{f}) \\
 &\cong \sum_j (\Delta x_j) (f_{\bullet\bullet j} - \bar{f}) \\
 &\cong \sum_j \alpha_j x_j (f_{\bullet\bullet j} - \bar{f}), \\
 \frac{1}{2} \Delta_P \bar{m} + \frac{1}{2} \Delta_P \bar{f} + \Delta_Q \bar{f} &\cong \sum_i x_i \alpha_i \left[\sum_k x_k (m_{ik\bullet} - \bar{m}) + \sum_k x_k (f_{ik\bullet} - \bar{f}) \right. \\
 &\quad \left. + (f_{\bullet\bullet i} - \bar{f}) \right] \\
 &= 3 \sum_i x_i \alpha_i^2.
 \end{aligned}$$

Proof of Lemma 2.

$$\begin{aligned}
 \Delta_P \bar{m} &= \Delta_P (\bar{u} \bar{v} \bar{\psi}) \\
 &\cong (\Delta_P \bar{u}) \bar{v} \bar{\psi} + \bar{u} (\Delta_P \bar{v}) \bar{\psi} + \bar{u} \bar{v} (\Delta_P \bar{\psi}) \\
 &\cong \Delta_P \bar{u} + \Delta_P \bar{\psi}, \\
 \Delta_P \bar{\psi} &= \sum_{ikj} (\Delta_P P_{ik}^*) Q_j^* \psi_{ikj} \\
 &= \sum_{ikj} (\Delta_P P_{ik}^*) Q_j^* (\psi_{ikj} - \bar{\psi}) \\
 &\cong \sum_{ikj} \left[\frac{(\Delta_P P_{ik}) u_{ik}}{\bar{u}} - \frac{(\Delta_P \bar{u}) P_{ik} u_{ik}}{\bar{u}^2} \right] Q_j^* (\psi_{ikj} - \bar{\psi}) \\
 &\cong \sum_{ikj} [\Delta P_{ik} - (\Delta_P \bar{u}) P_{ik}^*] Q_j^* (\psi_{ikj} - \bar{\psi}) \\
 &\cong \sum_{ikj} (\Delta P_{ik}) Q_j^* (\psi_{ikj} - \bar{\psi}) \\
 &\cong \sum_{ikj} (\Delta P_{ik}) Q_j (\psi_{ikj} - \bar{\psi}) \\
 &= \sum_{ikj} (\Delta P_{ik}) Q_j \psi_{ikj},
 \end{aligned}$$

and similarly for the other quantities in (8).

Proof of Lemma 3.

$$\begin{aligned}
 \Delta \bar{h}_Q &= \sum_i (\Delta Q_i) h_i \\
 &\cong \sum_i (\Delta x_i) h_i, \\
 \Delta \bar{h}_P &= \sum_{ij} (\Delta P_{ij}) h_{ij} \\
 &\cong \sum_{ij} [(\Delta x_i) x_j + x_i (\Delta x_j)] h_{ij} \\
 &= 2 \sum_{ij} (\Delta x_i) x_j h_{ij} \\
 &\cong 2 \sum_{ij} (\Delta x_i) Q_j h_{ij} \\
 &= 2 \sum_i (\Delta x_i) h_{i\bullet}, \\
 \Delta_Q \left[\sum_{ikj} P_{ik} Q_j \left(\frac{h_i + h_k}{2} \right) \right] &= \sum_{ikj} P_{ik} (\Delta Q_j) \left(\frac{h_i + h_k}{2} \right) \\
 &= 0, \\
 \Delta_P \left[\sum_{ikj} P_{ik} Q_j \left(\frac{h_i + h_k}{2} \right) \right] &= \sum_{ikj} (\Delta P_{ik}) Q_j \left(\frac{h_i + h_k}{2} \right) \\
 &= \sum_{ik} (\Delta P_{ik}) \left(\frac{h_i + h_k}{2} \right) \\
 &\cong \sum_{ik} [(\Delta x_i) x_k + x_i (\Delta x_k)] \left(\frac{h_i + h_k}{2} \right) \\
 &= \sum_i (\Delta x_i) h_i \\
 &\cong \Delta \bar{h}_Q, \\
 \Delta_P \left[\sum_{ikj} P_{ik} Q_j \left(\frac{h_j + h_k}{2} \right) \right] &= \sum_{ikj} (\Delta P_{ik}) Q_j \left(\frac{h_j + h_k}{2} \right) \\
 &= \sum_{ik} (\Delta P_{ik}) \left(\frac{h_{i\bullet} + h_{k\bullet}}{2} \right) \\
 &\cong \sum_{ik} [(\Delta x_i) x_k + x_i (\Delta x_k)] \left(\frac{h_{i\bullet} + h_{k\bullet}}{2} \right) \\
 &= \sum_i (\Delta x_i) h_{i\bullet} \\
 &\cong \frac{1}{2} \Delta \bar{h}_P,
 \end{aligned}$$

$$\begin{aligned}
\Delta_Q \left[\sum_{ikj} P_{ik} Q_j \left(\frac{h_{ij} + h_{kj}}{2} \right) \right] &= \sum_{ikj} P_{ik} (\Delta Q_j) \left(\frac{h_{ij} + h_{kj}}{2} \right) \\
&\cong \sum_{ikj} x_i x_k (\Delta x_j) \left(\frac{h_{ij} + h_{kj}}{2} \right) \\
&\cong \sum_{ikj} Q_i Q_k (\Delta x_j) \left(\frac{h_{ij} + h_{kj}}{2} \right) \\
&= \sum_j (\Delta x_j) h_{j\bullet} \\
&\cong \frac{1}{2} \Delta \bar{h}_P.
\end{aligned}$$

Proof of Lemma 4. Keeping \bar{h}_Q and $h_{i\bullet}$ for $i = 1, \dots, n$ constant, we have

$$\begin{aligned}
\Delta_Q(\bar{h}_Q) &= 0, \\
\Delta_Q \left[\sum_{ikj} P_{ik} Q_j \left(\frac{h_{i\bullet} + h_{k\bullet}}{2} \right) \right] &= \sum_{ikj} P_{ik} (\Delta Q_j) \left(\frac{h_{i\bullet} + h_{k\bullet}}{2} \right) \\
&= 0.
\end{aligned}$$

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