Sufficient conditions for polymorphism with cyclical selection in a subdivided population

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SUMMARY

The combined effect of multi-niche selection and cyclical selection is studied in a deterministic model. Sufficient conditions for protected polymorphism are derived for diploid populations with and without dominance and for haploid populations. These conditions appear to be broader than in the cases of only multi-niche selection or only cyclical selection.

1. INTRODUCTION

Since the first papers on models incorporating environmental heterogeneity (Levene (1953) on spatial variation in fitness, and Dempster (1955) on selection varying with time) there has been a continual extension of population genetics theory in this area. Recent reviews on the subject are given by Christiansen & Feldman (1975), Felsenstein (1976) and Hedrick, Ginevan & Ewing (1976).

The two basic types of variation in fitness: geographical and temporal, have almost exclusively been investigated separately.

In this paper I present a deterministic model in which the combined effect of spatial and temporal variability in fitness is considered. The model incorporates the generalized Levene model due to Strobeck (1974) and the general cyclical selection model of Hoekstra (1975).

2. DIPLOID POPULATIONS

Consider an autosomal locus with two alleles A_1 and A_2 in a diploid population, which is subdivided into n subpopulations living in different environments (ecological niches). The population is subjected to cyclical selection with a cycle-length of t generations.

Let $w_{i,k}$, 1, $v_{i,k}$ be the relative fitnesses of the genotypes A_1A_1, A_1A_2 and A_2A_2 in the ith niche in the kth generation of the cycle. After selection in the kth generation a proportion $c_{i,k}$ of the total population is in the ith niche, and then mating occurs as follows. Suppose there are m mating groups in each of which there is random mating, and let $a_{ij,k}$ be the proportion of adults from the ith

niche mating in the jth mating group in the kth generation. The proportion of the total population in the kth generation mating in the jth mating group is then

$$K_{j,k} = \sum_{i=1}^{n} c_{i,k} a_{ij,k}.$$

The offspring of each mating is dispersed at random, therefore the gene frequency of the A_1 allele before selection in the kth generation p_k is the same in all niches. Denoting the frequency of A_1 after selection in the ith niche in the kth generation by $p'_{i,k}$, the frequency of A_1 in the jth mating group in the kth generation will be

$$x_{j,k} = \sum_{i=1}^{n} c_{i,k} a_{ij,k} p'_{i,k} / K_{j,k} \tag{1}$$

and

$$p_{k+1} = \sum_{j=1}^{m} K_{j,k} x_{j\ k}. \tag{2}$$

Substitution of (1) into (2) gives

$$p_{k+1} = \sum_{j=1}^{m} \sum_{i=1}^{n} c_{i,k} a_{ij,k} p'_{i,k}$$

$$= \sum_{i=1}^{n} c_{i,k} p'_{i,k} \sum_{j=1}^{m} a_{ij,k} = \sum_{i=1}^{n} c_{i,k} p'_{i,k}. \tag{3}$$

As is observed by Christiansen & Feldman (1975) in their discussion of the model of Strobeck (1974), the frequencies of the genotypes $A_1 A_1$, $A_1 A_2$, and $A_2 A_2$ prior to selection in the kth generation are $p_k^2 + \text{var } x_{k-1}$, $2p_k(1-p_k) - 2 \text{ var } x_{k-1}$, and $(1-p_k)^2 + \text{var } x_{k-1}$, where var x_{k-1} is the variance of the A_1 frequencies in the mating groups of the preceding generation (Wahlund, 1928). Therefore

$$p'_{i,k} = \frac{(p_k^2 + \text{var } x_{k-1})(w_{i,k} - 1) + p_k}{(p_k^2 + \text{var } x_{k-1})(w_{i,k} + v_{i,k} - 2) + 2p_k(1 - v_{i,k}) + v_{i,k}}. \tag{4}$$

A sufficient condition for 'protection' (Prout, 1968) of allele A_1, which means that A_1 cannot be lost or fixed by selection, is that the trivial equilibrium $p = 0$ is unstable. When p is sufficiently small we may neglect second- and higher-order terms in p (and in x). Since var x_{k-1} has only second-order terms in x, equation (4) becomes (in the neighbourhood of 0)

$$p'_{i,k} = \frac{1}{v_{i,k}} p_k. \tag{5}$$

Substitution of (5) into (3) results in

$$p_{k+1} = p_k \sum_{i=1}^{n} \frac{c_{i,k}}{v_{i,k}}. \tag{6}$$

The recursion equation for the frequency of A_1 over a cycle of t generations is therefore

$$p_{t+1} = p_1 \prod_{k=1}^{t} \sum_{i=1}^{n} \frac{c_{i,k}}{v_{i,k}}.$$

Thus, allele A_1 is protected if

$$\prod_{k=1}^{t} \sum_{i=1}^{n} \frac{c_{i,k}}{v_{i,k}} > 1$$

or, if the geometric mean (taken over the different generations making up a cycle) of the weighted harmonic means of the fitnesses of the $A_2 A_2$ homozygote (taken over the different niches in each generation) is less than unity:

$$(V_H)_G = \prod_{k=1}^{t} \left\{ \sum_{i=1}^{n} \frac{c_{i,k}}{v_{i,k}} \right\}^{-1} < 1. \tag{7a}$$

Similarly, allele A_2 is protected if

$$(W_H)_G = \prod_{k=1}^{t} \left\{ \sum_{i=1}^{n} \frac{c_{i,k}}{w_{i,k}} \right\}^{-1} < 1. \tag{7b}$$

Conditions $(7a)$ and $(7b)$ reduce to those for cyclical selection in a single random mating population (see, for example, Hoekstra (1975)): $V_G < 1$ and $W_G < 1$ if $n = 1$ (a single population) or if $v_{i,k} = v_k$ and $w_{i,k} = w_k$ for all i (equal fitnesses in all niches), and they reduce to the conditions for protected polymorphism in the (generalized) Levene model: $V_H < 1$ and $W_H < 1$ if $t = 1$ (fitnesses not varying with time).

3. THE CASE OF DOMINANCE

I now proceed to investigate the special case of dominance. Suppose A_2 is completely dominant ($v_{i,k} = 1$ for all i and k). Then the stability of 0 depends on the second-order terms in p and x of equation (4). Substituting $v_{i,k} = 1$ and retaining first- and second-order terms in (4), one obtains

$$p'_{i,k} = (p_k^2 + \text{var } x_{k-1})(w_{i,k} - 1) + p_k$$

or, since

$$\text{var } x_{k-1} = \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1} - p_k^2,$$

$$p'_{i,k} = (w_{i,k} - 1) \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1} + p_k. \tag{8}$$

Substitution of (8) into (3) gives

$$p_{k+1} = \sum_{i=1}^{n} c_{i,k} p_k + \sum_{i=1}^{n} c_{i,k}(w_{i,k} - 1) \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1}$$

$$= p_k + \sum_{i=1}^{n} c_{i,k}(w_{i,k} - 1) \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1} \tag{9}$$

The recursion equation for a complete cycle of selection is then

$$p_{t+1} = p_1 + \sum_{k=1}^{t} \sum_{i=1}^{n} c_{i,k}(w_{i,k} - 1) \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1}. \tag{10}$$

From substitution of (8) into (1) is obtained that in the neighbourhood of 0

$$x_{j,k} = \frac{1}{K_{j,k}} \sum_{i=1}^{n} c_{i,k} a_{ij,k} (w_{i,k} - 1) \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1}$$

$$+ \frac{1}{K_{j,k}} \sum_{i=1}^{n} c_{i,k} a_{ij,k} p_k$$

$$= \frac{1}{K_{j,k}} \sum_{i=1}^{n} c_{i,k} a_{ij,k} (w_{i,k} - 1) \sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1} + p_k.$$

Therefore, $x_{j,k}^2 = p_k^2 + $ third- and higher-order terms in p and x. Since third- and higher-order terms are neglected, one obtains that in the neighbourhood of 0

$$\sum_{j=1}^{m} x_{j,k-1}^2 K_{j,k-1} = \sum_{j=1}^{m} p_{k-1}^2 K_{j,k-1} = p_{k-1}^2.$$

But it follows from (9) that

$$p_{k-1}^2 = p_{k-2}^2 + 0(px^2, x^4) = \ldots = p_1^2 + 0(px^2, x^4),$$

and therefore equation (10) becomes

$$p_{t+1} = p_1 + p_1^2 \sum_{k=1}^{t} \sum_{i=1}^{n} c_{i,k} (w_{i,k} - 1). \tag{11}$$

Therefore, 0 is unstable if

$$\sum_{k=1}^{t} \sum_{i=1}^{n} c_{i,k} (w_{i,k} - 1) > 0$$

or, if the arithmetic mean (taken over the generations) of the weighted arithmetic means of the fitnesses of the $A_1 A_1$ homozygote (taken over the niches) is greater than unity:

$$(W_A)_A = \sum_{k=1}^{t} \sum_{i=1}^{n} c_{i,k} w_{i,k} / t > 1. \tag{12}$$

Together with condition (7b), the condition for protected polymorphism if A_2 is dominant becomes

$$(W_H)_G < 1 < (W_A)_A. \tag{13}$$

Again, condition (13) reduces in the special case of $n = 1$ or $w_{i,k} = w_k$ for all i to the condition for protected polymorphism with dominance when there is cyclical selection in a single homogeneous population (Hoekstra, 1975): $W_G < 1 < W_A$, and (13) reduces for $t = 1$ to the corresponding condition in the (generalized) Levene model (Prout, 1968; Strobeck, 1974): $W_H < 1 < W_A$.

4. HAPLOID POPULATIONS

Gliddon & Strobeck (1975) showed that in haploid populations polymorphism can be maintained in the Levene model (under the same conditions as those for a protected polymorphism in diploid populations with complete dominance), while

temporal variation in fitness cannot maintain polymorphism in haploid populations.

In this section I will derive conditions for stable polymorphism in a subdivided haploid population undergoing cyclical selection.

Let the relative fitnesses of the genotypes A_1 and A_2 in the ith niche in the kth generation be 1 and $w_{i,k}$. The same assumptions are made as in the preceding section on diploid populations. Equations (1)–(3) still hold, and equation (4) becomes

$$p'_{i,k} = \frac{p_k}{p_k(1 - w_{i,k}) + w_{i,k}}. \tag{14}$$

Sufficiently close to the trivial equilibrium $p = 0$ equation (14) becomes

$$p'_{i,k} = \frac{1}{w_{i,k}} p_k. \tag{15}$$

Substitution of (15) into (3) gives

$$p_{k+1} = p_k \sum_{i=1}^{n} \frac{c_{i,k}}{w_{i,k}},$$

and the recursion equation over a cycle of selection is

$$p_{t+1} = p_1 \prod_{k=1}^{t} \sum_{i=1}^{n} \frac{c_{i,k}}{w_{i,k}}. \tag{16}$$

Therefore 0 is unstable if (compare (7a, b))

$$(W_H)_G < 1. \tag{17}$$

To investigate the stability of the other trivial equilibrium $p = 1$, $p_k = 1 - q_k$ is substituted into (14). Sufficiently close to 1 equation (14) then becomes

$$1 - q'_{i,k} = \frac{1 - q_k}{q_k(w_{i,k} - 1) + 1},$$

or

$$q'_{i,k} = \frac{w_{i,k} q_k}{q_k(w_{i,k} - 1) + 1}. \tag{18}$$

Neglecting second-order terms, (18) becomes $q'_{i,k} = w_{i,k} q_k$, which substituted into (3) produces

$$q_{k+1} = q_k \sum_{i=1}^{n} c_{i,k} w_{i,k}. \tag{19}$$

The recursion equation over a cycle of selection is then

$$q_{t+1} = q_1 \prod_{k=1}^{t} \sum_{i=1}^{n} c_{i,k} w_{i,k}. \tag{20}$$

Therefore, 1 is unstable if the geometric mean (over the generations) of the weighted arithmetic means of the fitnesses of A_2 (over the niches) is greater than unity:

$$(W_A)_G > 1. \tag{21}$$

Conditions (17) and (21) together form conditions for a stable polymorphism in a subdivided haploid population undergoing cyclical selection. Comparing these conditions with condition (13) (the case of dominance in diploid populations), it can be seen that for $t = 1$ (selection constant with time) (17) and (21) indeed reduce to (13), which agrees with the finding of Gliddon & Strobeck (1975). But in the general case of cyclical selection in a subdivided population, the conditions for stable polymorphism in haploid populations are narrower than in diploid populations with dominance, since the geometric mean is never greater than the arithmetic mean.

5. CONCLUSIONS

Sufficient conditions for a protected polymorphism in a subdivided population undergoing cyclical selection were derived. In particular, three situations were considered.

(1) The general case of one locus with two alleles in a diploid population; the relative fitnesses of the three genotypes in the ith niche in the kth generation are $w_{i,k}, 1, v_{i,k}$. There is stable polymorphism if there is overdominance of the geometric between-generations mean of the weighted harmonic between-niches mean fitnesses:

$$(W_H)_G < 1 > (V_H)_G.$$

(2) When there is complete dominance ($v_{i,k} = 1$ for all i and k, and therefore $(V_H)_G = 1$), then polymorphism is protected if the geometric between-generations mean of the weighted harmonic between-niches means of the recessive fitness is less than unity, but the arithmetic between-generations mean of the weighted arithmetic between-niches means of the recessive fitness is greater than unity:

$$(W_H)_G < 1 < (W_A)_A.$$

(3) In haploid populations where the relative fitnesses of the two genotypes in the ith niche in the kth generation are 1, $w_{i,k}$ there is a protected polymorphism if

$$(W_H)_G < 1 < (W_A)_G.$$

Thus it appears that conditions for protected polymorphism in a subdivided population undergoing cyclical selection are less stringent than in the cases where there is only spatial variation in fitness or where there is only temporal variation in fitness. Furthermore, conditions for protected polymorphism in haploid populations are not the same as those in diploid populations with complete dominance (as in the Levene model (Gliddon & Strobeck, 1975)), but they are more restricted in haploid populations when there is also cyclical selection.

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