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Polymorphism from environmental heterogeneity: models are only robust if the heterozygote is close in fitness to the favoured homozygote in each environment

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SUMMARY

The lack of robustness of models of the maintenance of polymorphism in a heterogeneous environment which has been pointed out by Maynard Smith & Hoekstra (1980), applies also to models based on habitat selection, on temporal variation and on density-regulated selection. Only if (partial) dominance 'switches' between environments such that the fitness of the heterozygote is always close to the favoured homozygote, is there reasonable robustness. This is true for all models considered. It is argued that there are good reasons for supposing that the favourable allele at a locus may show dominance, although the experimental evidence is still scanty.

1. INTRODUCTION

There is a large body of theoretical work on the problem of how genetic variation can be maintained in a varied environment, which has been reviewed by Felsenstein (1976) and Hedrick, Ginevan & Ewing (1976). Broadly speaking, temporal variation in selection coefficients at a single two-allelic locus in a diploid population brings about protected polymorphism (i.e. both alleles increase in frequency when rare) if there is geometric mean overdominance (averaged over time), while spatial fitness variation leads to protected polymorphism if there is harmonic mean overdominance (averaged over the subpopulations or niches). In the latter case, conditions for protected polymorphism become broader with decreasing amounts of migration between the subpopulations. The theory thus shows that environmental variation in fitness may maintain genetic polymorphism in the absence of (arithmetic mean) overdominance, which has been known for a long time as a potential variation preserving mechanism (Fisher, 1922), but which is also well known for a remarkable lack of empirical evidence concerning its operation in natural populations (Lewontin, 1974).

Already at an early stage of the formulation of the models for polymorphism in a varied environment, Maynard Smith (1966) had shown that in a special case of Levene's model (Levene, 1953) the conditions for stable polymorphism require

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the relative subpopulation sizes to lie in a very narrow range for small and moderate values of the selection coefficients. This disturbing lack of robustness also applies to a number of other models of polymorphism in a heterogeneous environment, as shown by Maynard Smith & Hoekstra (1980). They analysed various models on spatial fitness variation, but did not consider the robustness of models based on temporal variation in fitness, nor models relying on habitat selection or restricted migration. It has been claimed (e.g. Maynard Smith (1966), Jones (1980), Jones & Probert (1980)), that habitat selection may improve the robustness of the models considerably. The aim of this paper is to investigate the robustness displayed by the above-mentioned types of models, excluded in the analysis by Maynard Smith & Hoekstra (1980).

In Section 2 of this paper we explain the approach used to analyse robustness. Section 3 is devoted to the effect of habitat selection on the robustness of the models. Section 4 considers models based on temporal variation, while in Section 5 we ask whether the combined effect of spatial and temporal fitness variation may enhance robustness. Finally in Section 6 a model of density-regulated selection in a heterogeneous environment, proposed recently by Arnold & Anderson (1983) is considered.

2. OUTLINE OF THE APPROACH

The robustness of a model is analysed by considering the dependence of the model parameters upon each other as imposed by the conditions for protected polymorphism or, in other words, by examining the part of the parameter space, defined by these conditions. The robustness, ρ, with respect to one of these parameters is then defined as the range of values of this parameter for which there is protected polymorphism (for given values of the other parameters), expressed as a fraction of the total range of values it may take. We therefore have $0 \leqslant \rho \leqslant 1$. Thus a robustness of $\rho = 0{\cdot}1$ means that a critical model parameter (such as relative niche size) must adopt values in an interval which comprises only 10% of its total range, in order to guarantee a protected polymorphism; as soon as the parameter takes a value outside this interval polymorphism becomes unstable.

The general approach adopted in this paper is as follows. A special (but not atypical) case of the model under consideration is singled out in order to reduce the number of parameters. Thus generality is sacrificed to gain simplicity and transparency of the analysis. We consider only one locus diploid models, assuming equal and opposite selection in two environments (representing in the spatial models two niches or subpopulations, and in the temporal models two alternative selection regimes to which the population is subjected). The following basic patterns of fitness variation are studied:

(i) *Partial dominance of constant direction*

Relative fitnesses are as follows:

$$\left.\begin{array}{lccc} \text{Genotype} & A_1A_1 & A_1A_2 & A_2A_2 \\ \text{Environment 1} & 1 & 1-ks & 1-s \\ \text{Environment 2} & 1-s & 1-(1-k)s & 1 \end{array}\right\} \qquad (1)$$

$$(0 \leqslant s,\ k \leqslant 1)$$

For any value of k (partial) dominance has the same direction in both environments: for $k = 0$ allele A_1 is completely dominant with respect to fitness, for $0 \leqslant k \leqslant \frac{1}{2}$ A_1 is partially dominant, for $k = \frac{1}{2}$ there is additivity in fitness, for $\frac{1}{2} \leqslant k \leqslant 1$ allele A_2 is partially dominant, and for $k = 1$ A_2 is completely dominant.

(ii) *Partial dominance of varying direction*

Relative fitnesses are as follows:

$$\begin{array}{lccc}
\text{Genotype} & A_1A_1 & A_1A_2 & A_2A_2 \\
\text{Environment 1} & 1 & 1-ks & 1-s \\
\text{Environment 2} & 1-s & 1-ks & 1
\end{array} \Bigg\} \qquad (0 \leqslant s, k \leqslant 1) \qquad (2)$$

Now the direction of (partial) dominance differs between the two environments: A_1 is (partially) dominant in one environment and A_2 in the other environment. In the Discussion section we will comment on the plausibility of these fitness patterns.

3. HABITAT SELECTION

We adopt the model of habitat selection proposed by Maynard Smith (1966, 1970); the essential features of this model are:

(i) The environment is divided into two niches, characterized by different selective forces,

(ii) the adults produced in the two niches form a single random mating population,

(iii) there is habitat selection in the sense that females tend to return after mating to lay eggs in the niche in which they were raised.

The basic models of selection in a subdivided population were formulated by Levene (1953) and Dempster (1955). These models assume that the adults form a single random mating population, and that after mating females lay their eggs in one of a number of 'niches'; the selective values of the genotypes differ from niche to niche. There is an important difference between Levene's model and Dempster's model with regard to the way the population size is supposed to be regulated. In Levene's model each niche contains after selection a constant fraction of the total population, while in Dempster's model each niche has a constant fraction of the total population of zygotes before selection, and selection acts by differential survival of the zygotes to the time of migration. A number of consequences of this difference are discussed by Christiansen (1975), while Maynard Smith & Hoekstra (1980) present a simple general model from which Levene's and Dempster's models emerge as special cases.

We now analyse the robustness of Levene's model with habitat selection. Consider an autosomal locus with two alleles A_1 and A_2 in a diploid population, subdivided in two subpopulations living in different niches. The population is subjected to selection as indicated in the preceding section. After selection a proportion c of the total population is in niche 1 and a proportion $1-c$ in niche 2. Then global random mating occurs, after which a female raised in niche 1 lays a fraction $c+h(1-c)$ of its eggs in niche 1, and $1-c-h(1-c)$ in niche 2; similarly, a female raised in niche 2 lays a fraction $1-c+hc$ of its eggs in niche 2 and $c-hc$

in niche 1. Thus the parameter h measures the amount of habitat selection, ranging from 0 (no habitat selection) to 1 (complete habitat selection). The conditions for protected polymorphism in this model are given by Maynard Smith (1970). For our purpose they can be written in the following form:

(*a*) in the case of partial dominance of constant direction (1):

$$\frac{2-h+hks-2s}{(2-h)(2-s)} < c < \frac{2-h+hks}{(2-h)(2-s)}, \tag{3}$$

(*b*) in the case of partial dominance of varying direction (2):

$$\frac{k(2-h+hks-2s)}{(1-ks)(2-h)} < c < \frac{(1-k)(2-h+hks)}{(1-ks)(2-h)}. \tag{4}$$

Conditions (3) are shown in graphical form for three different values of k in Fig. 1, and conditions (4) in Fig. 2. We can now determine the robustness of the model with respect to the parameter c as it depends on s; that is, we observe the range of values c can take for various values of s in order to have protected polymorphism. It follows easily from conditions (3) that in the case of selection regime (1) the robustness is equal to

$$\rho = \frac{2s}{(2-h)(2-s)}. \tag{5}$$

For $s = 0{\cdot}01$ and $s = 0{\cdot}1$ the robustness is listed in Table 1. Clearly, in this model the robustness is very poor for small and moderate values of s, which is also apparent from Fig. 1. Furthermore, robustness is independent of k in this case, and although it increases with increasing h, the effect of habitat selection does not change the picture in a qualitative way. In the case of selection regime (2) (with corresponding conditions (4)) robustness very much depends on the value of the parameter k. Fig. 2 shows that if in both niches the heterozygote is close to the most fit homozygote (i.e. for a small value of k) there is considerable robustness. However, if the heterozygote is intermediate in fitness ($k = \frac{1}{2}$), the robustness is small, while for large values of k (the heterozygote close to the least fit homozygote) very large values of s are needed for polymorphism. Again, although habitat selection does increase robustness, the effect is insignificant for moderate selection ($s < 0{\cdot}1$).

We will also briefly examine the effect of habitat selection in a model proposed by Gillespie (1976). Maynard Smith & Hoekstra (1980) have shown that this model can be derived from Levene's model, and in fact it is the only model they analyse having a reasonable robustness. Gillespie's model is meant to apply to enzyme polymorphisms. He assumes the heterozygote to be phenotypically intermediate between the two homozygotes with respect to enzyme activity, but the relationship between fitness and activity to be convex. This leads to the situation that in each niche the heterozygote is closer to the most fit homozygote. As shown by Maynard Smith & Hoekstra (1980), Gillespie's model is equivalent to a Levene model with fitness scheme (2), if $k = \alpha/(\alpha+s)$, where the parameter α is estimated by Gillespie from experimental data to be 0·05. The robustness can be computed from conditions (3), and is shown in Table 1. Habitat selection improves the robustness only slightly.

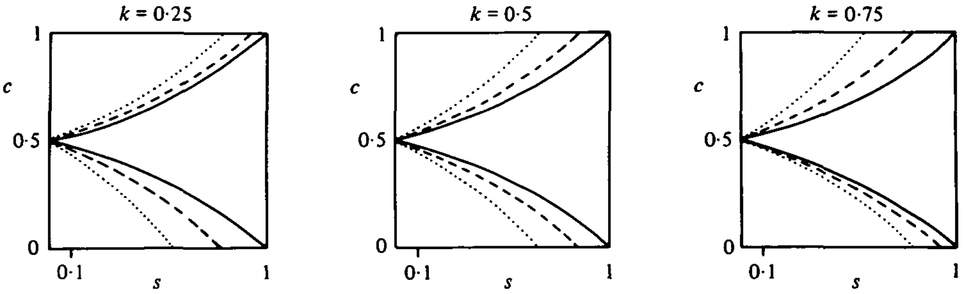

Fig. 1. Range of niche sizes, c, for which polymorphism is stable as a function of the selection coefficient s. The curves are for Levene's model with habitat selection ($h = 0$ —; $h = 0{\cdot}5$ ---; $h = 1$ ...), and with fitness regime (1) for three different degrees of dominance k.

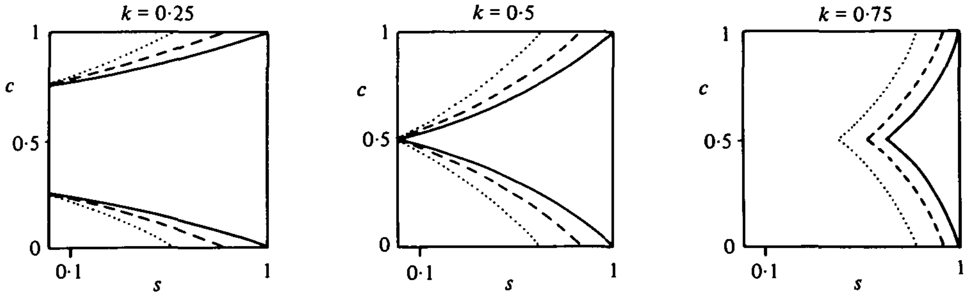

Fig. 2. Range of niche sizes, c, for which polymorphism is stable as a function of the selection coefficient s. The curves are for Levene's model with habitat selection ($h = 0$ —; $h = 0{\cdot}5$ ---; $h = 1$ ...), and with fitness regime (2) for three different degrees of dominance k.

In the same way as with Levene's model we can study the robustness of Dempster's model with habitat selection. The conditions for a protected polymorphism can be derived in a way analogous to the derivation of Maynard Smith (1970) for Levene's model. Thus one can show that when the frequencies p_1 and p_2 of A_1 in the two niches are sufficiently small, and the fitnesses of A_1A_1, A_1A_2 and A_2A_2 in the two niches are respectively w_1, 1, v_1 and w_2, 1, v_2, the following recursion equations are valid:

$$\begin{bmatrix} p_{1,t+1} \\ p_{2,t+1} \end{bmatrix} \simeq \begin{bmatrix} a & b \\ e & d \end{bmatrix} \begin{bmatrix} p_{1,t} \\ p_{2,t} \end{bmatrix} \tag{6}$$

where

$$a = (2cv_1 + h(1-c)v_2)/(2v_1(cv_1 + (1-c)v_2));$$

$$b = (1-c)(2-h)/(2(cv_1 + (1-c)v_2));$$

$$e = c(2-h)/(2(cv_1 + (1-c)v_2));$$

$$d = (2(1-c)v_2 + hcv_1)/(2v_2(cv_1 + (1-c)v_2)).$$

Table 1. *Robustness of the models discussed in Section 3*

		$s = 0·01$			$s = 0·1$		
		$h = 0$	$h = 0·5$	$h = 1$	$h = 0$	$h = 0·5$	$h = 1$
Levene's model with habitat selection; *fitness regime* (1)	All k	0·005	0·007	0·010	0·053	0·070	0·105
Idem; fitness regime (2)	$k = 0·25$	0·504	0·505	0·508	0·538	0·551	0·577
	$k = 0·50$	0·005	0·007	0·010	0·053	0·070	0·105
	$k = 0·75$	—	—	—	—	—	—
Gillespie's model with habitat selection	$k = 0·25$	—	—	—	0·538	0·551	0·577
	$k = 0·45$	0·096	0·098	0·101	—	—	—
Dempster's model with habitat selection; fitness regime (1)	All k	—	0·002	0·005	—	0·018	0·053
Idem; selection regime (2)	$k = 0·25$	0·500	0·501	0·504	0·500	0·514	0·541
	$k = 0·50$	—	0·002	0·005	—	0·018	0·053
	$k = 0·75$	—	—	—	—	—	—
Levene's model with habitat selection; mating within niches; fitness regime (1)	All k	0·005	0·010	($h = 0·9$) 0·050	0·053	0·105	($h = 0·9$) 0·526
Idem; fitness regime (2)	$k = 0·25$	0·504	0·508	($h = 0·9$) 0·538	0·538	0·577	($h = 0·9$) 0·885
	$k = 0·50$	0·005	0·010	0·050	0·053	0·105	0·526
	$k = 0·75$	—	—	—	—	—	—

Protection of allele A_1 is guaranteed if the leading eigenvalue of the gradient matrix in (6) exceeds one, which can be shown to be true if

$$h[cv_1^2+(1-c)\,v_2^2-(cv_1+(1-c)\,v_2)]+2v_1v_2 > 2v_1v_2(cv_1+(1-c)\,v_2). \qquad (7)$$

An exactly similar condition with w_i replacing v_i $(i = 1, 2)$ applies for the protection of A_2. These conditions become for selection regime (1): if

$$\left.\begin{array}{l} s<\dfrac{2-h}{2-hk} \quad \text{then} \quad c>\dfrac{(1-ks)\,[2(1-s)-h(1-ks)]}{(2-s)\,[(2-h)\,(1-s)-hs^2(1-k)^2]} \\ \text{otherwise} \quad c>0, \end{array}\right\} \qquad (8a)$$

and if

$$\left.\begin{array}{l} s<\dfrac{2-h}{s-h(1-k)} \quad \text{then} \quad c<\dfrac{(1-s)\,(1-ks)\,[2-h(1-ks)]}{(2-s)\,[(2-h)\,(1-s)-hs^2k^2]}, \\ \text{otherwise} \quad c<1. \end{array}\right\} \qquad (8b)$$

and for selection regime (2):

$$\beta < c < 1-\beta \qquad (9)$$

where

$$\beta = \frac{k[2\,(1-s)-h(1-ks)]}{2(1-s)-h(1-ks)+hs\,(1-k)(1-ks)}.$$

It is well-known that the conditions for protected polymorphism in Dempster's model are more restricted than in Levene's model. This is also apparent from a comparison between Figs. 3 and 4 (Dempster's model) and Figs. 1 and 2 (Levene's model). The effect of habitat selection on robustness is also in Dempster's model very limited for moderate selection (Table 1).

The rather surprising result that habitat selection does not have a significant effect on the robustness of these models might be due to the assumption of global random mating. To investigate this possibility, we replace the assumption of global random mating by random mating *within* each niche in Levene's model with habitat selection. The derivation of sufficient conditions for protected polymorphism is straightforward. Let the fitnesses of A_1A_1, A_1A_2 and A_2A_2 be equal to w_i, 1, v_i and the frequency of A_1 be p_i in niche i $(i = 1, 2)$. Sufficiently close to the equilibrium $p_1 = 0$, $p_2 = 0$ we obtain the following linear gene frequency transformation

$$\begin{bmatrix} p_{1,t+1} \\ p_{2,t+1} \end{bmatrix} \simeq \begin{bmatrix} (c+h(1-c))/v_1 & (1-c)\,(1-h)/v_2 \\ c(1-h)/v_1 & ((1-c)+hc)/v_2 \end{bmatrix} \begin{bmatrix} p_{1,t} \\ p_{2,t} \end{bmatrix}. \qquad (10)$$

Therefore, allele A_1 is protected if

$$c\{(1-h)\,(v_2-v_1)\} > (h-v_1)\,(1-v_2). \qquad (11a)$$

Similarly, allele A_2 is protected if

$$c\{(1-h)\,(w_2-w_1)\} > (h-w_1)\,(1-w_2). \qquad (11b)$$

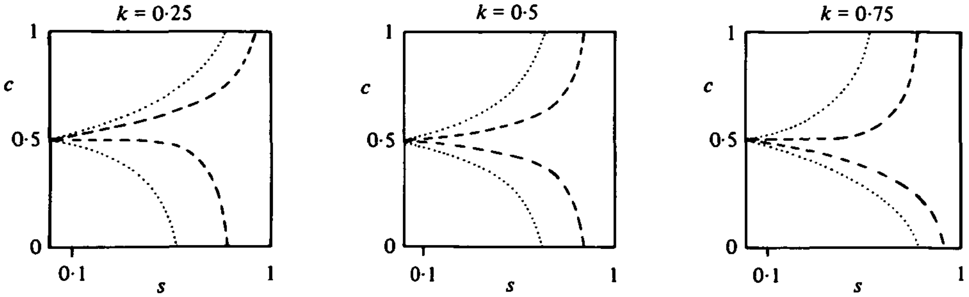

Fig. 3. Range of niche sizes, c, for which polymorphism is stable as a function of the selection coefficient s. The curves are for Dempster's model with habitat selection ($h = 0$: no polymorphism; $h = 0·5$ ---; $h = 1$ ...), and with fitness regime (1) for three different degrees of dominance k.

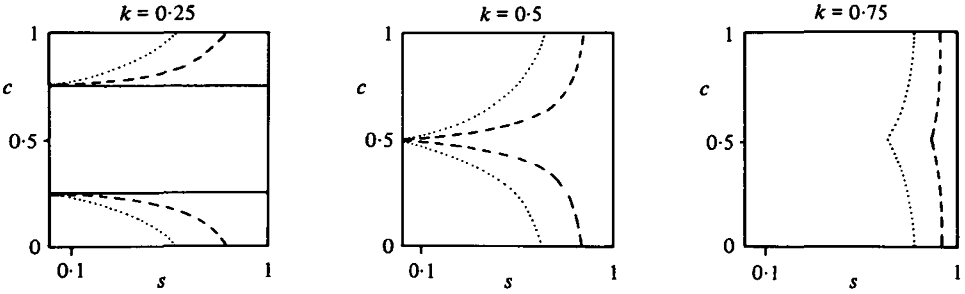

Fig. 4. Range of niche sizes, c, for which polymorphism is stable as a function of the selection coefficient s. The curves are for Dempster's model with habitat selection ($h = 0$ [only polymorphism for $k < 0·5$] —; $h = 0·5$; $h = 1$ ...), and with fitness regime (2) for three different degrees of dominance k.

For partial dominance of constant direction (selection regime (1)), (11) becomes

$$\frac{1-s-h(1-ks)}{(1-h)(2-s)} < c < \frac{1-h(1-ks)}{(1-h)(2-s)}, \tag{12}$$

and for partial dominance of varying direction (selection regime (2)), (11) becomes

$$\frac{k(1-s-h(1-ks))}{(1-h)(1-ks)} < c < \frac{(1-k)(1-h(1-ks))}{(1-h)(1-ks)}. \tag{13}$$

From conditions (12) and (13) the robustness can be calculated (see Table 1). Only very strong habitat selection causes a substantial increase in robustness; (in this model it is not meaningful to calculate robustness for $h = 1$, since that case corresponds with two separate populations without any gene flow between them; we have taken $h = 0·9$ instead).

4. TEMPORAL FITNESS VARIATION

In this section we study the robustness of temporal fitness variation models. Suppose a large random-mating population is in an environment which can be in one of two different states (defined by the selective values for the genotypes at an autosomal locus). We use the same selection schemes as in the preceding section. Thus, with partial dominance of constant direction – fitness regime (1) – environment 1 (where the genotypes A_1A_1, A_1A_2 and A_2A_2 have relative fitnesses $1, 1-ks$ and $1-s$ respectively) occurs with probability r, and environment 2 (with fitnesses $1-s$, $1-(1-k)s$ and 1) occurs with probability $1-r$. Similarly, with partial dominance of varying direction – fitness regime (2) – environment 1 (fitnesses 1, $1-ks$ and $1-s$) occurs with probability r, and environment 2 (fitnesses $1-s$, $1-ks$ and 1) with probability $1-r$. Therefore, with temporal fitness variation the parameter r plays the same role as the relative subpopulation size c in the spatial models of the preceding section. The conditions for protected polymorphism of this model were derived by Haldane & Jayaker (1963). For our purpose they can be written in the following form:

(*a*) in the case of partial dominance of constant direction:

$$\frac{\log\{1-(1-k)s\}}{\log\{(1-s)(1-(1-k)s)/(1-ks)\}} < r < \frac{\log\{(1-(1-k)s)/(1-s)\}}{\log\{(1-(1-k)s)/(1-ks)(1-s)\}}, \tag{14}$$

(*b*) in the case of partial dominance of varying direction:

$$\frac{\log\{1-ks\}}{\log\{1-s\}} < r < \frac{\log\{(1-s)/(1-ks)\}}{\log\{1-s\}}. \tag{15}$$

A graphical representation of conditions (14) is shown in Fig. 5*a*, and of conditions (15) in Fig. 5*b*. Just as in the case of the spatial models, robustness is only satisfactory when the heterozygote is close to the most fit homozygote in both environments ($k < \frac{1}{2}$ with partial dominance of varying direction). Table 2 shows the robustness figures (with respect to r) for weak and moderate selection ($s = 0{\cdot}01$ and $s = 0{\cdot}1$).

5. BOTH SPATIAL AND TEMPORAL FITNESS VARIATION

In this section we consider the robustness of a model in which selection varies spatially as well as temporally. Again we distinguish partial dominance of constant direction (selection regime (1)) and of varying direction (selection regime (2)). In the former case the fitnesses of the three genotypes A_1A_1, A_1A_2 and A_2A_2 are as follows:

$$\begin{array}{lll} & \text{In niche 1} & \text{In niche 2} \\ \text{With probability } r: & 1, 1-ks, 1-s & 1-s, 1-(1-k)s, 1 \\ \text{With probability } 1-r: & 1-s, 1-(1-k)s, 1 & 1, 1-ks, 1-s. \end{array} \tag{16}$$

In the latter case:

$$\begin{array}{lll} & \text{In niche 1} & \text{In niche 2} \\ \text{With probability } r: & 1, 1-ks, 1-s & 1-s, 1-ks, 1 \\ \text{With probability } (1-r): & 1-s, 1-ks, 1 & 1, 1-ks, 1-s. \end{array} \tag{17}$$

In both cases the niche sizes are assumed to be constant: a fraction c of the total population is in niche 1 and $1-c$ in niche 2. Thus the present model is a combination of Levene's model discussed in Section 3 and of the temporal model of Section 4. The conditions for protected polymorphism for this model were first

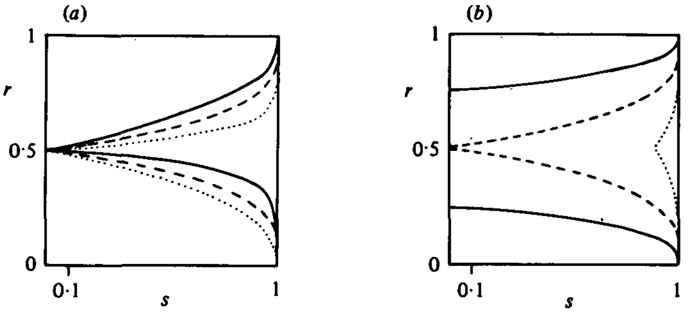

Fig. 5. Range of values of the probability r of occurrence of a particular environment, for which polymorphism is stable as a function of the selection coefficient s. The curves are for the temporal model for three different degrees of dominance ($k = 0{\cdot}25$ —; $k = 0{\cdot}5$ ---; $k = 0{\cdot}75$ ...); (*a*) fitness regime (1); (*b*) fitness regime (2).

Table 2. *Robustness of the models discussed in Section 4*

	$s = 0{\cdot}01$			$s = 0{\cdot}1$		
	$k = 0{\cdot}25$	$k = 0{\cdot}50$	$k = 0{\cdot}75$	$k = 0{\cdot}25$	$k = 0{\cdot}50$	$k = 0{\cdot}75$
Temporal model; fitness regime (1)	0·003	0·003	0·003	0·026	0·026	0·026
Idem; fitness regime (2)	0·502	0·003	—	0·519	0·026	—

derived by Hoekstra (1978). In the present special cases and in a suitable form for analysing robustness they are as follows:

(*a*) for selection regime (1):

$$\left.\begin{aligned} &\text{if } c < \tfrac{1}{2}: \quad \frac{\log\{(1-s)/b\}}{\log\{a/b\}} < r < \frac{\log\{(1-s)/d\}}{\log\{e/d\}} \\ &\text{if } c > \tfrac{1}{2}: \quad \frac{\log\{(1-s)/d\}}{\log\{e/d\}} < r < \frac{\log\{(1-s)/b\}}{\log\{a/b\}}, \end{aligned}\right\} \tag{18}$$

where

$$\begin{aligned} a &= c(1-ks)(1-s)+(1-c)(1-(1-k)s); \\ b &= c(1-(1-k)s)+(1-c)(1-ks)(1-s); \\ d &= c(1-(1-k)s)(1-s)+(1-c)(1-ks); \\ e &= c(1-ks)+(1-c)(1-(1-k)s)(1-s). \end{aligned}$$

(*b*) selection regime (2):

$$\left.\begin{aligned} &\text{if } c < \tfrac{1}{2}: \quad \frac{\log\{\alpha/\beta\}}{\log\{\gamma/\beta\}} < r < \frac{\log\{\alpha/\gamma\}}{\log\{\beta/\gamma\}} \\ &\text{if } c > \tfrac{1}{2}: \quad \frac{\log\{\alpha/\gamma\}}{\log\{\beta/\gamma\}} < r < \frac{\log\{\alpha/\beta\}}{\log\{\gamma/\beta\}}, \end{aligned}\right\} \tag{19}$$

where

$$\alpha = (1-s)/(1-ks)$$
$$\beta = 1-(1-c)\,s$$
$$\gamma = 1-cs.$$

We determine the robustness of this model with respect to the parameters c and r in conjunction for the same two values of s as in the preceding sections, namely $s = 0{\cdot}01$ (weak selection) and $s = 0{\cdot}1$ (moderate selection). Fig. 6*a* shows for which combinations of values of c and r selection regime (1) produces protected polymorphism (conditions (18)), and similarly Fig. 6*b* for selection regime (2) (conditions (19)). When partial dominance is of constant direction, there is again little robustness, as can be seen from Fig. 6*a*: when the model is very robust with respect to c, the robustness with respect to r is very small, and vice versa.

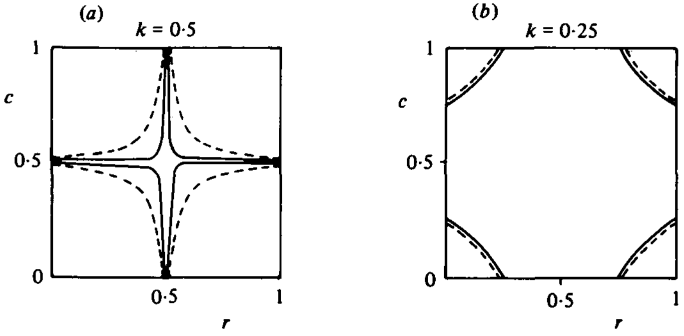

Fig. 6. Dependence of probability r of a particular environment and niche size c upon each other as imposed by the conditions for protected polymorphism in a model of both spatial and temporal fitness variation; (*a*) selection regime (1) and (*b*) selection regime (2). In (*a*) the conditions are nearly independent of k, while in (*b*) there is no polymorphism for $k > 0{\cdot}5$. —, $s = 0{\cdot}01$; ---, $s = 0{\cdot}1$.

Furthermore, robustness is nearly independent of k. For $s = 0{\cdot}01$ the model has a maximum robustness in the order of 0·1 (when c and r are both about 0·5), and for $s = 0{\cdot}1$ the maximum robustness is in the order of 0·2, again for intermediate values of c and r. As we have seen before, when dominance is allowed to vary from one allele to the other, the robustness is quite good for small values of k.

From this analysis it is clear that for both selection regimes the combination of spatial and temporal fitness variation produces a greater robustness than when there is only spatial or only temporal variation; however, the gain in robustness is not very great, and the qualitative difference in robustness associated with the difference between the selection regimes (1) and (2) remains.

6. THE MODEL OF ARNOLD AND ANDERSON

Arnold & Anderson (1983) have developed a model for density-regulated selection in a heterogeneous environment. The main features of their model are:

(i) the adults form a single random mating population,

(ii) there is a number of different habitats, each of which receives a constant fraction of the newly formed zygotes,

(iii) selection occurs in the habitats, and determines the fraction of adults contributed by each habitat to the mating pool.

Thus, their model is a form of Dempster's model, discussed in Section 3. Arnold & Anderson (1983) are aware of the fact that a number of models of selection in a heterogeneous environment lack robustness. However, in this section we show that their model is no exception in this respect.

In Arnold & Anderson's model the fitness of genotype $A_i A_j$ $(i, j = 1, 2)$ in habitat h is defined as

$$w_{ij}(h) = 1 + R_{ij}(h)[K_{ij}(h) - c(h) N]/K_{ij}(h). \tag{20}$$

This is the well-known logistic formulation, where R_{ij} is the intrinsic rate of increase, and K_{ij} the carrying capacity. N denotes the total population size, which is the sum of the subpopulation sizes. The following recursion describes the per generation change in subpopulation size in habitat h:

$$N'(h) = \overline{W}(h)\, N(h), \tag{21}$$

where $\overline{W}(h)$ is the mean fitness in habitat h.

To analyse the robustness of this model, we consider the 2 habitat case, and we reduce the number of parameters as follows. Suppose there is no variation in intrinsic rate of increase, so that there is only variation between habitats and genotypes in carrying capacity; (in the converse case of no variation in carrying capacity, polymorphism is impossible in this model). The conditions for protected polymorphism given by Arnold & Anderson (1983) the reduce to:

$$\frac{1}{c^2/K_{11}(1) + (1-c)^2/K_{11}(2)} < \frac{1}{c^2/K_{12}(1) + (1-c)^2/K_{12}(2)} > \frac{1}{c^2/K_{22}(1) + (1-c)^2/K_{22}(2)}. \tag{22}$$

If there is partial dominance of constant direction (selection regime (1)) with respect to the K_{ij}, then conditions (22) reduce to:

$$\frac{bd - \sqrt{abd}}{bd - a} < c < \frac{-d + \sqrt{abd}}{ab - d}, \tag{23}$$

where

$$a = 1 - (1-k)s$$
$$b = 1 - s$$
$$d = 1 - ks,$$

while for partial dominance of varying direction (selection regime (2)) the conditions become:

$$\left.\begin{aligned} & s > 1 - \left(\frac{1-c}{c}\right)^2 \left(\frac{1-k}{k}\right) \\ \text{and} \quad & \\ & s > 1 - \left(\frac{c}{1-c}\right)^2 \left(\frac{1-k}{k}\right). \end{aligned}\right\} \tag{24}$$

A graphical representation of conditions (23) and (24) is shown in respectively Figs. 7*a* and *b*. Although the conditions for protected polymorphism in this model are similar to those in Levene's model, this model is less robust (compare Fig. 7 with Figs. 1 and 2).

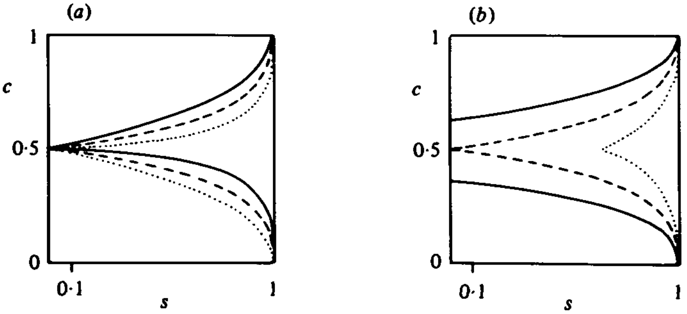

Fig. 7. Range of niche sizes, c, for which polymorphism is stable as a function of the selection coefficient s. The curves are for the model of Arnold & Anderson for three different degrees of dominance: $k = 0{\cdot}25$ (—), $k = 0{\cdot}5$ (---) and $k = 0{\cdot}75$ (...). (*a*) Fitness regime (1); (*b*) fitness regime (2).

We also have looked at a special case of Arnold & Anderson's model in which both the R_{ij} and the K_{ij} are allowed to vary, but with the constraint that the product of these parameters $R_{ij}\,K_{ij}$ is constant. The analytical analysis then runs into difficulties, but numerical computations show that there is no gain in robustness compared with the preceding case, in which there is only variation in the K_{ij}.

7. DISCUSSION

From an analysis of a number of models of spatial fitness variation, Maynard Smith & Hoekstra (1980) conclude that niche differentiation can maintain genetic polymorphism only if the selective differences between the genotypes at a single locus are large, or if in all niches the heterozygote has a higher fitness than the arithmetic mean of the homozygotes, as in a model proposed by Gillespie (1976).

In this paper we show that this general conclusion also holds when there is habitat selection, when fitnesses vary temporally, and when fitness varies both in space and in time.

The conclusion that habitat selection does not significantly improve the robustness of the models requires some further discussion. We have analysed habitat selection in a model formulated by Maynard Smith (1966, 1971) in which habitat selection is based on conditioning (females tend to return to the niche in which they were raised) rather than on genotypes selecting the niche in which they have the highest fitness. A model based on the latter possibility would in all probability be more robust, but seems to us of dubious plausibility, although there are some reports of cases in which habitat choice based directly on genotype may occur (see Jones (1980)). Apart from the fact that habitat selection based on conditioning seems more plausible than when based on the genotype itself, Maynard Smith's model is attractive because it can alternatively be interpreted as a model of restricted migration between subpopulations (especially in the case of random mating within the niches, which we have analysed). Moreover, Maynard Smith's model is applicable to animals as well as plants, whereas a model based on genotypes selecting the niche in which they are most fit, is clearly less applicable to plants.

We are then left with the conclusion that for weak and moderate selective differences, environmental heterogeneity is unlikely to maintain genetic polymorphism unless there is arithmetic mean overdominance, as displayed by fitness regime (2). A somewhat related result has been obtained by Avery (1978), who studied a model of two intermigrating subpopulations of finite size with selection acting in opposite directions in the subpopulations. He found that when the direction of dominance was different in the two subpopulations a higher average heterozygosity was established than when the direction of dominance was the same.

How likely is the 'switching' of dominance as implied by fitness scheme (2)? It seems to us that – at least with regard to enzyme loci – there are reasonably strong arguments in favour of some degree of dominance of the favourable allele. Kacser & Burns (1973, 1981) argue on the basis of a theoretical analysis of enzyme systems that one should expect to find dominance at the physiological level, even if there is strict additivity between the genotypes in enzyme activity. The assumption of Gillespie (1976) that enzyme activities are additive, but that the fitness of a genotype is a convex function of its enzyme activity, is in fact close in spirit to the conclusions of Kacser & Burns. The ideas of Kacser & Burns have been confirmed by Briscoe, Robertson & Malpica (1975), who found that the *Adh-F* allele was dominant over the *Adh-S* alternative with respect to survival on ethanol supplemented food, while the *in vitro* enzyme activity of *Adh* heterozygotes was intermediate between the two homozygotes. A similar finding has been reported by Van Delden, Boerema & Kamping (1978), although they found that the degree of dominance could vary between different populations. A second argument comes from the consideration that a heterozygote produces the same two molecules as the homozygotes produce. Thus, if there is a difference in specificity between the enzymes of the two homozygotes, the heterozygote will be able to perform both functions. Such a case has been found by Zouros & Van Delden (1982), at the *Est*-4 locus of *Drosophila mojavensis*. There is a difference in substrate specificity between two alleles at this locus. The heterozygote has both enzymes and is therefore able to perform equally well on both substrates.

A third argument for dominance at enzyme loci concerns multimeric enzymes. The different subunits of the molecule may interact in such a way that the hybrid molecule is not intermediate in the various characteristics, but resembles one of the monomers. This so-called 'oligomer effect' has for example been observed for *LDH*, a tetrameric enzyme, both in the case when the subunits of the hybrid molecule were derived from different isoenzymes (Braswell, 1975) and when different allozyme subunits hybridized (Place & Powers, 1984). In the latter case the hybrid molecule resembled one homomer in certain characteristics, but was similar to the other homomer in other characteristics. Of course, here the dominance is at the protein level, and the precise correspondence between biochemical characteristics and fitness is not known. But dominance with respect to fitness seems not unlikely – also in view of the other two arguments.

On the basis of these three arguments we accept the idea that for enzyme loci dominance of the favoured allele might be a common phenomenon. It is, however, unfortunate that there is very little evidence of different environments favouring different homozygotes at an enzyme locus (see Hedrick *et al.* 1976).

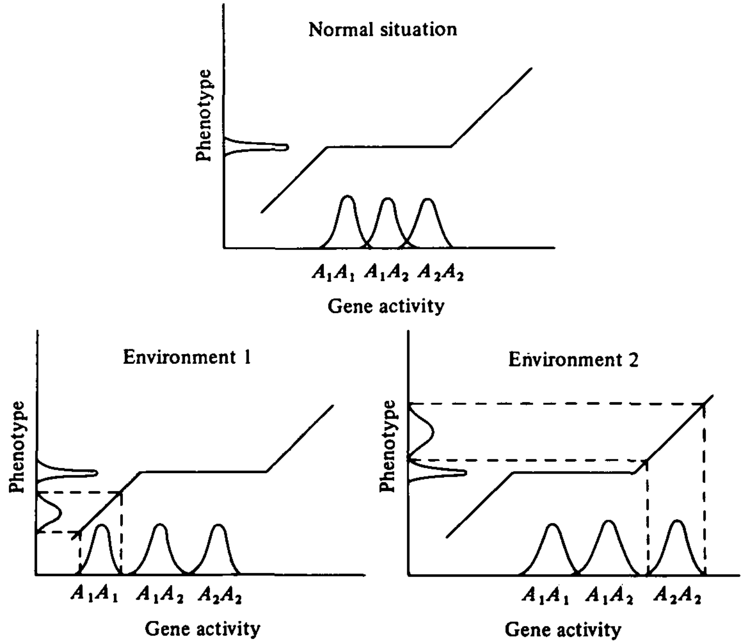

Fig. 8. (*a*) All three genotypes are canalized to produce the same phenotype; (*b*) A_1A_1 falls outside the canalized range; A_2 is dominant. (*c*) A_2A_2 falls outside the canalized range; A_1 is dominant. In both environments the heterozygote has the same fitness as the favoured (canalized) homozygote.

The above discussion concerns enzyme loci. What about loci coding for, say, morphological structures? Although it is known that artificial selection may reverse dominance relationships (Ford, 1940; Fisher & Holt, 1944), it seems doubtful that dominance 'switching' for these characters is common. Moreover, the arguments discussed above do not easily apply to this class of genes. In this connection we would like to suggest the following possibility. Suppose for a particular morphological characteristic the relationship between gene activity and phenotype is canalized (see Rendel, 1967). If different environments cause a shift in gene activity in opposite direction, then in each environment a different homozygote may fall outside the canalized range (see Fig. 8). When the canalized phenotype has the highest fitness, the favoured allele would be dominant (A_1 in environment 2 and A_2 in environment 1).

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