

# REGIONS OF STABLE EQUILIBRIA FOR MODELS OF DIFFERENTIAL SELECTION IN THE TWO SEXES UNDER RANDOM MATING

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## ABSTRACT

The equilibrium structure of models of differential selection in the sexes is investigated. It is shown that opposing additive selection leads to stable polymorphic equilibria for only a restricted set of selection intensities, and that for weak selection the selection intensities must be of approximately the same magnitude in the sexes. General models of opposing directional selection, with arbitrary dominance, are investigated by considering simultaneously the stability properties of the trivial equilibria and the curve along which multiple roots appear. Numerical calculations lead us to infer that the average degree of dominance determines the equilibrium characteristics of models of opposing selection. It appears that if the favored alleles are, on the average, recessive, there may be multiple polymorphic equilibria, whereas only a single polymorphic equilibrium can occur when the favored alleles are, on the average, dominant. The principle that the average degree of dominance controls equilibrium behavior is then extended to models allowing directional selection in one sex with overdominance in the other sex, by showing that polymorphism is maintained if and only if the average fitness in heterozygotes exceeds one.

ALL mechanisms that maintain genetic variability involve the balance of opposing forces. Such a balance may be the result of opposing mutation pressures, mutation opposing selection, multiple niche selection, or the well-known overdominant case, where an allele is favored in heterozygotes but is at a disadvantage in homozygotes. Differential selection in the two sexes is another mechanism that may produce stable internal equilibria. OWEN (1953) established a general mathematical framework for the analysis of differential selection in the two sexes, and considered situations that admit of more than a single stable

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equilibrium. BODMER (1965) noted that when fertility effects combine multiplicatively in mating pairs, viability and fertility models lead to qualitatively different results only in the case where selective effects are opposed in the two sexes. With some selective values (admittedly rather artificial) there may be as many as three polymorphic equilibrium states, with two of the equilibria stable. Under more reasonable assumptions it is quite possible to have both a stable and an unstable polymorphic equilibrium. In this paper, we delineate the regions of the parameter space, that is, regions in the space of selective values, where qualitatively different types of equilibrium behavior occur. The results show that for some models, only a restricted set of selection intensities leads to stable polymorphic equilibria.

THE MODEL

OWEN (1953) reduced the problem to one with only two independent parameters by considering the gene frequency ratio in the two sexes at equilibrium. In order to investigate regions of stability, we consider pairs of simultaneous equations for the two sexes. In the interest of completeness we begin with the general model. We consider a single diallelic locus with constant selective values, some of which differ between the two sexes, and normal Mendelian segregation. Selection is assumed to occur through viability (or fertility) differences, but with no dependence of the selection parameter on the mating pair. Discrete generations and random mating among selected adults are also assumed.

We denote the frequency of allele  $A_1$  in males and females in the mating pool by  $p_m$  and  $p_f$ , respectively. Similarly, the frequencies of allele  $A_2$  are  $q_m (=1-p_m)$  and  $q_f (=1-p_f)$ . Genotypic fitness values are designated  $w_{m1}$  ( $w_{f1}$ ),  $w_{m2}$  ( $w_{f2}$ ) and  $w_{m3}$  ( $w_{f3}$ ) corresponding to genotypes  $A_1A_1$ ,  $A_1A_2$  and  $A_2A_2$ , respectively, in males (females). The frequency before selection and the fitness of each genotype will be:

Genotype	$A_1A_1$	$A_1A_2$	$A_2A_2$
Frequency	$p_m p_f$	$p_m q_f + p_f q_m$	$q_m q_f$
Fitness, males	$w_{m1}$	$w_{m2}$	$w_{m3}$
Fitness, females	$w_{f1}$	$w_{f2}$	$w_{f3}$

After selection the genotypic frequencies are:

Genotype	$A_1A_1$	$A_1A_2$	$A_2A_2$
Frequency, males	$w_{m1} p_m p_f / \bar{w}_m$	$w_{m2} (p_m q_f + p_f q_m) \bar{w}_m$	$w_{m3} q_m q_f / \bar{w}_m$
Frequency, females	$w_{f1} p_m p_f / \bar{w}_f$	$w_{f2} (p_m q_f + p_f q_m) \bar{w}_f$	$w_{f3} q_m q_f / \bar{w}_f$

where

$$\bar{w}_m = w_{m1} p_m p_f + w_{m2} (p_m q_f + p_f q_m) + w_{m3} q_m q_f$$

$$\bar{w}_f = w_{f1} p_m p_f + w_{f2} (p_m q_f + p_f q_m) + w_{f3} q_m q_f$$

The frequency of the allele  $A_1$  in males after selection, *i.e.*, in the mating pool for the following generation, is:

$$p'_m = \frac{2w_{m1} p_m p_f + w_{m2} (p_m q_f + p_f q_m)}{2\bar{w}_m} \tag{1a}$$

and the corresponding frequency in females following selection is:

$$p'_f = \frac{2w_{f1}p_m p_f + w_{f2}(p_m q_f + p_f q_m)}{2\bar{w}_f} \tag{1b}$$

The changes in gene frequency are:

$$\Delta p_m = \frac{2w_{m1}p_m p_f + w_{m2}(p_m q_f + p_f q_m) - 2\bar{w}_m p_m}{2\bar{w}_m}$$

and

$$\Delta p_f = \frac{2w_{f1}p_m p_f + w_{f2}(p_m q_f + p_f q_m) - 2\bar{w}_f p_f}{2\bar{w}_f}$$

At equilibrium,  $\Delta p_m = \Delta p_f = 0$  whence, after some calculation:

$$p_m = \frac{2(w_{f2} - w_{f3})p_f^2 + (2w_{f3} - w_{f2})p_f}{(4w_{f2} - 2w_{f1} - 2w_{f3})p_f^2 + (2w_{f1} - 4w_{f2} + 2w_{f3})p_f + w_{f2}} \tag{2a}$$

$$p_f = \frac{2(w_{m2} - w_{m3})p_m^2 + (2w_{m3} - w_{m2})p_m}{(4w_{m2} - 2w_{m1} - 2w_{m3})p_m^2 + (2w_{m1} - 4w_{m2} + 2w_{m3})p_m + w_{m2}} \tag{2b}$$

The expression for  $p_m$  ( $p_f$ ) is the ratio of polynomials in  $p_f$  ( $p_m$ ). If we write  $p_m = f(p_f)$  and  $p_f = g(p_m)$  then, by substitution,  $p_m = f[g(p_m)]$ , a quintic equation in  $p_m$  which is easily reduced to a cubic by factoring out the trivial roots zero and one. It follows that at most there can be three polymorphic equilibria. The resulting cubic equation is, however, very difficult to analyze directly. In order to gain some insight into the behavior of models of opposing selection in the sexes, we begin by considering the case of additive selection.

*Opposing additive selection*

Under this model the fitness relations are parameterized as  $w_{m1}=1$ ,  $w_{m2}=1-.5s_m$ ,  $w_{m3}=1-s_m$ ,  $w_{f1}=1-s_f$ ,  $w_{f2}=1-.5s_f$  and  $w_{f3}=1$ , [ $s_m, s_f \in (0,1)$ ], so that  $A_1$  is favored in males but  $A_2$  is favored in females. Substitution and simplification of equations (2a) and (2b) yield:

$$p_m = \frac{-2s_f p_f^2 + (s_f + 2)p_f}{(2 - s_f)} \tag{3a}$$

$$p_f = \frac{2s_m p_m^2 + (2 - 3s_m)p_m}{(2 - s_m)} \tag{3b}$$

In this particular model, the equilibrium equations are quartic equations which can be reduced to quadratics by factoring out the trivial roots zero and one. Further simplification leads to the conclusion:

$$p_m = \frac{s_m - 1}{s_m} \pm \left( \frac{s_m s_f - s_m - s_f + 2}{2s_m s_f} \right)^{1/2}$$

Since  $0 < s_m, s_f \leq 1$ , the first term on the right-hand side is always negative, and the term under the radical is always positive. There are, therefore, always

two real roots. It also follows that the only root which can yield admissible solutions is:

$$p_m = \frac{s_m - 1}{s_m} + \left( \frac{s_m s_f - s_m - s_f + 2}{2s_m s_f} \right)^{1/2}$$

The region of admissible equilibria can be obtained by considering the boundaries  $p_m = 1$  and  $p_m = 0$  and determining  $s_f$  as a function of  $s_m$  for these two boundaries. For  $p_m = 0$  the relation between  $s_f$  and  $s_m$  bounding admissible solutions is:

$$s_f = \frac{s_m}{1 - s_m}$$

and for  $p_m = 1$ ,

$$s_f = \frac{s_m}{1 + s_m}$$

The equilibrium region for values of  $s_m$  and  $s_f$  is shown in Figure 1. Equilibrium gene frequencies can be easily computed, and such computations show (1) that equilibrium frequencies in the two sexes can be widely divergent, and (2) that average gene frequencies (over sexes) are intermediate ( $0.25 \leq \bar{p} \leq 0.75$ ) throughout most of the equilibrium region.

The most interesting conclusion that can be drawn from this analysis is that weaker selection intensities progressively restrict the parameter space yielding admissible equilibria; *e.g.*,  $s_m, s_f < 0.3$  can maintain variability only if the selec-

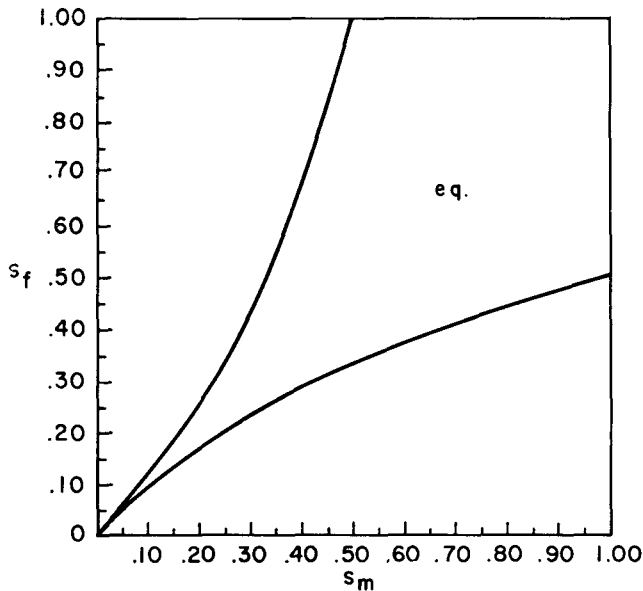


FIGURE 1.—Portion of the parameter space which yields stable internal equilibria as a function of the selection intensities in males ( $s_m$ ) and females ( $s_f$ ) for opposing additive selection.

tion intensities are approximately equal. Conversely, an allele which is lethal in one sex can be maintained if the selection intensity against the alternative allele in the opposite sex is greater than 0.5. Questions regarding the stability of polymorphic equilibria are taken up in a more general context in a later section. We simply note here that polymorphic equilibria are always stable under opposing additive selection. This model represents a special case of partial dominance. It is therefore of interest to examine the influence of dominance parameters on the equilibrium structure of these models.

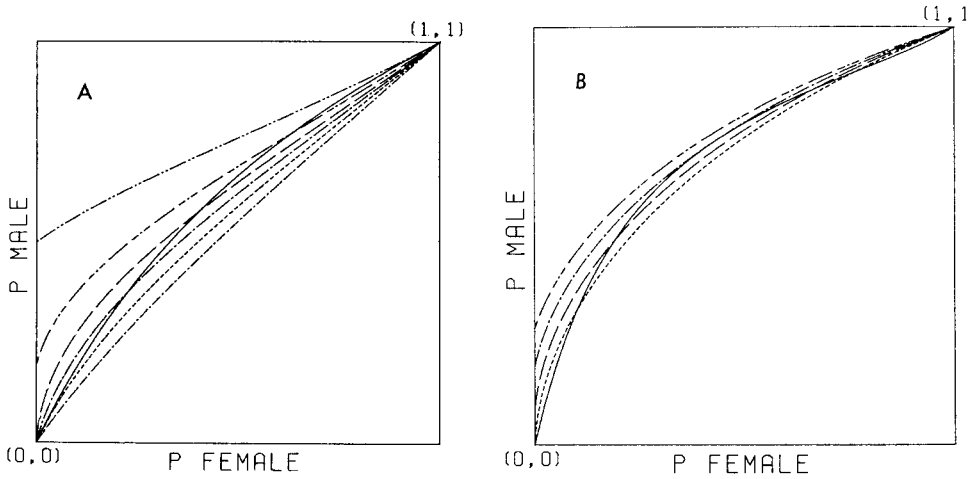


FIGURE 2.—Graphs of equations (2a) and (2b). Solid lines are the graphs of equation (2a). FIGURE 2a.—Change of equilibrium gene frequency with variation in the strength of selection.  $h_f = 0.7, s_f = 0.5, h_m = 0.3$

- · — · —  $s_m = 0.2$ . Selection in the female drives out the  $A_1$  gene and there is no equilibrium.
- · · · ·  $s_m = 1/3$ . The dotted line, *i.e.*, the graph of equation (2b), is tangent to the solid line. The trivial equilibrium at (0,0) is changing from stable to unstable.
- · — · —  $s_m = 0.45$ , — — —  $s_m = 0.55$ , and — · — · —  $s_m = 0.70$ . As  $s_m$  increases from the value  $1/3$ , a stable, nontrivial equilibrium moves in through the (0,0) equilibrium. The equilibrium values of  $p_f$  and  $p_m$  are the coordinates of the points where the dotted line equation, (2b), meets the solid line equation, (2a). As  $s_m$  increases,  $p_f$  and  $p_m$  move along the graph of equation (2a).
- · — · —  $s_m = 1.0$ . The graph of equation (2b) is tangent to that of equation (2a) at (1,1).

The internal equilibrium has moved to coincide with the trivial equilibrium at (1,1).

FIGURE 2b.—The birth of paired equilibria.  $h_f = 0.9, s_f = 0.7, h_m = 0.6$ . The allele which is deleterious in females,  $A_1$ , has the greater dominance so if exactly one trivial equilibrium is stable it must be the one where  $A_1$  is eliminated. For all four values of  $s_m$  shown in Figure 2b, this equilibrium is stable and that with  $A_2$  absent is unstable.

- · — · —  $s_m = 0.85$ . There is no equilibrium. The  $A_1$  gene is necessarily eliminated.
- · — · —  $s_m = 0.80$ . The graph of equation (2b) has become tangent to that of equation (2a). There is a single nontrivial equilibrium, but it is unstable and  $A_1$  will still be eliminated.
- · — · —  $s_m = 0.75$ . The single equilibrium at  $s_m = 0.80$  has bifurcated into two, one stable and one unstable. If  $A_1$  starts at high frequency, the polymorphism will be maintained. If  $A_1$  starts at low frequency, it will be eliminated.
- · · · ·  $s_m = 0.70$ . The qualitative picture is similar to that for  $s_m = 0.75$ , but the equilibria have moved further apart.

*Opposing selection with arbitrary dominance*

For any given selective values, it is easy to graph equations (2a) and (2b) and to obtain the equilibria by observing where the graphs intersect. Figure 2a, 2b, and 2c show the graphs for some representative choices of the selective values. At a later point the degrees of dominance will be important and their role can be seen in Figure 2. In it we parameterize the selective values as  $w_{f1} = 1 - s_f$ ,  $w_{f2} = 1 - h_f s_f$ ,  $w_{f3} = 1$ ,  $w_{m1} = 1$ ,  $w_{m2} = 1 - h_m s_m$ , and  $w_{m3} = 1 - s_m$ .

As the selective values vary, the equilibrium point, or points, move about in the  $(p_f, p_m)$  space. The values of  $w_{f1}$ ,  $w_{f2}$ , and  $w_{f3}$  determine the graph of equation (2a); suppose we hold these values constant. If we then vary the selection values for the males, only the graph of equation (2b) changes and the equilibrium—the intersection of the graphs—moves along the fixed graph of equation (2a).

As  $w_{m1}$ ,  $w_{m2}$ , and  $w_{m3}$  vary, the equilibrium can be lost either by moving through  $(0,0)$  or  $(1,1)$  and out of the allowable region (see Figures 2a and 2c) or by the graph of (2b) moving to become tangent to that of (2a) and then losing contact with the latter (see Figures 2b and 2c). Values where equilibria appear or disappear play a central role when we describe the way the system behaves.

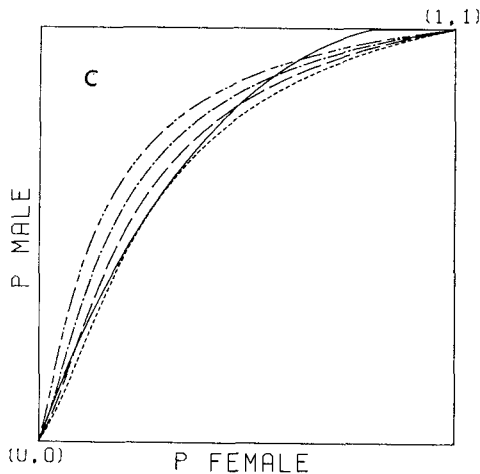


FIGURE 2c.—A nontrivial equilibrium moves through one of the trivial equilibria.  $h_f = 0.6$ ,  $s_f = 0.8$ ,  $h_m = 0.9$ .

- $s_m = 0.70$ . There is a single unstable equilibrium. The  $A_2$  allele will be lost. The situation is identical with one of those in Fig. 2b, except that the parameter values for the two sexes have been interchanged.
- $s_m = 0.75$ . The bifurcation has taken place and the equilibria move apart.
- $s_m = 0.80$ . The unstable equilibrium where  $A_1$  is relatively rare has moved to coincide with the trivial equilibrium at  $(0,0)$ . The graphs of equations (2b) and (2a) are tangent at  $(0,0)$ .
- $s_m = 0.85$ . The unstable internal equilibrium has been lost. The equilibrium at  $(0,0)$  has changed from stable to unstable. The polymorphism will be preserved no matter what the initial gene frequencies may be.

The graphs of equations (2a) and (2b) always pass through the trivial equilibria at (0,0) and (1,1). If a point of the intersection moves towards (0,0) then the tangent to equation (2b) and (0,0) moves closer and closer to that of equation (2a) and, at the instant when the equilibrium is lost, the two tangents coincide.

Following OWEN (1953) we introduce

$$a_f = 2w_{f1}/w_{f2} - 1$$

and

$$b_f = 2w_{f3}/w_{f2} - 1$$

(In OWEN's notation,  $a_f = C_1$ ,  $b_f = c_1$ .) Now equation (2a) assumes the form  $p_m = f(p_f; a_f, b_f)$ , where

$$f(p; a, b) = \frac{(1-b)p^2 + bp}{1 + p(1-p)(a + b - 2)}$$

The slope of the tangent at (0,0) is  $b$  and at (1,1) it is  $a$ .

With the obvious notation, equation (1b) is  $p_f = f(p_m; a_m, b_m)$ , so the slope of the tangent to its graph at (0,0) is

$$\frac{dp_m}{dp_f} = 1/f'(0; a_m, b_m) = \frac{1}{b_m}$$

Thus the tangents to equations (2a) and (2b) at (0,0) coincide when  $b_f b_m = 1$ . Similarly, those at (1,1) coincide when  $a_f a_m = 1$ .

The condition  $b_f b_m = 1$  is important for another reason, too. If we let

$$g(r, s; a, b) = \frac{(a+1)rs + r(1-s) + s(1-r)}{(a+1)rs + r(1-s) + s(1-r) + (b+1)(1-r)(1-s)}$$

then the equations (1a) and (1b) are:

$$\begin{aligned} p_f &= g(p_f, p_m; a_f, b_f) \\ p_m &= g(p_m, p_f; a_m, b_m). \end{aligned}$$

The Jacobian matrix at (0,0) is:

$$\begin{bmatrix} \frac{1}{b_f+1} & \frac{1}{b_f+1} \\ \frac{1}{b_m+1} & \frac{1}{b_m+1} \end{bmatrix}$$

whose dominant eigen-value is

$$\lambda = \frac{1}{b_f+1} + \frac{1}{b_m+1} \tag{4a}$$

Similarly the dominant eigen-value of the Jacobian matrix evaluated at (1,1) is

$$\lambda = \frac{1}{a_f+1} + \frac{1}{a_m+1} \tag{4b}$$

The trivial equilibrium at (0,0) is stable when (4a) is less than 1, *i.e.*, when  $b_f b_m > 1$ . The equilibrium is unstable when  $b_f b_m < 1$ . Similarly the curve  $a_f a_m = 1$  separates parameter values where (1,1) is stable from those where it is an unstable equilibrium. It follows that a trivial equilibrium changes its stability at precisely those parameter values where a polymorphic equilibrium comes to coincide with the trivial equilibrium.

It is more difficult to determine those parameter values where the graphs of equations (2a) and (2b) become tangent—the values where equilibria are created or destroyed in pairs. As OWEN (1953) shows, such values lie on the solution of

$$4\alpha^3 + 4\beta^3 - 3\alpha^2\beta^2 - 6\alpha\beta + 1 = 0 \tag{5}$$

where

$$3\alpha = a_f b_m + b_f + a_m \tag{6a}$$

and

$$3\beta = a_m b_f + b_m + a_f. \tag{6b}$$

If one parameterizes equation (5) by  $u = (\alpha + \beta)/2$ , an elementary but arduous calculation shows that  $\alpha = u + v$  and  $\beta = u - v$  where  $v$  is a root of the biquadratic equation

$$3(v^2)^2 - 6(u^2 + 4u + 1)v^2 + 3u^4 - 8u^3 + 6u^2 - 1 = 0.$$

These algebraic formulas are too complicated to convey any biological insight directly, but they provide a means of delineating the regions of the parameter space where the system exhibits a particular biological behavior. Meaningful two-dimensional graphs can be obtained by fixing two parameters and numerically finding values of  $u$  which yield solutions of equations (6a) and (6b) within the allowable range of two other parameters. This procedure can be applied to any parameterization of the selection scheme. In what follows, dominance is separated from the intensity of selection by setting:

$$\begin{aligned} w_{f1} &= 1 - s_f; w_{f2} = 1 - h_f s_f; w_{f3} = 1, \\ w_{m1} &= 1; w_{m2} = 1 - h_m s_m; w_{m3} = 1 - s_m. \end{aligned}$$

Using this parameterization the trivial equilibria are unstable when:

$$s_m < \frac{(1 - h_f) s_f}{h_m (1 - s_f)} \tag{7a}$$

$$s_m > \frac{h_f s_f}{1 - h_m + h_f s_f} \tag{7b}$$

FIGURE 3.—Boundaries of regions of equilibria as a function of  $s_m$  and  $s_f$  for fixed choices of  $h_m$  and  $h_f$ . The solid line (—) is the line along which (0,0) in the  $p_m, p_f$  plane goes from stability to instability. The dashed line (---) divides the regions of stability and instability of (1,1) and the dotted line (----) is the line along which equilibria appears in pairs (*i.e.*, the solution to equation 5). The regions with octagons are characterized by no polymorphic equilibria. Either (0,0) is unstable and (1,1) is stable or (0,0) is stable and (1,1) is unstable. The regions with a triangle ( $\Delta$ ) are characterized by a single stable polymorphic equilibrium. The regions with an inverted triangle ( $\nabla$ ) are characterized by a single unstable equilibrium. The region with the star (\*) contain one unstable and one stable equilibrium, so that one trivial equilibrium is unstable while the other is stable.



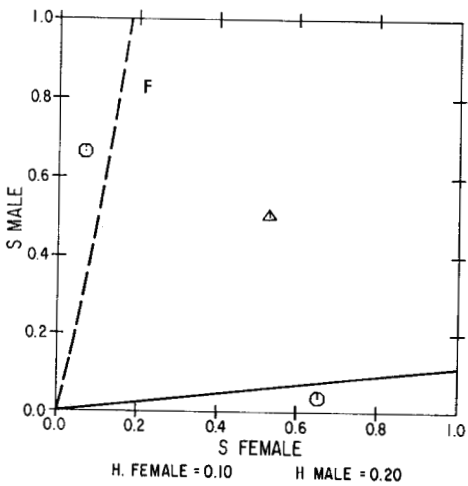
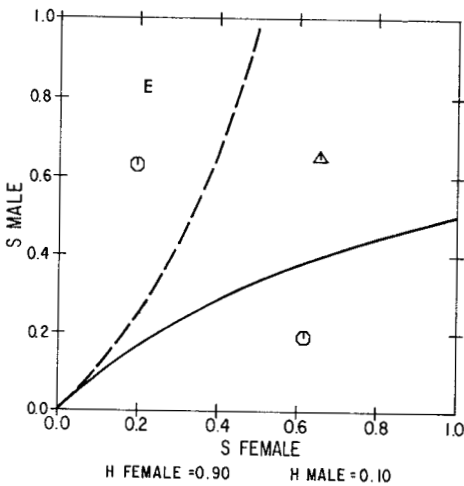
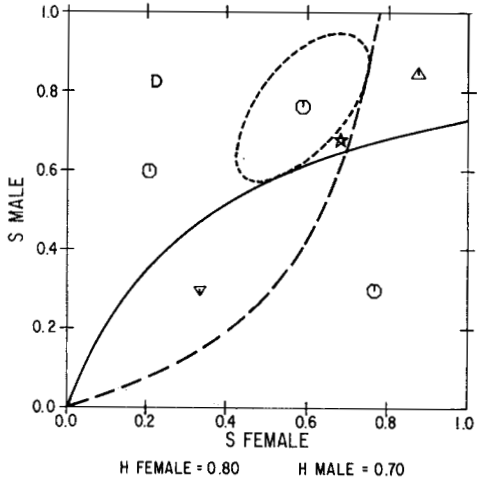
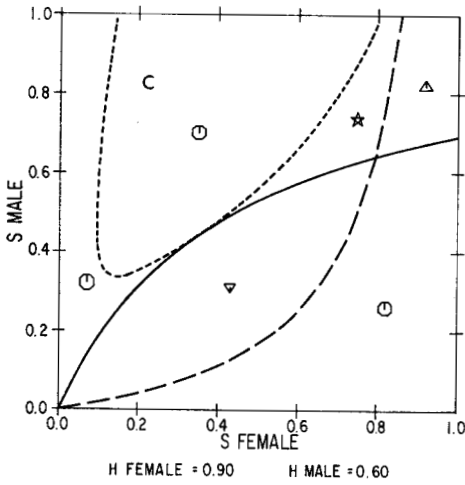
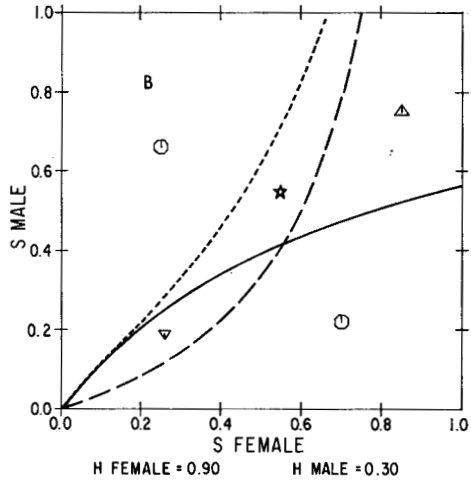
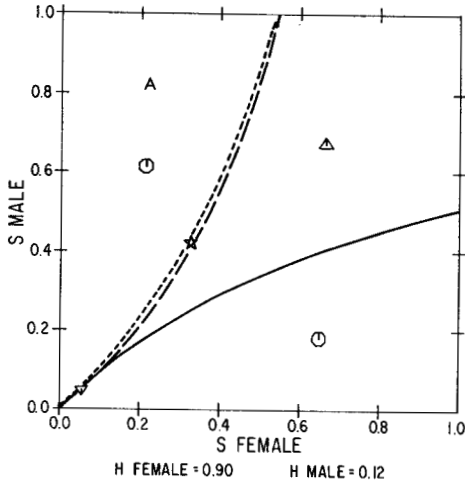


Figure 3 shows some representative graphs of the equilibrium regions in the  $s_m, s_f$  parameter space for fixed values of  $h_m$  and  $h_f$ . The region admitting of stable equilibria may include points outside the region bounded by equations (7a) and (7b). These are points where there is more than one equilibrium, (see, for example, Figure 3b).

An interesting special case arises when the slopes of the equations formed from the inequalities (7a) and (7b) coincide at  $s_m = s_f = 0$ . (This, of course, occurs when internal equilibria are simultaneously entering and exiting through the (0,0), (1,1) corners in the  $p_m, p_f$  plane). When this condition is satisfied, the dominance parameters obey the constraint  $h_m + h_f = 1$ , and the conditions for instability of the trivial equilibria become:

$$s_m < \frac{s_f}{1-s_f}$$

$$s_m > \frac{s_f}{1+s_f} ,$$

identical to the case of additive selection. It appears that the relation  $h_m + h_f = 1$  divides the equilibrium properties of this model into two classes: (1) when  $h_m + h_f > 1$ , more than a single internal equilibrium may occur, and the region admitting of stable equilibria includes points outside the region bounded by equations (7a) and (7b) (Figures 3a, b, c, d); and (2) when  $h_m + h_f < 1$ , only a single stable polymorphic equilibrium occurs, and consequently equations (7a) and (7b) bound the entire equilibrium region. Finally, when the dominance parameters are perfectly complementary, the region admitting of stable internal equilibria is identical to that for additive selection. Figure 3e presents one example of complementary dominance relations, whereas Figure 3f shows the increase in the equilibrium area over that shown in Figure 3e when  $h_m + h_f < 1$ .

Some corollaries of the above results are: (1) for  $h_f = 0$  any choice of  $s_m$  and  $s_f$  to the right of the curve

$$s_m = \frac{s_f}{h_m(1-s_f)}$$

will yield a stable polymorphic equilibrium, (2) for  $h_m = 0$  all pairs of  $s_m$  and  $s_f$  above the curve

$$s_m = \frac{h_f s_f}{1-h_f s_f}$$

produce stable polymorphic equilibria, and (3) when  $h_m = h_f = 0$  all  $s_m, s_f \in [0,1]$  give stable polymorphic equilibria.

The biological implications of these results are that the region of polymorphic equilibria increases as the degree of dominance decreases. If the detrimental alleles are completely recessive in both sexes, then any nonzero selection in the two sexes will produce a balanced polymorphism. On the other hand, opposing selection against characters which are, on the average, dominant ( $h_m + h_f > 1$ ) results in a greater complexity of equilibrium behavior. This situation is charac-

terized by (1) more than a single polymorphic equilibrium and therefore a dependence of equilibrium achieved on starting conditions, and (2) a restriction of the equilibrium region towards the corner of strong selection as  $h_m + h_f$  goes from 1.0 to 2.0 (e.g.,  $s_m, s_f > 0.5$  for  $h_m + h_f > 1.5$ , Figure 3e).

#### *Overdominance in females and directional selection in males*

Let the female viabilities be  $w_{f1} = 1-a$ ,  $w_{f2} = 1$ , and  $w_{f3} = 1-b$  and assume that the  $A_1$  allele is favored in the males with viabilities  $w_{m1} = 1$ ,  $w_{m2} = 1-hs$ ,  $w_{m3} = 1-s$ . The condition for the equilibrium with  $A_1$  absent to be unstable is  $\frac{1}{1-b} + \frac{1-hs}{1-s} > 2$ . This is always the case, since each term on the left is greater than 1. It is obvious on biological grounds that this equilibrium is necessarily unstable because when  $A_1$  is rare it is favored in the females as well as in the males.

The condition for the other trivial equilibrium to be unstable is  $\frac{1}{1-a} + 1-hs > 2$  or  $hs < \frac{a}{1-a}$ . Thus, the polymorphism will be maintained if, and only if, selection against male heterozygotes is not too strong. When heterosis is very strong (specifically if the female heterozygote has more than twice the survival probability of the  $A_1A_1$  homozygote), even a gene which is a dominant lethal in males will be maintained in the population.

The quantitative relationship is most easily described if the selection parameters are renormalized so that  $w_{f1} = w_{m1} = 1$ . Since there is overdominance in females and directional selection in males,  $w_{f1} = 1 < w_{f2}, w_{f3} < w_{f2}$ , and  $w_{m1} > w_{m2} > w_{m3}$ . The polymorphism will be maintained if and only if  $w_{f2} + w_{m2} > 1$ .

#### DISCUSSION AND CONCLUSIONS

Models of differential selection in the two sexes have been considered by a number of authors (BODMER 1965; HALDANE 1962; LI 1963; MÉRAT 1969; OWEN 1953). The main result of these earlier investigations has been to identify the number of possible equilibria associated with different patterns of selection. Thus, MÉRAT (1969) shows that overdominance in one sex coupled with underdominance in the other sex constitutes the only model of selection which will yield three equilibria. He also shows that two equilibria can arise under models of opposing directional selection. It is highly unlikely that patterns of selection during the reproductive phases of the life cycle are identical for males and females. Indeed, if a genotype manifests itself in the reproductive component of fitness, then almost certainly the effects will be sex dependent (PROUT 1971). Consequently, patterns of opposing selection between the sexes provide another opportunity for the maintenance of genetic variation in organisms with complex and varied life histories.

The major result of this investigation has been to illustrate the dependence of equilibrium region on the average degree of dominance over the sexes. In particular, we assert that the relation  $h_m + h_f = 1$  divides models of opposing selec-

tion into classes yielding only a single internal equilibrium ( $h_m + h_f < 1$ ) and classes yielding more than one internal equilibrium ( $h_m + h_f > 1$ ). A natural question to consider concerns the power of opposing selection in the sexes as a force in the maintenance of genetic variability. To consider this question we need some standard of comparison. The classic model of single-locus overdominance provides a ready comparison, and hence we need only determine the constraints that the average selective values over sexes must satisfy to maintain polymorphism. It is readily seen from equations (4a) and (4b) that the conditions for instability of the trivial equilibria are:

$$\frac{1}{2} \left( \frac{1}{w_{f1}} + \frac{1}{w_{m1}} \right) > 1$$

and

$$\frac{1}{2} \left( \frac{1}{w_{f3}} + \frac{1}{w_{m3}} \right) > 1$$

when the parameterization is chosen relative to  $w_{m2} = w_{f2} = 1$ . It follows that a sufficient, but not necessary, condition for a stable polymorphism is that the heterozygous fitness values exceed the harmonic mean of the homozygote fitness values. Therefore, opposing selection in the sexes will maintain polymorphism over a wider range of fitness values than will the classical model of overdominant selection. If  $h_m + h_f > 1$ , then stable polymorphisms can arise which violate the requirement that the harmonic mean of the homozygote fitness values be less than that of the heterozygote, further widening the conditions under which polymorphism will be maintained. It therefore appears that opposing selection in the sexes can be a potentially important mechanism in the maintenance of genetic variation.

One further aspect of the model of opposing selection in the sexes which bears comment is its apparent similarity to the LEVENE (1953) model of multi-niche selection. Sufficient conditions for instability of the trivial equilibria appear to be identical; however, it is not immediately clear whether the wider conditions of PROUT (1968) are also satisfied. Furthermore, the algebraic structure of the general model (assuming two niches) differs in the specification of the mating pattern. The multi-niche model assumes random mating throughout the population, whereas the model of opposing selection in the sexes requires a disassortative pattern of mating (*i.e.*, in the niche context, individuals from niche 1 can mate only with individuals from niche 2, and conversely). The effect of this restriction of the mating pattern is to produce greater heterozygosity in the sex model. Hence, direct extrapolation of the present results to the two-niche model is not justified. However, these results may provide some guidance in the further study of multi-niche selection. For example, the similarity of the trivial equilibria would suggest that average degree of dominance over niches may also play a role in describing the global equilibrium structure of multi-niche selection models.

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