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On the product mean fitness and population growth in sexual and asexual populations

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ABSTRACT

We examine situations that have frequently been invoked as advantageous for sex. In a constant environment with one diallelic locus determining viability that differs between the sexes, complete genotypic frequency dynamics are obtained in a symmetric case. The product of male and female mean fitnesses may not increase over time. In models with periodic or random environments, the numbers of sexuals and asexuals in pure populations of each can be compared. In agreement with previous studies, sexual populations are shown to grow at a faster rate than asexual populations.

Keywords: failure of optimality, global stability, multiple equilibria, population size, random environments.

INTRODUCTION

One of the most famous results in theoretical population genetics is Fisher's (1930) Fundamental Theorem of Natural Selection. One form of this theorem states that if genotypes A_iA_j at a single locus have viabilities w_{ij}, and if x_i and x_i' are the frequencies of A_i at the present and next generation respectively, then the mean viability W satisfies

$$W' = \sum_i \sum_j w_{ij} x_i' x_j' \geq W = \sum_i \sum_j w_{ij} x_i x_j$$

(Kingman, 1961). This result is not generally true if viability is determined by two or more loci (Moran, 1964), or if fitness is measured in terms other than viability, for example fertility (Pollack, 1978).

When the viabilities of single-locus genotypes differ between the sexes, the possible extension of Fisher's theorem, originally suggested by MacArthur (1965), involves the product $\bar{M}\bar{F}$ of the average genotypic viabilities in males and females. Spieth (1974) observed a numerical case in which $\bar{M}\bar{F}$ did not increase monotonically over time. A more detailed analytical study by Lessard (1989) revealed that $\bar{M}\bar{F}$ may not be maximized at a

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stable equilibrium of the complete dynamical system even if such an equilibrium has equal allele frequencies in the two sexes. Karlin and Lessard (1986: ch. 7; see also Selgrade and Ziehe, 1987) showed that, for a single diallelic locus with female and male viability differences, there are at most three interior equilibria and that from every initial genotype frequency vector there is convergence to one of these equilibria.

Roughgarden (1991) studied a one-locus, two-allele model in which each of the three genotypes produced eggs and sperm in different proportions, allowing average egg and sperm production, W and V respectively, to be computed at each generation. This model can be re-expressed in the form used by Karlin and Lessard (1986), Selgrade and Ziehe (1987) or Lessard (1989) by appropriate adjustments of the census time. Using local analysis near the genotypic fixations, Roughgarden claimed that the product WV would be maximized as evolution proceeded under random mating. In the first part of this paper, we explicitly determine all equilibria and present an analysis of the global stability of all equilibrium points that are possible in a special case of Roughgarden's model, and show that his optimization principle is not always valid.

In models that incorporate both ecological and genetic properties, the change in the population size is usually governed by the change in mean fitness. From the first part of this paper, it might be inferred that population size is not monotone over time and, indeed, may not increase faster with sex present than without. The second part of the paper uses a one-locus, two-allele model to compare asexual and sexual populations, first in a cyclical and then in a random environment. In the first case, a simple model with genotypic viabilities is used to show that, under random mating, the size of the sexual population ultimately exceeds that of a comparable asexual population. In the second case, we show that diploid genotypes A_1A_1 and A_2A_2 increase in numbers faster than haploid asexual types A_1 and A_2, respectively, in comparable random environments, and that the number of A_1A_2 grows faster than the product of the haploid asexual numbers of A_1 and A_2. The models considered in this section are closely related to that studied by Christiansen (1984).

THE MODEL

The genetic system is diploid with one locus and two alleles A_1 and A_2. The frequencies of the three genotypes A_1A_1, A_1A_2 and A_2A_2 at the present generation are x_{11}, x_{12} and x_{22}, respectively, with $x_{ij} \geq 0$ and $x_{11} + x_{12} + x_{22} = 1$. Each parental genotype A_iA_j produces eggs and sperm at rates w_{ij} and v_{ij}, respectively. Thus, the average egg production per individual in the present generation is

$$W = w_{11}x_{11} + w_{12}x_{12} + w_{22}x_{22} \tag{1}$$

and the average sperm production is

$$V = v_{11}x_{11} + v_{12}x_{12} + v_{22}x_{22} \tag{2}$$

In the 'sperm pool', the frequencies of the alleles A_1 and A_2 are, therefore,

$$p_s = \frac{v_{11}x_{11} + \frac{1}{2}v_{12}x_{12}}{V} \quad \text{and} \quad q_s = \frac{v_{22}x_{22} + \frac{1}{2}v_{12}x_{12}}{V} \tag{3}$$

respectively. In the same way, for eggs, the frequencies of A_1 and A_2 in the 'egg pool' are

$$p_e = \frac{w_{11}x_{11} + \frac{1}{2}w_{12}x_{12}}{W} \quad \text{and} \quad q_e = \frac{w_{22}x_{22} + \frac{1}{2}w_{12}x_{12}}{W} \tag{4}$$

respectively.

Suppose mating occurs randomly so that each egg is fertilized at random from the sperm pool. Then the genotypic frequencies after mating are

$$\begin{aligned} x'_{11} &= p_s p_e \\ x'_{12} &= p_s q_e + p_e q_s \\ x'_{22} &= q_s q_e \end{aligned} \tag{5}$$

Therefore, we have the following transformation of frequencies from (x_{11}, x_{12}, x_{22}) in the present generation to $(x'_{11}, x'_{12}, x'_{22})$ at the next generation:

$$\begin{aligned} x'_{11} &= [(v_{11}x_{11} + \tfrac{1}{2}v_{12}x_{12})(w_{11}x_{11} + \tfrac{1}{2}w_{12}x_{12})]/VW \\ x'_{12} &= [(v_{11}x_{11} + \tfrac{1}{2}v_{12}x_{12})(w_{22}x_{22} + \tfrac{1}{2}w_{12}x_{12}) + (v_{22}x_{22} + \tfrac{1}{2}v_{12}x_{12})(w_{11}x_{11} + \tfrac{1}{2}w_{12}x_{12})]/VW \\ x'_{22} &= [(v_{22}x_{22} + \tfrac{1}{2}v_{12}x_{12})(w_{22}x_{22} + \tfrac{1}{2}w_{12}x_{12})]/VW \end{aligned} \tag{6}$$

System (6) is in the form discussed by Roughgarden (1991); we use this representation. It is important to note that an equivalent model with the recursion in terms of allele frequencies in the two kinds of gametes was studied by Karlin and Lessard (1986: eq. 7.2). In what follows, we study a special case of this model, produce all of its equilibrium points, and analyse their stability properties.

EQUILIBRIUM POINTS FOR A SYMMETRIC CASE

We denote by $\mathbf{P} = (x_{11}, x_{12}, x_{22})$ any population state with $x_{ij} \geq 0$ and $x_{11} + x_{12} + x_{22} = 1$. It is easy to verify that $\mathbf{P}_1^* = (1, 0, 0)$ and $\mathbf{P}_2^* = (0, 0, 1)$ are equilibrium points corresponding to fixation of A_1 and A_2, respectively. All other equilibrium points are polymorphic with $x_{ij} > 0$ for all three genotypes A_iA_j.

In general, the polymorphic equilibria for this model are given by the roots of a cubic equation that is difficult to use explicitly. Therefore, we assume that the sperm and egg production parameters v_{ij} and w_{ij} are *symmetric*, so that

$$v_{12} = w_{12} = 1,\ v_{11} = v_{22} = v,\ w_{11} = w_{22} = w;\ v \neq w \tag{7}$$

Under these symmetry assumptions, the recursions (6) are given by

$$x'_{11} = [(vx_{11} + \tfrac{1}{2}x_{12})(wx_{11} + \tfrac{1}{2}x_{12})]/VW \tag{8}$$

$$x'_{12} = [(vx_{11} + \tfrac{1}{2}x_{12})(wx_{22} + \tfrac{1}{2}x_{12}) + (vx_{22} + \tfrac{1}{2}x_{12})(wx_{11} + \tfrac{1}{2}x_{12})]/VW \tag{9}$$

$$x'_{22} = [(vx_{22} + \tfrac{1}{2}x_{12})(wx_{22} + \tfrac{1}{2}x_{12})]/VW \tag{10}$$

where the average sperm and egg productions V and W are

$$V = v + (1 - v)x_{12} \quad \text{and} \quad W = w + (1 - w)x_{12} \tag{11}$$

respectively.

To find the equilibrium points, set $x'_{ij} = x_{ij}$, and subtract (10) from (8) giving

$$VW(x_{11} - x_{22}) = vw(x_{11}^2 - x_{22}^2) + \tfrac{1}{2}(v + w)x_{12}(x_{11} - x_{22}) \tag{12}$$

at equilibrium. Therefore, at equilibrium

$$x_{11} = x_{22} \text{ or } VW = vw(x_{11} + x_{22}) + \tfrac{1}{2}(v + w)x_{12} \tag{13}$$

If $x_{11} = x_{22} > 0$, then $2vx_{11} + x_{12} = V \neq W = 2wx_{22} + x_{12}$, and from (9) we obtain $\hat{x}_{12} = \frac{1}{2}$ and, since $\hat{x}_{11} = \hat{x}_{22}$, this will be called the *central symmetric polymorphism*, $\mathbf{P}_3^* = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$. If, on the other hand, $VW = vw(x_{11} + x_{22}) + \frac{1}{2}(v + w)x_{12}$, then (11) gives

$$[v + (1 - v)x_{12}][w + (1 - w)x_{12}] = vw(1 - x_{12}) + \tfrac{1}{2}(v + w)x_{12} \tag{14}$$

since $x_{11} + x_{22} = 1 - x_{12}$. Now (14) can be rewritten as the quadratic equation

$$(1 - v)(1 - w)x_{12}^2 - \tfrac{1}{2}x_{12}(2vw - v - w) = 0 \tag{15}$$

whose solutions are

$$\hat{x}_{12} = 0 \text{ or } \hat{x}_{12} = \frac{2vw - v - w}{2(1 - v)(1 - w)} \tag{16}$$

If $\hat{x}_{12} = 0$, then from (9) either $\hat{x}_{11} = 0$ or $\hat{x}_{22} = 0$, and we retrieve the two fixation equilibria $\mathbf{P}_1^*$ and $\mathbf{P}_2^*$.

We have therefore to determine conditions on v and w that permit the existence of polymorphic equilibrium points $\mathbf{P} = (x_{11}, x_{12}, x_{22})$ with

$$\hat{x}_{12} = \frac{2vw - v - w}{2(1 - v)(1 - w)} = \frac{v}{2(v - 1)} + \frac{w}{2(w - 1)} \tag{17}$$

Since $V = v + (1 - v)x_{12}$ and $W = w + (1 - w)x_{12}$, substituting (17) into (8) and (10) results in the quadratic equation

$$x^2 + \frac{v + w - 2}{2(v - 1)(w - 1)}x + \frac{(2vw - v - w)^2}{16vw(v - 1)^2(w - 1)^2} = 0 \tag{18}$$

Then, two solutions for $\hat{x}_{11}$ and $\hat{x}_{22}$ are given by

$$\hat{x}_{11} = \frac{2 - v - w}{4(v - 1)(w - 1)} \pm \frac{(w - v)\sqrt{1 - (1/vw)}}{4(v - 1)(w - 1)} \tag{19}$$

Thus, equation (17) determines two equilibrium points, provided $x_{12} > 0$ and equation (18) has positive solutions. Equation (18) has valid solutions of $vw \geq 1$, and both are positive if

$$\frac{2 - v - w}{(v - 1)(w - 1)} > 0$$

Thus, (18) has two positive solutions if either $v < 1 < w$ and $vw > 1$, or $w < 1 < v$ and $vw > 1$. Coupling these with the conditions for $x_{12} > 0$, we conclude that there are two additional equilibrium points, $\mathbf{P}_4^*$ and $\mathbf{P}_5^*$, determined by (17) and (19), if, and only if, either

$$v < 1 < w \text{ and } \frac{1}{w} < v < \frac{w}{2w - 1} \text{ or } w < 1 < v \text{ and } \frac{1}{v} < w < \frac{v}{2v - 1} \tag{20}$$

or, equivalently,

$$1 < vw < \frac{v+w}{2} \tag{21}$$

We have thus secured:

Result 1. *There are always three equilibrium points* $\mathbf{P}_1^* = (1, 0, 0)$, $\mathbf{P}_2^* = (0, 0, 1)$ *and* $\mathbf{P}_3^* = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$. *If, in addition, conditions (20) or (21) hold, then two asymmetric polymorphic equilibria* $\mathbf{P}_4^*$ *and* $\mathbf{P}_5^*$ *exist, where* $\mathbf{P}_4^* = (A^*, B^*, C^*)$, $\mathbf{P}_5^* = (C^*, B^*, A^*)$ *such that*

$$A^* = \frac{2-v-w}{4(v-1)(w-1)} + \frac{(w-v)\sqrt{1-(1/vw)}}{4(v-1)(w-1)} \tag{22}$$

$$B^* = \frac{v}{2(v-1)} + \frac{w}{2(w-1)} \tag{23}$$

$$C^* = \frac{2-v-w}{4(v-1)(w-1)} - \frac{(w-v)\sqrt{1-(1/vw)}}{4(v-1)(w-1)} \tag{24}$$

Remark. The analysis of Karlin and Lessard (1986) and Selgrade and Ziehe (1987) also revealed three possible interior polymorphisms in terms of the roots of a cubic polynomial.

STABILITY ANALYSIS FOR THE SYMMETRIC CASE

In this section, we give a complete stability analysis of all equilibrium points, including some global stability properties, for the symmetric model. The reader should consult Selgrade and Ziehe (1987) for a different proof. In the course of the analysis, we will make use of the following propositions.

Proposition 1. *Independent of the present state, after one generation the heterozygote frequency* $x_{12} \le 1/2$.

Proof. Let $A_1 = vx_{11} + \frac{1}{2}x_{12}$, $A_2 = vx_{22} + \frac{1}{2}x_{12}$, $B_1 = wx_{11} + \frac{1}{2}x_{12}$, $B_2 = wx_{22} + \frac{1}{2}x_{12}$. Then $V = A_1 + A_2$ and $W = B_1 + B_2$ and we may rewrite (9) as

$$x'_{12} = \frac{A_1B_1 + A_2B_2 + A_1B_2 + A_2B_1}{2(A_1 + A_2)(B_1 + B_2)} + \frac{A_1B_2 + A_2B_1 - A_1B_1 - A_2B_2}{2(A_1 + A_2)(B_1 + B_2)} \tag{25}$$

Thus,

$$x'_{12} = \frac{1}{2} - \frac{vw(x_{11} - x_{22})^2}{2WV} \tag{26}$$

Hence, no matter what the initial value of x_{12}, after one generation we have $x_{12} \le \frac{1}{2}$.

Proposition 2. *For* $0 \le y \le 1$, *let*

$$F(y) = \frac{\frac{1}{2}(v+w)y + vw(1-y)}{[v(1-y)+y][w(1-y)+y]} \tag{27}$$

(i) *If* $vw < 1$, *then* $0 < F(y) < 1$ *for all* $0 < y \leq \frac{1}{2}$.
(ii) *If* $vw > 1$, *then* $F(y) > 1$ *in some neighbourhood of* $y = \frac{1}{2}$.
(iii) *If* $2vw - v - w > 0$, *then* $F(y) > 1$ *for* $0 < y \leq \frac{1}{2}$.
(iv) *If* $2vw - v - w < 0$, *then* $F(y) < 1$ *in some neighbourhood of* $y = 0$.

The proof of Proposition 2 is given in Appendix 1.

We are now ready to discuss the stability properties of the equilibria $\mathbf{P}_i^*$. We start with the *central symmetric polymorphism* $\mathbf{P}_3^*$ and show:

Result 2. *Stability of central polymorphism.*

1. *If* $vw < 1$, *then the central polymorphism* $\mathbf{P}_3^* = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ *is globally stable.*
2. *If* $vw > 1$, *then* $\mathbf{P}_3^*$ *is not locally stable.*

The proofs of the two parts of Result 2 are given in Appendix 2.

Remark. It should be pointed out that, from any point on the plane $x_{11} = x_{22}$, there will always be convergence to $\mathbf{P}_3^*$.

Result 3.

1. *If* $2vw - v - w > 0$, *then both fixations* $\mathbf{P}_1^*$ *and* $\mathbf{P}_2^*$ *are locally stable. In fact, for any* $\mathbf{P} = (x_{11}, x_{12}, x_{22})$, $\mathbf{P}^{(n)} \rightarrow \mathbf{P}_1^*$ *when* $x_{11} > x_{22}$ *and* $\mathbf{P}^{(n)} \rightarrow \mathbf{P}_3^*$ *when* $x_{22} > x_{11}$, *so that* $\mathbf{P}_1^*$ *and* $\mathbf{P}_2^*$ *are globally stable.*
2. *If* $2vw - v - w < 0$, *then neither* $\mathbf{P}_1^*$ *nor* $\mathbf{P}_2^*$ *are locally stable.*

For the proof, suppose we start with $\mathbf{P} = (x_{11}, x_{12}, x_{22})$ where $x_{22} > x_{11}$. Then by Proposition 1 and using the superscript $^{(n)}$ to denote the nth iteration, we have $x_{12}^{(n)} \leq \frac{1}{2}$ for all $n \geq 1$. Since $2vw - v - w > 0$, Proposition 2 implies that $F(x_{12}^{(n)}) \geq 1$ for $n \geq 1$, and, using (A3), the sequence $\{u_n\}_{n=1}^{\infty}$, with $u_n = x_{22}^{(n)} - x_{11}^{(n)}$, is a positive increasing and bounded sequence. Thus,

$$\lim_{n\to\infty} (x_{22}^{(n)} - x_{11}^{(n)}) = \lim_{n\to\infty} u_n = u \tag{28}$$

where $u > 0$. Hence from (A3), $\lim_{n\to\infty} F(x_{12}^{(n)}) = 1$. But $F(y) \geq 1$ with equality only when $y = 0$. Thus, the continuity of $F(y)$ implies that $\lim_{n\to\infty} x_{12}^{(n)} = 0$. Therefore, since $\lim_{n\to\infty}(x_{22}^{(n)} + x_{11}^{(n)}) = 1$ and $\lim_{n\to\infty}(x_{22}^{(n)} - x_{11}^{(n)}) = u$, we infer that

$$\lim_{n\to\infty} \mathbf{P}^{(n)} = \left(\frac{1-u}{2}, 0, \frac{1+u}{2}\right)$$

Because of the continuity of the transformation $\mathbf{P} \rightarrow \mathbf{P}'$, the limit $\lim_{n\to\infty} \mathbf{P}^{(n)}$ is an equilibrium point, and the only equilibrium of this form is $\mathbf{P}_2^*$. Hence $\lim_{n\to\infty} \mathbf{P}^{(n)} = (0, 0, 1) = \mathbf{P}_2^*$. Similarly, when $x_{22} < x_{11}$ and $2vw - v - w > 0$, $\lim_{n\to\infty} \mathbf{P}^{(n)} = \mathbf{P}_1^*$.

If $2vw - v - w < 0$, then by Proposition 2, $0 < F(y) < 1$ for some neighbourhood of $y = 0$. Thus if, for example, $\mathbf{P}$ is near $\mathbf{P}_2^*$ with $x_{22} > x_{11}$, then by virtue of (A3) the sequence $\{u_n\}_{n=1}^{\infty}$, where $u_n = x_{22}^{(n)} - x_{11}^{(n)}$, is decreasing and so cannot converge to 1. Thus $\mathbf{P}_2^*$ is not locally stable. A similar argument works for $\mathbf{P}_1^*$.

For the stability of the asymmetric polymorphic equilibria $\mathbf{P}_4^*$ and $\mathbf{P}_5^*$, we have the following result.

Result 4. *Suppose that conditions (20) or, equivalently, (21) hold, so that the two asymmetric polymorphisms* $\mathbf{P}_4^*$ *and* $\mathbf{P}_5^*$ *exist. Then both* $\mathbf{P}_4^*$ *and* $\mathbf{P}_5^*$ *are locally stable. In light of the result of Karlin and Lessard (1986: theorem 7.1), these equilibria are globally stable under the same conditions, with domains of attraction separated by* $\mathbf{P}_3^*$.

The proof is omitted. Table 1 summarizes the existence and stability criteria for all of the equilibria. The reader is referred to Karlin and Lessard (1986: 218) for a geometric representation of the appropriate domains of attraction.

IS THE PRODUCT OF THE AVERAGE SPERM AND EGG PRODUCTION MAXIMIZED?

In his discussion of the present model, Roughgarden (1991) claimed that, in the course of evolution, selection tends to maximize the product VW of the average sperm and egg production. It should be recalled that Karlin and Lessard (1986: 224) showed that the product increases from one equilibrium to the next attainable after new alleles are introduced one at a time. Lessard (1989: 226) showed the related result that a mutant allele invades a symmetric equilibrium (including fixation states) if, and only if, VW increases from one generation to the next after a long enough time provided the mutant allele is sufficiently rare. We examine the change in VW locally and globally, using the analysis presented in the previous sections.

The stability analysis implies that, in the course of evolution, three mutually exclusive cases occur:

- *Case 1:* the two fixations $\mathbf{P}_1^*$ and $\mathbf{P}_2^*$ are globally stable.
- *Case 2:* the central symmetric polyphorphism is globally stable.
- *Case 3:* the two asymmetric polymorphic equilibria $\mathbf{P}_4^*$ and $\mathbf{P}_5^*$ are globally stable and the other equilibria are not stable.

Consider the product $S = VW$ of the average sperm and egg production, and in the symmetric case observe that

Table 1. Equilibrium structure

Equilibrium	Existence conditions	Stability conditions
Fixations		
$\mathbf{P}_1^* = (1, 0, 0)$ $\mathbf{P}_2^* = (0, 0, 1)$	always exist	$2vw - v - w > 0$
Central polymorphism		
$\mathbf{P}_3^* = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$	always exists	$wv < 1$
$\mathbf{P}_4^* = (A^*, B^*, C^*)$ $\mathbf{P}_5^* = (C^*, B^*, A^*)$	$1 < vw < (v + w)/2$	$1 < vw < (v + w)/2$

$$S = S(x_{12}) = [v + x_{12}(1 - v)][w + x_{12}(1 - w)] \tag{29}$$

$$= vw + x_{12}(v + w - 2vw) + x_{12}^2(1 - v)(1 - w) \tag{30}$$

Proposition 3.

1. *If* $vw < 1$, *then* $S(x_{12})$ *is an increasing function of* x_{12} *for* $0 \le x_{12} \le \frac{1}{2}$.
2. *If* $v + w - 2wv < 0$, *then* $S(x_{12})$ *is a decreasing function of* x_{12} *for* $0 \le x_{12} \le 1$.

Proof. From equation (30), using the notation $S'(\cdot)$ to indicate the derivative,

$$S'(x_{12}) = (v + w - 2vw) + 2x_{12}(1 - v)(1 - w) \tag{31}$$

Hence

$$S'(0) = v + w - 2vw,\ S'(\tfrac{1}{2}) = 1 - vw,\ S'(1) = 2 - v - w \tag{32}$$

If $vw < 1$, then $vw < \sqrt{vw} \le (v + w)/2$, which implies that $S'(\frac{1}{2}) > 0$ and $S'(0) > 0$. Therefore, as $S'(x_{12})$ is linear in x_{12}, $S'(x_{12}) > 0$ for $0 \le x_{12} \le \frac{1}{2}$.

If $v + w - 2vw < 0$, then $S'(0) < 0$. Also, $vw > 1$ and $(v + w)/2 \ge \sqrt{vw} > 1$, which implies that $S'(1) < 0$. Therefore, since $S'(x_{12})$ is linear in x_{12}, $S'(x_{12}) < 0$ for all $0 \le x_{12} \le 1$ and $S(x_{12})$ is a decreasing function of x_{12} for $0 \le x_{12} \le 1$.

Observe that, when the two asymmetric polymorphic equilibria $\mathbf{P}_4^* = (A^*, B^*, C^*)$ and $\mathbf{P}_5^* = (C^*, B^*, A^*)$ are stable, $S'(B^*) = 0$ and $S''(B^*) = 2(1 - v)(1 - w) < 0$, and the product $S(x_{12})$ has its global maximum in the interval $0 \le x_{12} \le 1$ at $x_{12} = B^*$, namely at $\mathbf{P}_4^*$ and $\mathbf{P}_5^*$.

When the two fixations $\mathbf{P}_1^* = (1, 0, 0)$ and $\mathbf{P}_2^* = (0, 0, 1)$ are stable, $v + w - 2vw < 0$, so that $S(x_{12})$ is a decreasing function of x_{12} for $0 \le x_{12} < 1$ and attains its global maximum at $x_{12} = 0$. That is, VW is globally maximized at $\mathbf{P}_1^*$ and $\mathbf{P}_2^*$.

The case in which the only stable equilibrium is the central symmetric polymorphism $\mathbf{P}_3^* = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ is more complex. In this case, $S(x_{12})$ is an increasing function of x_{12}. Hence, by (32) the global maximum of $S(x_{12})$ is attained at a point $\tilde{x}_{12}$ with $\frac{1}{2} < \tilde{x}_{12} \le 1$. Now $\tilde{x}_{12} = 1$ when $v + w \le 2$. Otherwise, if $v + w > 2$, then from (31)

$$\tilde{x}_{12} = \frac{2vw - v - w}{2(1 - v)(1 - w)}$$

Thus, it is possible that $\mathbf{P}_3^* = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ is stable and the product VW is not globally maximized at $\mathbf{P}_3^*$. But, as we know, by Proposition 1, $x_{12}^{(n)} \le \frac{1}{2}$ for $n \ge 1$, no matter what the starting population state $\mathbf{P} = (x_{11}, x_{12}, x_{22})$ (i.e. $n = 0$). On the other hand, $S(\frac{1}{2})$ is the maximal value of S for $0 \le x_{12} \le \frac{1}{2}$. Therefore, at least from the second generation and on $(n \ge 1)$, $V^{(n)}W^{(n)} \le V^*W^* = S(\frac{1}{2})$ and, of course, $V^{(n)}W^{(n)} \xrightarrow{n\to\infty} V^*W^*$. It is of course possible that the initial state $VW > V^*W^*$, if initially $x_{12} > \frac{1}{2}$.

Proposition 4. *If* $vw < 1$, *then the sequence* V^nW^n *is increasing from some generation.*

Proof. By (26)

$$x_{12}^{(n+1)} = \frac{1}{2} - \frac{vw(x_{11}^{(n)} - x_{22}^{(n)})^2}{2V^nW^n} \tag{33}$$

And, by equations (8) and (10)

$$x_{22}^{(n+1)} - x_{11}^{(n+1)} = F(x_{12}^{(n)})(x_{22}^{(n)} - x_{11}^{(n)}) \tag{34}$$

where $F(\cdot)$ is defined in (27).

Result 2 implies that $x_{12}^{(n)} \to \frac{1}{2}$ and Proposition 1 implies that, for any $n > 1$, $x_{12}^{(n)} < \frac{1}{2}$. Hence, there exists an N such that

$$x_{12}^{(N)} < x_{12}^{(N+1)} \tag{35}$$

We show by induction that the sequence $x_{12}^{(n)}$ is an increasing sequence for $n \geq N$. By (35) this holds for $n = N$. Assume that, for $n > N$

$$x_{12}^{(n)} < x_{12}^{(n+1)} \tag{36}$$

Proposition 1 implies that WV is an increasing function of x_{12}. Therefore

$$W^{(n)}V^{(n)} < W^{(n+1)}V^{(n+1)} \tag{37}$$

Proposition 2 implies that

$$(x_{22}^{(n+1)} - x_{11}^{(n+1)})^2 < (x_{22}^{(n)} - x_{11}^{(n)})^2 \tag{38}$$

since

$$x_{12}^{(n+2)} = \frac{1}{2} - \frac{vw(x_{11}^{(n+1)} - x_{22}^{(n+1)})^2}{2V^{(n+1)}W^{(n+1)}} \tag{39}$$

We conclude by (37) and (38) that

$$x_{12}^{(n+2)} > \frac{1}{2} - \frac{vw(x_{11}^{(n)} - x_{22}^{(n)})^2}{2V^{(n)}W^{(n)}} = x_{12}^{(n+1)} \tag{40}$$

By Proposition 1, WV is an increasing function of x_{12}; hence, for any $n \geq N$, $W^{(n)}V^{(n)} \leq W^{(n+1)}V^{(n+1)}$.

Remark. Proposition 4 relates to the result of Lessard (1989: 226), in that we have here made no restriction on the frequency of a mutant allele that would change the fitnesses and therefore affect VW. Thus Proposition 4 supports earlier claims about the long-term behaviour of VW.

EXAMPLES WHERE $V'W' < VW$

Here we produce examples where the product VW of the average sperm and egg production goes down; first, when the central polymorphism $\mathbf{P}_3^*$ is stable and, second, when the two fixations $\mathbf{P}_1^*$ and $\mathbf{P}_3^*$ are stable.

If $\mathbf{P}_3^*$ is stable, $vw < 1$ and $VW = S(x_{12})$ is an increasing function of x_{12}. Thus, to produce an example where $V'W' < VW$, it is sufficient to identify cases when $x'_{12} < x_{12}$. Following (26), $x'_{12} < x_{12}$ if, and only if,

$$\frac{1}{2}VW - \frac{vw(x_{11} - x_{22})^2}{2} < VWx_{12} \tag{41}$$

where $V = v(x_{11} + x_{22}) + x_{12}$, $W = w(x_{11} + x_{22}) + x_{12}$. For a given vector (x_{11}, x_{12}, x_{22}), inequality (41) is continuous in v and w. If $v = w = 1$, then (41) becomes

$$\tfrac{1}{2} - \tfrac{1}{2}(x_{11} - x_{22})^2 < x_{12} \tag{42}$$

Let $a = x_{11} + x_{22}$, $x_{12} = 1 - a$, $x_{11} = \xi$. Then, (42) can be written as

$$G(a, \xi) = \tfrac{1}{2} - \tfrac{1}{2}(a - 2\xi)^2 - (1 - a) < 0 \tag{43}$$

For $\xi \approx 0$ or $\xi \approx a$, clearly $G(a, \xi) < 0$. Thus, by continuity, if $vw < 1$ but $v \approx 1$ and $w \approx 1$, one can find a starting population state $\mathbf{P} = (x_{11}, x_{12}, x_{22})$ where $x_{11} \approx 0$, $x_{12} < \tfrac{1}{2}$ such that at the next generation the frequencies $\mathbf{P}' = (x'_{11}, x'_{12}, x'_{22})$ satisfy $x'_{12} < x_{12}$ and so $V'W' < VW$.

If $\mathbf{P}_1^*$ and $\mathbf{P}_2^*$ are stable, $2vw > v + w$ and $VW = S(x_{12})$ is a decreasing function of x_{12}. Therefore, for $V'W' < VW$, we must have $x'_{12} > x_{12}$. When $v = w = 1$ so that $2vw = v + w$, $x'_{12} > x_{12}$ if

$$\tfrac{1}{2} - \tfrac{1}{2}(a - 2\xi)^2 > (1 - a) \tag{44}$$

When $\xi = a/2$, (44) becomes $a > \tfrac{1}{2}$. This is generally the case, because after the second generation, $1 - a = 1 - x_{11} - x_{22} = x_{12} \leq \tfrac{1}{2}$. Thus, again by continuity, when $2vw > v + w$ with $v \approx 1$ and $w \approx 1$, there is an initial population state $\mathbf{P} = (x_{11}, x_{12}, x_{22})$ with $x_{12} < \tfrac{1}{2}$ and $x_{11} \approx x_{22}$ such that the frequencies in the next generation, $\mathbf{P}' = (x'_{11}, x'_{12}, x'_{22})$, satisfy $x'_{12} > x_{12}$ and so $V'W' < VW$.

In the case of asymmetric parameters, where $v_{11} \neq v_{22}$ and $w_{11} \neq w_{22}$, it is possible that the sequence $W^n V^n$ is actually a decreasing sequence. For example, let $v_{11} = 1.2$, $v_{22} = 0.9$, $w_{11} = 0.3$, $w_{22} = 0.6$ with $v_{12} = w_{12} = 1$ and the initial state be $x_{11} = 0.3$, $x_{12} = 0.5$ and $x_{22} = 0.2$. Then, for $n \geq 13$, the sequence $W^n V^n$ decreases (see Table 2).

ASEXUAL AND SEXUAL POPULATION GROWTH IN A PERIODIC ENVIRONMENT

Most hybrid models that include genotypically determined fitnesses that are functions of population size write the population size in generation $t + 1$, $N(t + 1) = \bar{U}(t)N(t)$, where $\bar{U}(t)$ is some measure of mean fitness at time t. In the two-sex case of the previous sections, $\bar{U}$ would probably be $\bar{V}\bar{W}$. The question arises as to whether the long-term value of N would be greater in the presence of two sexes, as above, than if sex were absent altogether. In this section, we consider the effect of meiosis, a central feature of sexual species, on the change in N.

Consider a diploid population and one locus with alleles A_1 and A_2. Assume that the fitness of A_iA_j fluctuates between two values $1 - a_{ij}$ and $1 + a_{ij}$, with the fitness at generation t given by

$$w_{ij}(t) = 1 + a_{ij}F(t) \tag{45}$$

where a_{ij} are constants and $F(t)$ is a periodic function, with period T, such that $|F(t)| < 1$, $F(t)$ is positive for $0 < t < T/2$, negative for $T/2 < t < T$, and the average of $F(t)$ over one period is zero.

We consider two kinds of populations – sexual and asexual – which differ only in that the sexual population undergoes meiosis and random union of gametes at the end of each generation. The sexual population begins each generation with its genotype frequencies in Hardy-Weinberg ratios, while the asexual population begins at whatever genotype frequencies result from the preceding generation.

We claim that although the average fitnesses of the three genotypes A_iA_j are the same, the fitness model defined by (45) can result in a growth advantage to the sexual system and can

Table 2. Example showing that V^nW^n may decrease*

Generation n	Genotype frequencies x_{11}	x_{12}	x_{22}	The product VW W^nV^n
1	0.300000	0.500000	0.200000	0.738400
2	0.280878	0.503657	0.215466	0.742035
3	0.266723	0.504342	0.228935	0.743697
4	0.255602	0.504396	0.240001	0.744742
5	0.246820	0.504100	0.249080	0.745388
6	0.239844	0.503642	0.256513	0.745784
7	0.234277	0.503129	2.262594	0.746024
8	0.229814	0.502620	0.267565	0.746165
9	0.226226	0.502146	0.271627	0.746245
10	0.223333	0.501721	0.274946	0.746287
11	0.220994	0.501349	0.277657	0.746307
12	0.219100	0.501028	0.279872	0.746313
13	0.217563	0.500755	0.281681	0.746312
14	0.216315	0.500526	0.283159	0.746307
15	0.215301	0.500333	0.284366	0.746299
16	0.214475	0.500173	0.285353	0.746292
17	0.213802	0.500040	0.286158	0.746284
18	0.213254	0.499929	0.286816	0.746277
19	0.212807	0.499839	0.287354	0.746271
20	0.212443	0.499764	0.287793	0.746265
21	0.212146	0.499702	0.288152	0.746260
22	0.211903	0.449651	0.288445	0.746256
23	0.211705	0.499610	0.288685	0.746253
24	0.211543	0.499576	0.288881	0.746250
25	0.211411	0.499548	0.289041	0.746247
26	0.211304	0.499525	0.289171	0.746245
27	0.211216	0.499506	0.289278	0.746244
28	0.211144	0.499491	0.289365	0.746243
29	0.211085	0.499479	0.289436	0.746241
30	0.211037	0.499468	0.289495	0.746240
31	0.210998	0.499460	0.289542	0.746240
32	0.210966	0.499453	0.289581	0.746239
33	0.210940	0.499448	0.289613	0.746239
34	0.210918	0.499443	0.289639	0.746238
35	0.210901	0.499439	0.289660	0.746238
36	0.210887	0.499436	0.289677	0.746237
37	0.210875	0.499434	0.289691	0.746237
38	0.210865	0.499432	0.289703	0.746237
39	0.210858	0.499430	0.289712	0.746237
40	0.210851	0.499429	0.289720	0.746237

* $v_{11} = 1.2$, $v_{22} = 0.9$, $w_{11} = 0.3$, $w_{22} = 0.6$, $v_{12} = w_{12} = 1$.

also determine the interval between successive meioses. In the special case where meiosis occurs at specific times, $t_n = (T/2)n$, the sexual system is shown to have a growth advantage.

The asexual population grows according to a continuous model in which $N_{ij}(t)$ are the numbers of A_iA_j at time t. Then, from the discrete-time equations, we have the following continuous time representation:

$$\frac{\mathrm{d}N_{11}}{\mathrm{d}t} = a_{11}(t)N_{11}(t), \frac{\mathrm{d}N_{12}}{\mathrm{d}t} = a_{12}(t)N_{12}(t), \frac{\mathrm{d}N_{22}}{\mathrm{d}t} = a_{22}(t)N_{22}(t) \tag{46}$$

Let $G(t) = \int_0^t F(x)\mathrm{d}x$. Then, $|G(t)| \leq T/2$. From equations (46), the size of the asexual population at time t is given by

$$\begin{aligned} N(t) &= N_{11}(t) + N_{12}(t) + N_{22}(t) \\ &= \mathrm{e}^t[N_{11}(0)\,\mathrm{e}^{a_{11}G(t)} + N_{12}(0)\,\mathrm{e}^{a_{12}G(t)} + N_{22}(0)\,\mathrm{e}^{a_{22}G(t)}] \leq H\,\mathrm{e}^t \end{aligned} \tag{47}$$

where H is some constant.

For the sexual population there is selection according to a similar continuous model and mating is by random union of gametes. We assume that meiosis occurs at the specific time points $t_n = (T/2)n$. Let $M_{ij}(t)$ be the number of A_iA_j at time t. In each interval $t_n < t < t_{n+1}$ we have the differential equations

$$\frac{\mathrm{d}M_{11}}{\mathrm{d}t} = a_{11}(t)M_{11}(t), \frac{\mathrm{d}M_{12}}{\mathrm{d}t} = a_{12}(t)M_{12}(t), \frac{\mathrm{d}M_{22}}{\mathrm{d}t} = a_{22}(t)M_{22}(t) \tag{48}$$

with initial conditions at t_n that are determined by the numbers of A_iA_j after the meiosis and random union of gametes at t_n. Let $M(t)$ be the population size at time t:

$$M(t) = M_{11}(t) + M_{12}(t) + M_{22}(t) \tag{49}$$

Let $L = \int_0^{T/2} F(t)\mathrm{d}t$, and in (45) set $a = La_{11}$, $b = La_{22}$ and $c = La_{12}$. We have:

Proposition 5. *If $a < c$ and $b < c$, or $c < a$ and $c < b$, then*

$$\lim_{n\to\infty} \frac{M(t_n)}{N(t_n)} = \infty \tag{50}$$

For the proof, first let x'_n, y'_n and z'_n be the numbers of A_1A_1, A_2A_2 and A_1A_2, respectively, before the occurrence of meiosis at times $t_n = (T/2)n$. Then

$$x'_n = x_{n-1}\,\mathrm{e}^{a(-1)^{n-1}}\,\mathrm{e}^{t_n}, y'_n = y_{n-1}\,\mathrm{e}^{b(-1)^{n-1}}\,\mathrm{e}^{t_n}, z'_n = z_{n-1}\,\mathrm{e}^{c(-1)^{n-1}}\,\mathrm{e}^{t_n} \tag{51}$$

where x_n, y_n and z_n are the numbers, divided by e^{t_n}, of A_1A_1, A_2A_2 and A_1A_2, respectively, after meiosis at t_n. Let $S_n = x_n + y_n + z_n$. Then

$$x_n = \frac{[x_{n-1}\,\mathrm{e}^{a(-1)^{n-1}} + \tfrac{1}{2}z_{n-1}\,\mathrm{e}^{c(-1)^{n-1}}]^2}{S_n} \tag{52}$$

$$y_n = \frac{[y_{n-1}\,\mathrm{e}^{b(-1)^{n-1}} + \tfrac{1}{2}z_{n-1}\,\mathrm{e}^{c(-1)^{n-1}}]^2}{S_n} \tag{53}$$

and

$$z_n = \frac{2(y_{n-1}\,\mathrm{e}^{b(-1)^{n-1}} + \tfrac{1}{2}z_{n-1}\,\mathrm{e}^{c(-1)^{n-1}})(x_{n-1}\,\mathrm{e}^{a(-1)^{n-1}} + \tfrac{1}{2}z_{n-1}\,\mathrm{e}^{c(-1)^{n-1}})}{S_n} \tag{54}$$

Clearly,

$$e^{t_n} S_n = x'_n + y'_n + z'_n = M(t_n) \tag{55}$$

By equation (47)

$$N(t_n) \leq H\, e^{t_n} \tag{56}$$

Hence

$$\frac{M(t_n)}{N(t_n)} \geq \frac{S_n}{H} \tag{57}$$

Therefore, to prove Proposition 5, it is sufficient to show that

$$\lim_{n\to\infty} S_n = \infty \tag{58}$$

To prove (58), we require the following propositions, whose proofs are given in Appendix 3.

Proposition 6. *Let U_n and V_n be defined by*

$$U_n = x_n + \frac{z_n}{2} \text{ and } V_n = y_n + \frac{z_n}{2} \tag{59}$$

Then, the sequences U_{2n} and V_{2n} are increasing if $c < a$ and $c < b$ or $c > a$ and $c > b$.

Proposition 7. *If $c < a$ and $c < b$ or $c > a$ and $c > b$, then* $\lim_{n\to\infty} S_{2n} = \infty$.

Then, using Propositions 6 and 7, we can finish the proof of Proposition 5. Since

$$S_{2n+1} = e^a x_{2n} + e^b y_{2n} + e^c z_{2n} \geq e^{\min(a,b,c)} S_{2n} \tag{60}$$

we conclude not only that $\lim_{n\to\infty} S_{2n} = \infty$, but also $\lim_{n\to\infty} S_{2n+1} = \infty$. This implies that

$$\lim_{n\to\infty} S_n = \infty \tag{61}$$

as desired.

DYNAMIC INEQUALITIES FOR SEXUAL AND ASEXUAL POPULATIONS IN A RANDOM ENVIRONMENT

We consider two kinds of population, one in which the genetic system is haploid with one locus and two alleles A_1 and A_2 and the frequencies of the two gametes A_1 and A_2 at the nth generation are x'_n and y'_n, respectively. The second population is diploid with one locus and two alleles A_1 and A_2, and meiosis occurs every generation. The frequencies of the three genotypes A_1A_1, A_1A_2 and A_2A_2 at the nth generation in the second case are x_n, z_n and y_n, respectively.

We assume that the fitnesses of the alleles A_1 and A_2 change randomly, and that the fitness of the genotype A_iA_j is the average of the fitnesses of alleles A_i and A_j. Let P_n and Q_n be two sequences of random variables which take the values 1 and –1 with probabilities

$$\Pr[P_n = 1] = \Pr[P_n = -1] = \tfrac{1}{2} \tag{62}$$

and

$$\Pr[Q_n = 1] = \Pr[Q_n = -1] = \tfrac{1}{2} \tag{63}$$

We assume that, in the haploid population, the fitnesses of gametes A_1 and A_2 at the nth generation are $L + P_n$ and $L + Q_n$ respectively. In the sexual population, the fitnesses of the three genotypes A_1A_1, A_2A_2 and A_1A_2 at the nth generation are given by

$$w^n_{11} = L + P_n,\ w^n_{22} = L + Q_n,\ w^n_{12} = L + \frac{P_n + Q_n}{2} \tag{64}$$

respectively.

The haploid population grows under selection only, so that

$$x'_{n+1} = (L + P_n)x'_n \qquad y'_{n+1} = (L + Q_n)y'_n \tag{65}$$

The diploid population undergoes selection, then meiosis and random union of gametes. Hence

$$x_{n+1} = \frac{[(L + P_n)x_n + \frac{1}{2}(L + (P_n + Q_n)/2)z_n]^2}{(L + P_n)x_n + (L + Q_n)y_n + (L + (P_n + Q_n)/2)z_n} \tag{66}$$

$$z_{n+1} = \frac{2[(L + P_n)x_n + \frac{1}{2}(L + (P_n + Q_n)/2)z_n][(L + Q_n)y_n + \frac{1}{2}(L + (P_n + Q_n)/2)z_n]}{(L + P_n)x_n + (L + Q_n)y_n + (L + (P_n + Q_n)/2)z_n} \tag{67}$$

$$y_{n+1} = \frac{[(L + Q_n)y_n + \frac{1}{2}(L + (P_n + Q_n)/2)z_n]^2}{(L + P_n)x_n + (L + Q_n)y_n + (L + (P_n + Q_n)/2)z_n} \tag{68}$$

In Appendix 4, we prove:

Proposition 8.

1. *For any* N, $x'_N/x'_1 < x_N/x_1$ *and* $y'_N/y'_1 < y_N/y_1$.
2. $\lim_{n\to\infty} x_n y_n / x'_n y'_n = \infty$, *where the limit is in the sense of probability.*

This proposition shows that a population that undergoes meiosis can have a higher long-term growth rate than that of a comparable asexual population.

DISCUSSION

The symmetric model studied here allows for a more detailed specification of the equilibria and domains of attraction than in Karlin and Lessard (1986), although the qualitative picture that emerges from the analyses is the same. The latter analysis was made in terms of allele frequencies in each of the sexes, whereas here we used the genotypes for comparison with Roughgarden (1991). Result 10.5 of Lessard (1989) entails that, in his model also, the product mean fitness may not increase to equilibrium. It is reasonable to speculate that results like Kingman's (1961) for viability selection that is the same in both sexes will not be generally true for the product mean fitness in any two-sex selection system.

The existence of multiple equilibria in two-sex viability systems has been well established since the work of Owen (1953; see also Karlin, 1972), although there has been little discussion of how the presence of multiple stable states affects the time-trajectory of the product mean fitness. Here we see that, even for the simple symmetric model, when the fixations are stable, or the central polymorphism is stable, the product mean fitness may not increase. In asymmetric models, such as that of Table 2, the product mean fitness may first increase and then decrease to equilibrium.

In his analysis, Roughgarden (1991) was interested in linear relationships between sperm and egg fitnesses. It is not obvious how to express an array of genotypic fitnesses in this form, although the well-studied case of sex-determination represents a simple example. In this case, $w_{ij} = 1 - v_{ij}$, and his local stability condition (13) reduces to $(v_{12} - v_{11})(1 - 2v_{11}) > 0$ for initial increase of A_2 near fixation of A_1. Thus, if $v_{11} < \frac{1}{2}$, A_2 increases when rare if it brings the sex ratio closer to even. The general form of such results can be found in Eshel and Feldman (1982a,b). Following the initial increase, however, the dynamics can be quite complicated, especially in multi-allelic (Karlin and Lessard, 1986) or multi-locus (Liberman *et al.*, 1990) contexts.

The analysis of periodic and random environments here can be viewed in a group-selection context. If one is willing to compare population growth rates as criteria for success, then our periodic environment model produces the conclusion that a diploid random mating system will out-compete a comparable asexual one. Our random environment model differs from those of Hines and Moore (1981), Roughgarden (1991) and Robson *et al.* (1999), in that we compare growth rates for the number of copies of A_1 and A_2 in the haploid asexual and diploid sexual cases. The basic result, however, is the same as in these earlier studies: with randomness in the environment, the numbers of both A_1 and A_2 grow faster with meiosis than without. It should be stressed that the evolution of genes that control meiosis is a much more complicated dynamical problem than is addressed here by comparing two systems that do not actually compete.

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APPENDIX 1: PROOF OF PROPOSITION 2

It is clear that $F(y) > 0$ for all $0 \le y \le 1$. Also, if $g(y)$ is given by

$$g(y) = \tfrac{1}{2}(v + w)y + vw(1 - y) - [v(1 - y) + y][w(1 - y) + y] \tag{A1}$$

then clearly $F(y) < 1(F(y) > 1)$ if, and only if, $g(y) > 0(g(y) < 0)$. Now $g(y) = yh(y)$, where

$$h(y) = y(v + w - vw - 1) + vw - \frac{v + w}{2} \tag{A2}$$

determines the sign of $g(y)$ for $0 < y \le 1$. Observe that $h(0) = vw - (v + w)/2$ and $h(\tfrac{1}{2}) = (vw - 1)/2$. Hence, if $vw < 1$, then $vw < \sqrt{vw} \le (v + w)/2$, so $h(0) \le 0$ and $h(\tfrac{1}{2}) < 0$. Since $h(y)$ is linear in y, $h(y) < 0$ for all $0 < y \le \tfrac{1}{2}$ and, therefore, $g(y) < 0$ for $0 < y < \tfrac{1}{2}$, which proves (i).

If $vw > 1$, then $h(\tfrac{1}{2}) > 0$ and also $g(\tfrac{1}{2}) > 0$. This, in turn, ensures that $g(y) > 0$ for some neighbourhood of $y = \tfrac{1}{2}$, which proves (ii).

If $2vw - v - w > 0$, then $vw > 1$, otherwise $vw \le \sqrt{vw} < (v + w)/2$ and $2vw - v - w < 0$. Hence $h(0) > 0$ and $h(\tfrac{1}{2}) > 0$. Therefore, $g(y) > 0$ for all $0 \le y \le \tfrac{1}{2}$ and $F(y) > 1$ for all $0 < y \le \tfrac{1}{2}$, as (iii) claims.

Finally, if $2vw - v - w < 0$, $h(0) < 0$ and, as in the proof of (ii), $F(y) < 1$ in some neighbourhood of $y = 0$.

APPENDIX 2: PROOF OF RESULT 2

Let $\mathbf{P}^{(n)} = (x_{11}^{(n)}, x_{12}^{(n)}, x_{22}^{(n)})$ be the population state after n generations starting with the population state $\mathbf{P} = (x_{11}, x_{12}, x_{22})$. We would like to show first that if $vw < 1$ and $\mathbf{P} \ne \mathbf{P}_1^*$, $\mathbf{P} \ne \mathbf{P}_2^*$ (recall that $\mathbf{P}_4^*$ and $\mathbf{P}_5^*$ do not exist when $vw < 1$), then $\mathbf{P}^{(n)} \xrightarrow{n \to \infty} \mathbf{P}_3^*$. Observe that from the transformation equations (8) and (10) we have

$$x_{22}^{(n+1)} - x_{11}^{(n+1)} = F(x_{12}^{(n)})(x_{22}^{(n)} - x_{11}^{(n)}) \tag{A3}$$

where $F(y)$ is given by (27).

By Proposition 1, $0 < x_{12}^{(n)} \le \frac{1}{2}$ for all $n = 1, 2, \ldots$, and so by Proposition 2, $0 < F(x_{12}^{(n)}) \le 1$ for all n. Hence the sequence $\{u_n\}_{n=1}^{\infty}$, where $u_n = x_{22}^{(n)} - x_{11}^{(n)}$, is either an increasing or decreasing bounded sequence depending on whether $x_{22} \ge x_{11}$ or $x_{22} \le x_{11}$. Suppose, for example, that $x_{22} \ge x_{11}$. Then $\{u_n\}_{n=1}^{\infty}$ is increasing and bounded in [0, 1] and so has a limit u,

$$\lim_{n\to\infty} (x_{22}^{(n)} - x_{11}^{(n)}) = \lim_{n\to\infty} u_n = u \tag{A4}$$

that is non-negative.

Suppose $u > 0$. Then, from (A3) with (A4), $\lim_{n\to\infty} F(x_{12}^{(n)}) = 1$. But, according to Proposition 2, $0 < F(y) < 1$ for all $0 < y < \frac{1}{2}$ and $F(0) = 1$. Thus, since $F(y)$ is continuous, $\lim_{n\to\infty} x_{12}^{(n)} = 0$, so that $\lim (x_{11}^{(n)} + x_{22}^{(n)}) = 1$. But then $\lim_{n\to\infty} x_{22}^{(n)} = (1 + u)/2$ and $\lim_{n\to\infty} x_{11}^{(n)} = (1 - u)/2$. The only equilibrium of the form

$$\left(\frac{1-u}{2}, 0, \frac{1+u}{2}\right)$$

is (0, 0, 1), with $u = 1$, but since $u^{(n)}$ is decreasing and initially $u < 1$, (0, 0, 1) is not attainable. Hence $u = 0$.

Now observe that

$$\frac{vx_{11}^{(n)} + \frac{1}{2}x_{12}^{(n)}}{V^{(n)}} = \frac{[v(x_{11}^{(n)} + x_{22}^{(n)}) + x_{12}^{(n)}]}{2V^{(n)}} + \frac{v(x_{11}^{(n)} - x_{22}^{(n)})}{2V^{(n)}} \tag{A5}$$

where $V^{(n)} = v(x_{11}^{(n)} + x_{22}^{(n)}) + x_{12}^{(n)}$ and $W^{(n)} = w(x_{11}^{(n)} + x_{22}^{(n)}) + x_{12}^{(n)}$. In fact

$$\frac{vx_{11}^{(n)} + \frac{1}{2}x_{12}^{(n)}}{V^{(n)}} = \frac{1}{2} + \frac{v(x_{11}^{(n)} - x_{22}^{(n)})}{2V^{(n)}} \tag{A6}$$

so that by (A4),

$$\lim_{n\to\infty} \frac{vx_{11}^{(n)} + \frac{1}{2}x_{12}^{(n)}}{V^{(n)}} = \frac{1}{2} \tag{A7}$$

Similarly,

$$\lim_{n\to\infty} \frac{wx_{11}^{(n)} + \frac{1}{2}x_{12}^{(n)}}{W^{(n)}} = \frac{1}{2} \tag{A8}$$

Therefore, returning to (8) and using (A7) and (A8),

$$x_{11}^{(n+1)} = \frac{(vx_{11}^{(n)} + \frac{1}{2}x_{12}^{(n)})(wx_{11}^{(n)} + \frac{1}{2}x_{12}^{(n)})}{V^{(n)}W^{(n)}} \tag{A9}$$

from which we conclude that $\lim_{n\to\infty} x_{11}^{(n)} = \frac{1}{4}$. Similarly, $\lim_{n\to\infty} x_{22}^{(n)} = \frac{1}{4}$ and so $\lim_{n\to\infty} x_{12}^{(n)} = \frac{1}{2}$. Thus, when $vw < 1$, for all starting $\mathbf{P} \ne \mathbf{P}_1^*$, $\mathbf{P}_2^*$, we have proved that $\lim_{n\to\infty} \mathbf{P}^{(n)} = \mathbf{P}_3^*$ and $\mathbf{P}_3^*$ is globally stable.

When $vw > 1$, by Proposition 2, $F(y) > 1$ for some neighbourhood of $y = \frac{1}{2}$. This implies that whenever $\mathbf{P}$ is near $\mathbf{P}_3^*$ and $x_{22} \ne x_{11}$, $\mathbf{P}^{(n)}$ cannot converge to $\mathbf{P}_3^*$. If $x_{22} = x_{11}$, then following equations (8), (9) and (10), $\mathbf{P}^{(n)} = \mathbf{P}_3^*$ for $n \ge 1$. In general, when $vw > 1$, $\mathbf{P}_3^*$ is not locally stable.

APPENDIX 3: PROOF OF PROPOSITIONS 6 AND 7

Proof of Proposition 6. Equations (52), (53) and (54) imply that, for all n,

$$U_n = x_n + \frac{z_n}{2} = e^{a(-1)^{n-1}}\, x_{n-1} + \tfrac{1}{2}\, e^{c(-1)^{n-1}}\, z_{n-1} \tag{A10}$$

Hence

$$U_{2n+2} = e^{-a} x_{2n+1} + \tfrac{1}{2}\, e^{-c} z_{2n+1} \tag{A11}$$

Equivalently,

$$U_{2n+2} = e^{-c}\left(x_{2n+1} + \frac{z_{2n+1}}{2}\right) + x_{2n+1}\,(e^{-a} - e^{-c}) \tag{A12}$$

or

$$U_{2n+2} = e^{-c} U_{2n+1} + x_{2n+1}(e^{-a} - e^{-c}) \tag{A13}$$

From (A13) we conclude that

$$U_{2n+2} = U_{2n} + x_{2n}(e^{-(c-a)} - 1) + x_{2n+1}\,(e^{-a} - e^{-c}) \tag{A14}$$

Equations (52), (53) and (54) imply that, for all n, $z_n = 2\sqrt{x_n y_n}$. Hence, by direct computation

$$\begin{aligned} x_{2n+1} - e^{a} x_{2n} &= \frac{(e^{a} x_{2n} + \frac{1}{2} e^{c} z_{2n})^2}{e^{a} x_{2n} + e^{b} y_{2n} + e^{c} z_{2n}} - e^{a} x_{2n} \\ &= \frac{x_{2n} y_{2n}\,(e^{2c} - e^{(a+b)})}{S_{2n+1}} \end{aligned} \tag{A15}$$

Hence, we conclude that

$$x_{2n}\,(e^{-(c-a)} - 1) + x_{2n+1}\,(e^{-a} - e^{-c}) = \frac{x_{2n} y_{2n}\,(e^{2c} - e^{(a+b)})\,(e^{-a} - e^{-c})}{S_{2n+1}} \tag{A16}$$

Equations (A14) and (A16) imply that

$$U_{2n+2} = U_{2n} + \frac{x_{2n} y_{2n}\,(e^{2c} - e^{(a+b)})(e^{-a} - e^{-c})}{S_{2n+1}} \tag{A17}$$

This implies that, if $c < a$ and $c < b$, or $c > a$ and $c > b$, then $U_{2n+2} > U_{2n}$. Similarly, we can show that V_{2n} is an increasing sequence.

Proof of Proposition 7. Since $S_{2n} = V_{2n} + U_{2n}$, it is sufficient to show that

$$\lim_{u\to\infty} U_{2n} = \infty \text{ or } \lim_{n\to\infty} V_{2n} = \infty \tag{A18}$$

By Proposition 6, U_{2n} and V_{2n} are increasing sequences. Suppose that the two sequences converge to finite limits M_1 and M_2, respectively, so that S_{2n} converges to $M = M_1 + M_2$.

Since U_{2n} and V_{2n} are increasing and positive sequences, there exists $K > 0$, such that for all n,

$$V_{2n}U_{2n} = \left(x_{2n} + \frac{z_{2n}}{2}\right)\left(y_{2n} + \frac{z_{2n}}{2}\right) > K \tag{A19}$$

By equations (52), (53) and (54), for all n, $z_n = 2\sqrt{x_n y_n}$. Hence, (A19) yields

$$2x_{2n}y_{2n} + (x_{2n} + y_{2n})\sqrt{x_{2n}y_{2n}} > K \tag{A20}$$

Now for all n

$$x_{2n} + y_{2n} \le S_{2n} < M \tag{A21}$$

Equation (A20) implies that there is a positive constant $D > 0$ such that for all n, $x_{2n}y_{2n} > D$. By equation (A17) we conclude that if $c < b$ and $c < a$, or $c > a$ and $c > b$, then

$$U_{2n+2} - U_{2n} = \frac{(\mathrm{e}^{-c} - \mathrm{e}^{-a})x_{2n}y_{2n}\,(\mathrm{e}^{(a+b)} - \mathrm{e}^{2c})}{S_{2n+1}} > \frac{D(\mathrm{e}^{-c} - \mathrm{e}^{-a})\,(\mathrm{e}^{(a+b)} - \mathrm{e}^{2c})}{M} = T > 0 \tag{A22}$$

This implies that

$$\lim_{n\to\infty} U_{2n} = \infty \tag{A23}$$

which proves our proposition that $\lim_{n\to\infty} S_{2n} = \infty$

APPENDIX 4: PROOF OF PROPOSITION 8

Consider the two populations after the Nth generation. Let $E_i(N)$ for $1 \le i \le 6$ be the sets defined by:

1. $E_1(N) = \{n \le N : P_n = Q_n = 1\}$
2. $E_2(N) = \{n \le N : P_n = Q_n = -1\}$
3. $E_3(N) = \{n \le N : P_n = -Q_n = 1 \text{ and } y_n > x_n\}$
4. $E_4(N) = \{n \le N : P_n = -Q_n = 1 \text{ and } y_n \le x_n\}$
5. $E_5(N) = \{n \le N : -P_n = Q_n = 1 \text{ and } y_n > x_n\}$
6. $E_6(N) = \{n \le N : -P_n = Q_n = 1 \text{ and } y_n \le x_n\}$

Assume that $Q_n = -P_n$. Then, equation (66) implies that

$$x_{n+1} = \frac{L^2(x_n + \tfrac{1}{2}z_n)^2 + 2LP_n x_n(x_n + \tfrac{1}{2}z_n) + P_n^2 x_n^2}{L(x_n + y_n + z_n) + P_n x_n + Q_n y_n} \tag{A24}$$

From equations (66), (67) and (68), $z_n = 2\sqrt{x_n y_n}$. Hence $(x_n + \tfrac{1}{2}z_n)^2 = x_n(x_n + y_n + z_n)$ and (A24) can be written as

$$\frac{x_{n+1}}{x_n} = \frac{L^2(x_n + y_n + z_n) + 2LP_n(x_n + \tfrac{1}{2}z_n) + P_n^2 x_n}{L(x_n + y_n + z_n) + P_n x_n + Q_n y_n} \tag{A25}$$

By direct computation

$$\frac{x_{n+1}}{x_n} - (L + P_n) = \frac{y_n}{L(x_n + y_n + z_n) + P_n x_n + Q_n y_n} \tag{A26}$$

We conclude that, for any $n \in U_{i=3}^{6} E_i(N)$,

$$\frac{x_{n+1}}{x_n} \geq L + P_n \tag{A27}$$

Moreover, if $n \in E_3(N) \cup E_5(N)$, then $y_n \geq x_n$; this implies that $y_n \geq \frac{1}{2} z_n$. Hence

$$\frac{y_n}{L(x_n + y_n + z_n) + P_n x_n + Q_n y_n} \geq \frac{y_n}{(4L+1)y_n} = \frac{1}{4L+1} \tag{A28}$$

Let $M = 1/(4L+1)$. Then, for $n \in E_3(N) \cup E_5(N)$,

$$\frac{x_{n+1}}{x_n} \geq L + P_n + M \tag{A29}$$

If $P_n = Q_n$, then from equation (66) and using $z_n = 2\sqrt{x_n y_n}$, we have

$$\frac{x_{n+1}}{x_n} = L + P_n \tag{A30}$$

We conclude that

$$\frac{x_N}{x_1} = \frac{x_2}{x_1}\frac{x_3}{x_2} \cdots \frac{x_N}{x_{N-1}} \geq \tag{A31}$$
$$(L+1)^{|E_1(N)|}(\mathrm{L}-1)^{|E_2(N)|}(L+1+M)^{|E_3(N)|}(L+1)^{|E_4(N)|}$$
$$(L-1+M)^{|E_5(N)|}\,(L-1)^{|E_6(N)|}$$

Similarly,

$$\frac{y_n}{y_1} \geq (L+1)^{|E_1(N)|}(L-1)^{|E_2(N)|}(L-1)^{|E_3(N)|}(L-1+M)^{|E_4(N)|} \tag{A32}$$
$$(L+1)^{|E_5(N)|}(L+1+M)^{|E_6(N)|}$$

Let $B_1(N) = E_3(N) \cup E_4(\mathrm{N})$ and $B_2(N) = E_5(N) \cup E_6(N)$. Then

$$\frac{x'_N}{x'_1} = (L+1)^{|E_1(N)| + |B_1(N)|}(L-1)^{|E_2(N)| + |B_2(N)|} \tag{A33}$$

and

$$\frac{y'_N}{y'_1} = (L+1)^{|E_1(N)| + |B_2(N)|}(L-1)^{|E_2(N)| + |B_1(N)|} \tag{A34}$$

We conclude from (A31), (A32), (A33) and (A34) that, for any N,

$$\frac{x'_N}{x'_1} < \frac{x_N}{x_1} \quad \text{and} \quad \frac{y'_N}{y'_1} < \frac{y_N}{y_1} \tag{A35}$$

For the second part of Proposition 8, equations (A31) and (A33) imply that

$$\frac{x_N}{x'_N} \geq \left(\frac{L+1+M}{L+1}\right)^{|E_3(N)|} \left(\frac{L-1+M}{L-1}\right)^{|E_5(N)|} \frac{x'_1}{x_1} \tag{A36}$$

and equations (A32) and (A34) imply that

$$\frac{y_N}{y'_N} \geq \left(\frac{L+1+M}{L+1}\right)^{|E_6(N)|} \left(\frac{L-1+M}{L-1}\right)^{|E_4(N)|} \frac{y'_1}{y_1} \tag{A37}$$

As $\Sigma_{i=3}^{6} \, |E_i(N)|/(N)$ converges in probability to $\frac{1}{2}$, we conclude from (A36) and (A37) that

$$\frac{x_n y_n}{x'_n y'_n} \to \infty \tag{A38}$$

This proves the proposition.