Nonlinear frequency-dependent selection at a single locus with two alleles and two phenotypes[*]

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Abstract. The paper investigates the discrete frequency dynamics of two phenotype diploid models where genotypic fitness is an exponential function of the expected payoff in the matrix game. Phenotypic and genotypic equilibria are defined and their stability compared to frequency-dependent selection models based on linear fitness when there are two possible phenotypes in the population. In particular, it is shown that stable equilibria of both types can exist in the same nonlinear model. It is also shown that period-doubling bifurcations emerge when there is sufficient selection in favor of interactions between different phenotypes.

Key words: Discrete diploid dynamic – Natural selection – ESS – Period-doubling bifurcation – Chaos

1. Introduction

The matrix game model is one of the most important theoretical models in evolutionary game theory. As pointed out by Lessard (1984),

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theoretical population biology models based on random pairwise interactions are an important source of ideas and principles that provide basic insights into intraspecific selection. The standard matrix game model always operates on the phenotypic level. This implies an assumption of parthenogenetic inheritance (Maynard Smith, 1982). However, most populations of interest have sexual diploid inheritance. Maynard Smith (1982) pointed out that if the phenotype (pure or mixed strategy) produced by a genetic homozygote is an evolutionarily stable strategy (ESS), then a sexual population with that genotype will be stable against invasion by any mutant allele.

If the ESS cannot be produced by a genetic homozygote, Maynard Smith also analyzed whether a genetically polymorphic population with two alleles can generate the ESS proportions, and if so whether such a population will be stable. This matrix game diploid model, but with multi-alleles, has been investigated by many authors (Maynard Smith, 1981, 1982; Eshel, 1982; Hofbauer et al., 1982; Hines and Bishop, 1984a,b; Lessard, 1984; Cressman and Hines, 1984; Hofbauer & Sigmund, 1988; Cressman, 1988ab, 1992; Gayley and Michod, 1990; Hines, 1994a,b; Cressman et al., 1996). In particular, Lessard (1984) analyzed a discrete time multi-allele, single-locus, two-phenotype diploid viability selection model. In this model, the individual fitness is assumed to be a linear function of phenotype frequency and can be identified with the expected payoff in a standard matrix game. Lessard defined the concepts of phenotypic and genotypic equilibria: phenotypic equilibria are characterized by equal phenotypic fitnesses and genotypic equilibria arise from constraints inherent in the underlying genetic system that are analogous to standard viability schemes (see Definition 1). Lessard's results (see also Cressman, 1992) show that:

 (I) the mean strategy of the population evolves monotonically to equilibrium;
 (II) a phenotypic equilibrium is (locally) stable if and only if it is an ESS of the matrix game;
(III) a genotypic equilibrium is stable if and only if its expected payoff is higher than all nearby average population payoffs (in particular, it must correspond to a (local) extremum of the mean strategy that is closer to the ESS than all nearby population mean strategies).

Vincent and Fisher (1988) and Tao et al. (1997) also investigated a discrete time evolutionary game model (but for a haploid species). They suggested that the individual fitness should be an exponential function of population density and of strategy frequency in order guarantee that the fitness is non-negative.

In this paper, we investigate the frequency dynamics of two discrete time two-phenotype diploid models where genotypic fitness is given through exponential functions of expected payoff. These two models, introduced in Sect. 2, are the pure-strategy model and the mixed-strategy model. They differ only in the interpretation of the strategy used by an individual with a given genotype. The paper compares the resultant dynamics of these two models with each other and with existing results for linear fitness models when the population has two possible phenotypes. Of particular interest is the relationship between the ESS analysis of the matrix game and the dynamic stability of equilibria for our frequency dynamic. However, complex dynamic behavior away from equilibrium is also exhibited through an application of the theory of discrete time nonlinear maps to our models.

It is shown in Theorem 1 that a stable phenotypic equilibrium must still be an ESS just as in Lessard's model (one direction of result II above). However, the evolution of the mean strategy need not be monotone. Furthermore, an ESS equilibrium that includes a mixture of both phenotypes can be unstable. This is especially true if selection pressure is sufficiently large (Theorem 1b) in which case period doubling bifurcations and chaos emerge (Example 1). The stability criterion of monomorphic genotypic equilibria (i.e., those with only one allele present) is given in Theorem 2a and is again the same as in Lessard's model (result III above). It is the existence and stability of polymorphic genotypic equilibria where the contrasts among the models is the most pronounced as discussed in Sect. 4 (see Theorem 3 and Example 3). However, by Theorem 2b, these can only occur when there is over or under dominance.[1] In such a case, Example 3 shows stable polymorphic genotypic equilibria can coexist with stable interior phenotypic equilibria for the mixed strategy model.

2. Population dynamics, fitness and payoff

Consider an infinite diploid population with nonoverlapping discrete generations in which an individual's fitness is its viability (i.e., probability of survival to reproductive age) and this is determined at a single autosomal locus with two possible alleles, A_1 and A_2. Let $F_{A_iA_j}$ be the average viability of individuals with genotype A_iA_j. When we assume random mating, Mendelian segregation, sex-independent viabilities,

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[1] Example 2 shows a case where there is an additive effect between the alleles and the dynamics resemble the haploid model of Tao et al. (1997).

equal fecundity and sex ratio of offspring, then

$$p' = p[pF_{A_1A_1} + (1 - p)F_{A_1A_2}]/\bar{F}. \qquad (1)$$

Here, p and p' are the the frequencies of allele A_1 in the current generation and in the next generation respectively, and

$$\bar{F} = p^2F_{A_1A_1} + 2p(1 - p)F_{A_1A_2} + (1 - p)^2F_{A_2A_2}$$

is the *mean fitness* of the current population. The discrete-time dynamic (1) is used extensively in the biological literature for models of single-locus, two-allele, frequency-independent natural selection (e.g., Fisher, 1930; Roughgarden, 1979) where the viability constants $F_{A_iA_j}$ are usually written as w_{ij} and also for frequency-dependent models (see Gayley and Michod (1990) and the references therein) where $F_{A_iA_j}$ are functions of p.

In this paper, our focus is on the latter model, especially when fitness is given through payoffs generated by random interactions between pairs of individuals who are characterized by their strategy (or behavior) that they use in these contests – the standard assumption underlying the matrix-game model of evolutionary game theory. We assume throughout that, in any given contest, an individual in the population can use one of two possible behaviors which are called the pure strategies R_1 and R_2. If the payoff matrix is

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix},$$

where a_{kl} ($k, l = 1, 2$) is the payoff of R_k competing against R_l, then the expected payoffs to R_1 and R_2 in random contests are given by

$$\varphi_1 = xa_{11} + (1 - x)a_{12} \quad \text{and} \quad \varphi_2 = xa_{21} + (1 - x)a_{22} \qquad (2)$$

respectively, where x is the proportion of individuals using strategy R_1 in the current population. We say x is the *mean strategy* of the population.[2]

We analyze the dynamic (1) in two models developed later in this section that differ only in how mean strategies and payoffs are related to allele frequencies and genotypic fitnesses respectively. We are particularly interested in the resultant equilibria of (1) and their stability properties. Since there are only two-strategies, only two classes of equilibria are possible; namely, the phenotypic and genotypic equilibria introduced by Lessard (1984).

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[2] This is a slight abuse of terminology since the mean strategy is actually $(x, 1 - x)$ where x is the proportion using R_1 and so $1 - x$ is the proportion using R_2.

Definition 1. *A* phenotypic equilibrium *is a population where all pure strategies in current use have equal expected payoff. A* genotypic equilibrium[3] *is a non-phenotypic equilibrium where the effective fitness of all alleles present in the current population are equal. The* effective fitness *of allele A_i is defined to be $pF_{A_1A_i} + (1 - p)F_{A_iA_2}$. The effective fitness, also called the "inclusive" or "marginal" fitness in population genetics (e.g. Ewens (1979)) is closely connected to the concept of effective strategy used later in our model.*

If all individuals in the population use the same pure strategy (i.e., $x = 0$ or 1), we are by definition at a phenotypic equilibrium called a *boundary phenotypic equilibrium.* On the other hand, at an *interior phenotypic equilibrium* with $0 < x < 1$, individuals using R_1 receive the same payoff as those using R_2 in each contest and this will translate into $F_{A_1A_1} = F_{A_1A_2} = F_{A_2A_2}$ and so $p = p'$ in (1). Similarly, if $p = 0$ or 1, the population is *monomorphic* and so at a genotypic equilibrium by default (unless all these homozygotes are using the same strategy and this corresponds to a phenotypic equilibrium). Otherwise, in a *polymorphic population* (i.e., $0 < p < 1$), a genotypic equilibrium satisfies $pF_{A_1A_1} + (1 - p)F_{A_1A_2} = pF_{A_1A_2} + (1 - p)F_{A_2A_2}$ and so $p = p'$ in (1). These are the only circumstances in which the population is in equilibrium.

There are two ways to interpret individual strategies. The first is the pure-strategy model in which each individual plays the same pure strategy in all contests throughout its lifetime. However, not all individuals of a particular genotype need play the same pure strategy. We assume a fraction u_{ij} of individuals of genotype A_iA_j play pure strategy R_1 and so $1 - u_{ij}$ play R_2.[4]

One possibility is that each individual plays in one contest in its lifetime. If payoffs translate directly into individual fitness, then $F_{A_iA_j}$ equals the average payoff to all individuals of genotypye A_iA_j given by

$$u_{ij}\varphi_1 + (1 - u_{ij})\varphi_2.$$

This model is commonly used in the continuous-time dynamic of frequency-dependent natural selection (Hofbauer and Sigmund, 1988; Cressman, 1992) where $F_{A_iA_j}$ is considered to be the rate of change of the number of A_iA_j individuals in the population (and so can be

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[3] Throughout the paper, phenotypic equilibria are denoted by p^* and genotypic equilibria by $\hat{p}$.

[4] Of course, if $u_{ij} = 0$ or 1, then all A_iA_j individuals play the same pure strategy. We assume u_{11}, u_{12}, u_{22} are not all equal throughout the paper (otherwise, the dynamics we consider all degenerate to $p' = p$ for all p).

negative). It is less appropriate for our discrete-time model unless the payoffs a_{kl} are all probabilities (or at least positive).

We feel a more realistic interpretation of payoffs in the discrete model is that each individual engages in a large but fixed number of random contests over its lifetime. The average payoff per contest is then φ_1 and φ_2 respectively for individuals using pure strategy R_1 and R_2 respectively and the individual fitnesses are taken to be $e^{\varphi_1} \equiv \exp\{\varphi_1\}$ and e^{φ_2} respectively. Such fitness functions[5] have appeared elsewhere in the literature on discrete population dynamics (e.g. May, 1973; Vincent and Fisher, 1988) where they are interpreted as per capita growth rates as well as on frequency-dependent selection (e.g. Tao et al., 1997) where a background fitness parameter W is often included (i.e., fitnesses are taken to be $\exp\{W + \varphi_1\}$ and $\exp\{W + \varphi_2\}$ respectively). The parameter W has no effect on our frequency dynamic (1) and so will be ignored hereafter. Thus

$$F_{A_i A_j} = u_{ij}e^{\varphi_1} + (1 - u_{ij})e^{\varphi_2}. \tag{3}$$

and the dynamic (1) becomes

$$p' = p\,\frac{p(u_{11}e^{\varphi_1} + (1 - u_{11})e^{\varphi_2}) + (1 - p)(u_{12}e^{\varphi_1} + (1 - u_{12})e^{\varphi_2})}{\bar{F}},$$

$$= p\,\frac{(pu_{11} + (1-p)u_{12}) + (p(1-u_{11}) + (1-p)(1-u_{12}))\exp\{\varphi_2 - \varphi_1\}}{x + (1-x)\exp\{\varphi_2 - \varphi_1\}}$$

$$= p\,\frac{x_{A_1} + (1 - x_{A_1})\exp\{\varphi_2 - \varphi_1\}}{x + (1 - x)\exp\{\varphi_2 - \varphi_1\}} \tag{4}$$

where $x_{A_1} = pu_{11} + (1 - p)u_{12}$ is the *effective strategy* of allele A_1 (the effective strategy of allele A_2 is $x_{A_2} = pu_{12} + (1 - p)u_{22}$). Furthermore, $\bar{F} = xe^{\varphi_1} + (1 - x)e^{\varphi_2}$ since

$$x(p) = p^2 u_{11} + 2p(1 - p)u_{12} + (1 - p)^2 u_{22}$$

$$= px_{A_1} + (1 - p)x_{A_2}$$

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[5] An alternative justification of fitness functions of this form is to assume the payoff from each contest gives the relative change in reproductive success (e.g., an individual who receives a payoff of ln(10) produces 10 times as many offspring as an individual who receives payoff 0). These fitnesses then accumulate multiplicatively over the n contests during an individual's lifetime to yield (3) where the payoff entries a_{kl} are adjusted by the factor n. It is interesting to note that this multiplicative effect is similar to assumptions in discrete-time models of two-locus natural selection (Hofbauer and Sigmund, 1988).
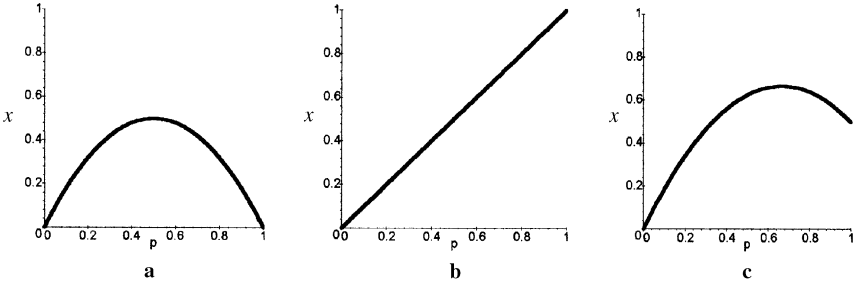
Fig. 1. The mean strategy map for **a** Example 1 with $u_{11} = u_{22} = 0$ and $u_{12} = 1$, **b** Example 2 with $u_{11} = 1$, $u_{12} = \frac{1}{2}$ and $u_{22} = 0$, **c** Example 3 with $u_{11} = 1/2$, $u_{12} = 1$ and $u_{22} = 0$.

is the population mean strategy here and for the following mixed-strategy model.

The second interpretation of individual strategies is the mixed-strategy model where all individuals of the same genotype play the same, possibly mixed, strategy. A mixed strategy is specified by its probability u that pure strategy R_1 is played in any given contest and so R_2 is played with probability $1 - u$. For example, $A_i A_j$ individuals who play the strategy specified by $u_{ij} = 1/2$ can be visualized as tossing a fair coin before each contest and then using the pure strategy that corresponds to the outcome. The average payoff per contest during the lifetime of each $A_i A_j$ individual is now $u_{ij}\varphi_1 + (1 - u_{ij})\varphi_2$ and so fitness is

$$F_{A_i A_j} = \exp\{u_{ij}\varphi_1 + (1 - u_{ij})\varphi_2\} \tag{5}$$

for all $i, j = 1, 2$. The frequency dynamic (1) can be rewritten as

$$p' = p\,\frac{\Phi_1}{p\Phi_1 + (1 - p)\Phi_2}, \tag{6}$$

where

$$\Phi_1 = (1 - p) + p\exp\{(u_{12} - u_{11})(\varphi_2 - \varphi_1)\}$$

$$\Phi_2 = p + (1 - p)\exp\{(u_{12} - u_{22})(\varphi_2 - \varphi_1)\}.$$

Both (4) and (6) are examples of nonlinear frequency-dependent selection mechanisms. The nonlinearities enter only through the multiplicative effect that accumulated individual payoff has on lifetime fitness since we have maintained a linear dependence of payoff on strategy frequency due to our assumption of random pairwise interactions. This contrasts with the usual development of nonlinear frequency-dependent selection in the literature where nonlinear payoffs are typically introduced through playing-the-field assumptions (Maynard

Smith, 1982; Gayley and Michod, 1990). In this literature, if the respective lifetime payoffs to R_1 and R_2 are the general nonlinear functions ψ_1 and ψ_2 of strategy frequency x, then the frequency dynamic has always been based on the pure-strategy scenario. Thus, the equilibrium structure and stability results in these references are most closely related to those of (4) with e^{φ_1} and e^{φ_2} replaced by ψ_1 and ψ_2 respectively.

The nonlinear fitness functions (3) and (5) respectively, on which (4) and (6) respectively are based, differ mathematically only in when the convex combination corresponding to mixed strategies is taken into account. In (3), convex combinations of fitnesses of the pure strategies are taken whereas, in (5), convex combinations of the payoffs of pure strategies are taken. We will see, especially in the Section 4, that this seemingly minor difference in the interpretation of mixed strategies can have a major impact on the equilibrium and stability structure of the dynamic.[6]

3. Phenotypic equilibria and ESS's

From Definition 1, an interior phenotypic equilibrium occurs when $\varphi_2 = \varphi_1$ in (2). Since

$$\varphi_2 - \varphi_1 = x(a_{21} - a_{11}) + (1 - x)(a_{22} - a_{12})$$
$$= (a_{12} - a_{22} + a_{21} - a_{11})x - (a_{12} - a_{22}),$$

when $\gamma \equiv a_{12} - a_{22} + a_{21} - a_{11} = 0$, either there is no interior phenotypic equilibrium (when $a_{12} - a_{22} \neq 0$) or else any population with mean strategy $0 < x < 1$ is an interior phenotypic equilibrium. To avoid these degeneracies, we assume hereafter that $\gamma \neq 0$. Lessard (1984) introduced the concept of *heterogeneity advantage* for the case $\gamma > 0$ (since $a_{12} + a_{21} > a_{11} + a_{22}$) and *homogeneity advantage* otherwise. Then, with $\zeta \equiv (a_{12} - a_{22})/\gamma$,

$$\varphi_2 - \varphi_1 = \gamma(x - \zeta). \tag{7}$$

The above definitions of γ and ζ are closely related to the evolutionarily stable strategy (ESS) concept of Maynard Smith (1982) for the 2×2 payoff matrix $[a_{kl}]_{k,l=1,2}$.

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[6] When fitnesses are assumed to accumulate additively over an individual's lifetime there is no difference in the frequency dynamic between the pure-strategy and the mixed-strategy models. In particular, when payoffs depend linearly on frequency, we obtain the standard matrix-game discrete dynamic of evolutionary game theory (Maynard Smith, 1982; Cressman, 1992).

To summarize, when $0 < \zeta < 1$, $x^* = \zeta$ is an interior ESS if and only if $\gamma > 0$; both $x^* = 0$ and $x^* = 1$ are boundary ESS's if and only if $\gamma < 0$. Furthermore, if $\zeta \leqq 0$, then $x^* = 0$ is an ESS if and only if $\gamma > 0$; $x^* = 1$ is an ESS if and only if $\gamma < 0$. Similarly, if $\zeta \geqq 1$, then $x^* = 0$ is an ESS if and only if $\gamma < 0$; $x^* = 1$ is an ESS if and only if $\gamma > 0$. It is also well-known that, in the standard two-strategy matrix-game haploid dynamic of evolutionary game theory (with either the discrete- or continuous-time dynamic), population mean strategy evolves monotonically towards an equilibrium and an equilibrium is locally asymptotically stable if and only if it is an ESS.[7]

We will investigate below how these properties of ESS's generalize to the diploid dynamics (4) and (6). In particular, the following theorem concerns the local asymptotic stability of phenotypic equilibria. A population at an equilibrium p^* is called (locally asymptotically) *stable* if, for all initial states p sufficiently close to p^*, all future states under (1) remain close to p^* and eventually converge to p^*.

Theorem 1. *Suppose p^* is a phenotypic equilibrium corresponding to the population mean strategy $x^* \equiv x(p^*)$.*

(a) *Suppose p^* is a boundary phenotypic equilibrium (i.e. $x^* = 0$ or $x^* = 1$). Then p^* is stable if and only if x^* is a ESS.*

(b) *Suppose p^* is an interior phenotypic equilibrium (i.e., $0 < x^* < 1$). If x^* is not an ESS, then p^* unstable. If x^* is an ESS, then there is some critical level of heterogeneity advantage (i.e., some $\gamma_{cr} > 0$) such that p^* is stable for $0 < \gamma < \gamma_{cr}$ and unstable when $\gamma > \gamma_{cr}$.[8]*

Proof. (a) Let us first consider a boundary phenotypic equilibrium. Without loss of generality, assume $x^* = 0$. For this mean strategy to be attainable, at least one of u_{11} and u_{22} is 0. Let us assume $u_{22} = 0$ and so $p^* = 0$ is a phenotypic equilibrium. Since p' depends continuously on p in both (4) and (6),[9] p^* is stable if and only if $p' < p$ whenever p is

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[7] These dynamic results follow from the equivalent characterization (Hofbauer and Sigmund, 1988) of an ESS in matrix games as a strategy for which payoffs (and therefore fitnesses) are strictly greater than the average population payoff when the population mean strategy is sufficiently close (but not equal) to the ESS. It can be shown that attainable ESS's in our model are strategies for which fitnesses given in either (3) or (5) are strictly greater than the average population fitness when the population mean strategy is sufficiently close (but not equal) to the ESS.

[8] In degenerate cases, γ_{cr} may be infinity in which case p^* is then stable for all $\gamma > 0$ when x^* is an ESS.

[9] This follows since $\bar{F}$ in (1) is always positive using either (3) or (5).

positive and sufficiently small.

$p' < p$

$\Leftrightarrow pF_{A_1A_1} + (1-p)F_{A_1A_2} < p^2F_{A_1A_1} + 2p(1-p)F_{A_1A_2} + (1-p)^2F_{A_2A_2}$

$\Leftrightarrow pF_{A_1A_1} + (1-2p)F_{A_1A_2} - (1-p)F_{A_2A_2} < 0$

Thus $p' < p$ for all positive p sufficiently small if and only if either

  (i) $F_{A_1A_2}(p) < F_{A_2A_2}(p)$ or
 (ii) $F_{A_1A_2}(p) = F_{A_2A_2}(p)$ and $F_{A_1A_1}(p) < F_{A_1A_2}(p)$.

For the pure-strategy model, $F_{A_iA_j} = u_{ij}e^{\varphi_1} + (1-u_{ij})e^{\varphi_2}$. Since $u_{22} = 0$,
(i) holds if and only if

$$u_{12}(e^{\varphi_1} - e^{\varphi_2}) < 0. \tag{8}$$

Assume $u_{12} \neq 0$ (i.e. $u_{12} > 0$). From (2), (i) holds for positive p sufficiently small (i.e., positive $x(p)$ sufficiently close to 0) if and only if either $a_{12} < a_{22}$ or both $a_{12} = a_{22}$ and $a_{11} < a_{12}$. These are the exact conditions for $x^* = 0$ to be an ESS. Furthermore, if $u_{12} = 0$, then $F_{A_1A_2}(p) = F_{A_2A_2}(p)$ and $u_{11} > 0$. In this case, (ii) holds if and only if $\varphi_1 < \varphi_2$. That is, if and only if $x^* = 0$ is an ESS. The calculations for the mixed-strategy model are identical except that, from (5), (8) is replaced with $\exp\{u_{12}(\varphi_1 - \varphi_2)\} < 1$. Since p' depends continuously on p and we have discarded degenerate situations where all u_{ij} are identical or where $\gamma = 0$, no positive p sufficiently close to $p^* = 0$ is an equilibium and so any p^* that is not stable will be unstable.

(b) For the remainder of the proof, assume that p^* is an interior phenotypic equilibrium (i.e., $0 < x^* = \zeta < 1$). If $p^* = 0$ or 1 (i.e., for monomorphic populations), an argument similar[10] to the above proof shows that p^* is stable if and only if x^* is an ESS (and p^* is unstable otherwise). Thus, we may assume $0 < p^* < 1$. From the theory of one-dimensional discrete-time dynamical systems, p^* is stable if $|\frac{dp'}{dp}|_{p=p^*} < 1$.[11] For the pure-strategy model,

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[10] Specifically, if $p^* = 0$ and $\zeta = x^* = u_{22}$, then (i) holds in the pure or mixed strategy model if and only if $(u_{12} - u_{22})(\varphi_1 - \varphi_2) < 0$ if and only if $(u_{12} - u_{22})(u_{22} - x(p))\gamma < 0$. Since $x(p)$ is on the same side of u_{22} as u_{12} for positive p sufficienty small, the result follows.

[11] We could also use this technique at boundary phenotypic equilibria. For instance, if $x^* = 0$ and $p^* = 0$, then $\frac{dp'}{dp}|_{p=0} = \frac{u_{12} + (1-u_{12}\exp\{\gamma(u_{22}-\zeta)\}}{u_{22} + (1-u_{22})\exp\{\gamma(u_{22}-\zeta)\}}$ is positive. Since $u_{22} = 0$, if $u_{12} > 0$, then $0 < \frac{dp'}{dp}|_{p=0} < 1$ if and only if $\gamma\zeta < 0$ if and only if (8) holds. If $\zeta \neq 0$, this is the condition for $x^* = 0$ to be an ESS. If $\zeta = 0$, we must consider case (ii) in the above proof.

from (4) and $\varphi_1(x^*) = \varphi_2(x^*)$,

$$\left.\frac{dp'}{dp}\right|_{x=x^*} = 1 - 2p^*(1-p^*)[x_{A_1}(p^*) - x_{A_2}(p^*)]^2\gamma, \qquad (9)$$

since $\varphi_2 - \varphi_1 = \gamma(x - x^*)$ and $\frac{dx}{dp} = 2(x_{A_1} - x_{A_2})$. A similar calculation using (6) yields the same derivative as (9) for the mixed-strategy model at an interior phenotypic equilibrium.

Assume $x_{A_1}(p^*) \neq x_{A_2}(p^*)$ for now. From (9), if $\gamma < 0$, then we obviously have $\frac{dp'}{dp}|_{x=x^*} > 1$. This means p^* is unstable if x^* is not an ESS. On the other hand, if x^* is an ESS (i.e., $\gamma > 0$), let

$$\gamma_{cr} = \frac{1}{p^*(1-p^*)[x_{A_1}(p^*) - x_{A_2}(p^*)]^2} > 0. \qquad (10)$$

For $0 < \gamma < \gamma_{cr}$, we have $|\frac{dp'}{dp}|_{x=x^*}| < 1$ and so p^* is stable. For $\gamma > \gamma_{cr}$, we have $\frac{dp'}{dp}|_{x=x^*} < -1$ and so p^* is unstable. Thus an interior phenotypic equilibrium corresponding to an ESS x^* can be stable or unstable depending on the level of heterogeneity advantage.[12]

For the remainder of the proof, assume $x_{A_1}(p^*) = x_{A_2}(p^*)$ and $0 < p^* < 1$. The local stability of p^* cannot be determined by (9). In this case, $(u_{11} - u_{12})(u_{22} - u_{12}) > 0$. Thus, if $p \neq p^*$, $x_{A_1} + (1 - x_{A_1})$ $\exp\{\varphi_2 - \varphi_1\} > x_{A_2} + (1 - x_{A_2})\exp\{\varphi_2 - \varphi_1\}$ if and only if $\gamma(x_{A_1} - x_{A_2})(x - x^*) < 0$. For the pure-strategy model, it is then easy to show from (4) that

$$\gamma(p - p')(p - p^*) > 0 \quad \text{for all } p \neq p^*.$$

If $\gamma < 0$, then p^* must be unstable since p' is farther from p^* than p. For $\gamma > 0$, p' is closer to p^* than p and, from $\frac{dp'}{dp}|_{p=p^*} = 1$, we know that there exists an $\varepsilon > 0$ such that

$$p' < p^* \text{ when } p \in (p^* - \varepsilon, p^*)$$

$$p' > p^* \text{ when } p \in (p^*, p^* + \varepsilon).$$

Thus p^* is stable if and only if $\gamma > 0$. A similar analysis involving (6) for the mixed-strategy model shows $\gamma(p - p')(p - p^*) > 0$ for all p sufficiently close but not equal to p^*. Thus, when $x_{A_1}(p^*) = x_{A_2}(p^*)$, an interior phenotypic equilibrium is stable for all $\gamma > 0$ and unstable for $\gamma < 0$.   □

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[12] It is easy to demonstrate that when $x = x^*$ and $\gamma = \gamma_{cr}$, the dynamic (1) satisfies the theorem of period-doubling bifurcation (Schuster, 1988; Argyris et al., 1994). This implies that more complex dynamical behavior is possible if $\gamma > \gamma_{cr}$ as discussed in Example 1 below.

The results of Theorem 1 on the local stability of phenotypic equilibria combine with similar results on genotypic equilibria in Sect. 4 below to give an overall understanding of general trajectories for the dynamic (1). As illustrated by the following example, this is especially true when the level of heterogeneity γ is below the critical level of Theorem 1b or when $\gamma < 0$. On the other hand, if γ is large in this example and there is an interior phenotypic equilibrium, complex dynamic behavior emerges including period-doubling bifurcations and chaos.

Example 1. *Let $u_{11} = u_{22} = 0$ and $u_{12} = 1$. Since (3) is identical to (5) for all i and j, the pure-strategy model and the mixed-strategy model coincide in this case.[13] The dynamic (1) can be rewritten as $p' = \delta_\gamma(p)$ where*

$$\delta_\gamma(p) \equiv p \, \frac{(1 - p) + p \exp\{\gamma(x - \zeta)\}}{x + (1 - x) \exp\{\gamma(x - \zeta)\}} \, . \tag{11}$$

Population mean strategy $x = 2p(1 - p)$ is plotted as a function of p in Fig. 1a from which it is clear that the set of attainable mean strategies is $\{x \,|\, x \in [0, \frac{1}{2}]\}$. Since $\delta_\gamma(p)$ is an anti-symmetric map about $p = \frac{1}{2}$ in the open interval $(0, 1)$ (i.e. $\delta_\gamma(1 - p) = 1 - \delta_\gamma(p)$) and $\delta_\gamma(p) \in (0, \frac{1}{2})$ if $p \in (0, \frac{1}{2})$ and $\delta_\gamma(p) \in (\frac{1}{2}, 1)$ if $p \in (\frac{1}{2}, 1)$, the trajectories in these two invariant subintervals are mirror images of each other reflected in the stationary trajectory corresponding to the equilibrium at $p = \frac{1}{2}$ (see Fig. 3 below).

Suppose $\zeta \leqq 0$ or $\zeta \geqq 1/2$. Then all interior trajectories evolve monotonically to an equilibrium. Specifically, if $x^* = 0$ is an ESS, then all initial states on one side of $p = \frac{1}{2}$ evolve to the closest boundary phenotypic equilibrium $p^* = 0$ or $p^* = 1$, both of which correspond to an ESS. On the other hand, if $x^* = 0$ is not an ESS, all interior trajectories evolve to $p = \frac{1}{2}$ which is a polymorphic genotypic equilibrium (unless $\zeta = \frac{1}{2}$ in which case $p^* = \frac{1}{2}$ is an interior phenotypic equilibrium corresponding to an ESS). In all these cases, the population evolves to an equilibrium as close as possible to an ESS given the fact that the genetics constrains population mean strategy to be in $\{x \,|\, x \in [0, \frac{1}{2}]\}$. This geometric intuition is used by Maynard Smith (1982) and by Gayley and Michod (1990).

The most interesting situation is when $0 < \zeta < \frac{1}{2}$. There are then two interior phenotypic equilibria (as well as the two boundary phenotypic equilibria and the genotypic equilibrium at $\hat{p} = \frac{1}{2}$); namely,

$$p^*_{1,2} = \frac{1}{2} \mp \frac{\sqrt{1 - 2\zeta}}{2} \, .$$

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[13] This coincidence of models occurs if and only if all individuals use pure strategies.
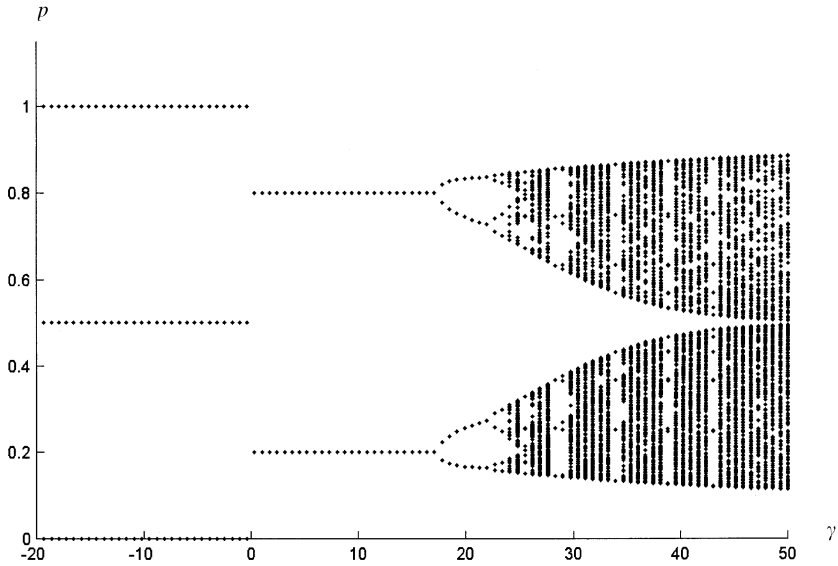
Fig. 2. The bifurcation diagram for Example 1. Here $\zeta = 0.32$ with $p_1^* = 0.2$ and $p_2^* = 0.8$ as the interior phenotypic equilibria. For $\gamma < \gamma_{cr} \simeq 17.4$, all interior trajectories converge to one of the stable equilibria indicated in the diagram (i.e., $p = 0, \frac{1}{2}, 1$ for $\gamma < 0$ and $p_{1,2}^*$ for $0 < \gamma < \gamma_{cr}$). As γ increases beyond γ_{cr}, there are first stable trajectories of period two, then period four around $\gamma \simeq 22$ until chaos occurs before period three at $\gamma \simeq 28$.
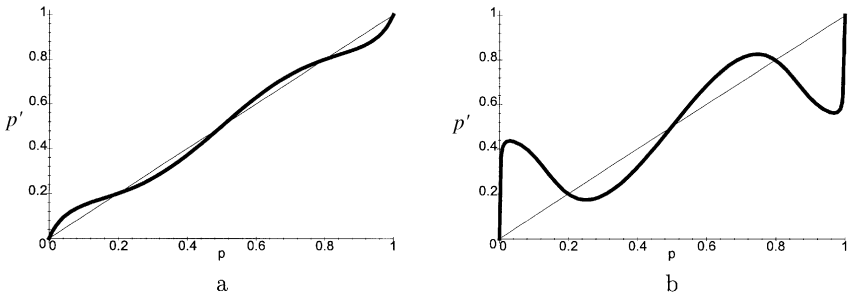
Fig. 3. The graphs of p' versus p for **a** $\gamma = 4$ and **b** $\gamma = 18$ in Example 1. The dynamic equilibria correspond to the points of intersection of these graphs with the line $p' = p$. Clearly, $p' \in (0, \frac{1}{2})$ if and only if $p \in (0, \frac{1}{2})$ for both levels of heterogeneity. For $\gamma = 4$, each trajectory evolves monotonically to equilibrium whereas there are stable cycles of period two near p_1^* and p_2^* when $\gamma = 18 > \gamma_{cr}$.

If $\gamma < 0$, then $x^* = 0$ is an ESS and so $p^* = 0$ and $p^* = 1$ are both stable by Theorem 1a. Furthermore, $\hat{p} = \frac{1}{2}$ is stable and $p_{1,2}^*$ are both unstable. All nonstationary interior trajectories monotonically evolve towards one of the three stable equilibria. These stability properties are indicated

in Fig. 2 since this bifurcation diagram shows $0, \frac{1}{2}, 1$ are the stable equilibrium values of p when the parameter γ is negative. For $\gamma > 0$, we have $\gamma_{cr} = \frac{2}{\zeta(1 - 2\zeta)}$ from (10). Obviously, if $\gamma < \frac{2}{\zeta(1 - 2\zeta)}$, then both $p^*_{1,2}$ are stable by Theorem 1b. In particular, p^*_1 attracts any initial state $p \in (0, \frac{1}{2})$ and p^*_2 attracts any initial state $p \in (\frac{1}{2}, 1)$. On the other hand, if $\gamma > \frac{2}{\zeta(1 - 2\zeta)}$, then both interior phenotypic equilibria are unstable. We only need to consider the dynamical properties of (11) in the open interval $(0, \frac{1}{2})$. It is easy to prove that the function $\delta_\gamma(p)$ is a one-dimensional map with two critical points in the open interval $(0, \frac{1}{2})$ for all $\gamma > \frac{2}{\zeta(1 - 2\zeta)}$. This implies that the dynamical properties of (11) in $(0, \frac{1}{2})$ are similar to the general one-dimensional cubic map (Schuster, 1988; Argyris et al., 1994). In particular, a period doubling bifurcation[14] occurs at γ_{cr}. Furthermore, when $\gamma > \frac{2}{\zeta(1 - 2\zeta)}$, the periodic and chaotic behaviours in the interval $(0, \frac{1}{2})$ are all possible with increasing γ as indicated clearly in the bifurcation diagram of Fig. 2.

4. Genotypic equilibria

The polymorphic genotypic equilibria, $0 < \hat{p} < 1$, for the pure-strategy model are generally different from those of the mixed-strategy model. To see this, from (4), a polymorphic population is in equilibrium for the pure-strategy model if and only if $(x_{A_1} - x_{A_2})(1 - \exp\{\gamma(x - \zeta)\}) = 0$. Thus, $\hat{p}$ is a polymorphic genotypic equilibrium if and only if $\hat{x} \equiv x(\hat{p}) \neq \zeta$ and $x_{A_1} - x_{A_2} = 0$. This can be rewritten as

$$x(\hat{p}) \neq \zeta \text{ and } \frac{\hat{p}}{1 - \hat{p}} = \frac{u_{12} - u_{22}}{u_{12} - u_{11}}. \tag{12}$$

On the other hand, from (6), a polymorphic population is in equilibrium for the mixed-strategy model if and only if $\Phi_1 = \Phi_2$. Thus, $\hat{p}$ is a polymorphic genotypic equilibrium for the mixed-strategy model if and only if

$$x(\hat{p}) \neq \zeta \text{ and } \frac{\hat{p}}{1 - \hat{p}} = \frac{1 - \exp\{\gamma(u_{12} - u_{22})(x - \zeta)\}}{1 - \exp\{\gamma(u_{12} - u_{11})(x - \zeta)\}}. \tag{13}$$

Thus, $\hat{p}$ is a polymorphic genotypic equilibrium for both the pure-strategy model and the mixed-strategy model if and only if

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[14] These types of bifurcations are the only interesting ones for a one-dimensional discrete dynamic. The fold bifurcation at $\gamma = 0$ is not interesting since the dynamics evolve to equilibria for all nearby parameters γ.

$u_{11} = u_{22}$, $\hat{p} = \frac{1}{2}$ and $x(\hat{p}) \neq \zeta$ as in Example 1. Although polymorphic genotypic equilibria are the most interesting, their stability properties are the most difficult to analyze, especially in the mixed-strategy model as we will see in Sect. 4.2 below. For this reason, we will begin our analysis with monomorphic genotypic equilibria (for both the pure and mixed strategy model) in the following theorem.

Theorem 2. (a) *Suppose $\hat{p} = 0$ or $\hat{p} = 1$ is a genotypic equilibrium (in particular $\hat{p}$ is not a phenotypic equilibrium). The following statements are equivalent.*
  (i) *$\hat{p}$ is stable.*
  (ii) *The strategy $x(\hat{p})$ has a strictly higher expected payoff than the average population payoff when the population mean strategy is $x(p)$ for all p sufficiently close but not equal to $\hat{p}$.*
  (iii) *The effective fitness of the monomorphic allele at $\hat{p}$ is greater than that of the absent allele.*
   (b) *If there is no over or under dominance[15], then there are no polymorphic genotypic equilibria.*

Proof. (a) We will only prove the result when $\hat{p} = 0$ is a genotypic equilibrium since the case $\hat{p} = 1$ is analogous. The proof follows the same steps as that of Theorem 2b. For both the pure- and mixed-strategy model, $\hat{p} = 0$ is stable if and only if, for all positive p sufficiently small, either $F_{A_1A_2} < F_{A_2A_2}$ or $F_{A_1A_2} = F_{A_2A_2}$ and $F_{A_1A_1} < F_{A_1A_2}$. From (4) and (6), this is equivalent to either $(u_{12} - u_{22})(\varphi_1 - \varphi_2) < 0$ or $(u_{12} - u_{22})(\varphi_1 - \varphi_2) = 0$ and $(u_{11} - u_{12})(\varphi_1 - \varphi_2) < 0$. From (7), note that $\varphi_1 \neq \varphi_2$ at a genotypic equilibrium. When the population mean strategy is $x(p)$ with φ_1 and φ_2 given by (2), the expected payoff to $x(\hat{p} = 0) = u_{22}$ minus the expected payoff to $x(p)$ is

$$p(2 - p)(u_{22} - u_{12})(\varphi_1 - \varphi_2) + p^2(u_{12} - u_{11})(\varphi_1 - \varphi_2).$$

Since $\varphi_1 \neq \varphi_2$ for all p sufficiently close to $\hat{p}$, the equivalence of (i), (ii) and (iii) is now straightforward.
   (b) If there is no over or under dominance, then $u_{12} - u_{22}$ and $u_{12} - u_{11}$ have opposite sign. Thus, from both (12) and (13), $\frac{\hat{p}}{1-\hat{p}}$ would have to be negative at a polymorphic genotypic equilibrium which is clearly impossible.   □

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[15] That is, u_{12} is a convex combination of u_{11} and u_{22}. In this case, the expected payoff of the heterozygote is between that of the two homozygotes. This is called semi-dominance in Cressman and Hines (1984) and incomplete dominance in Cressman (1992).

Statements (ii) and (iii) of Theorem 2 are related to the effect of introducing a mutant allele into a system already at equilibrium as discussed in Lessard (1984). In this paper, $\hat{p} = 0$ can be interpreted as meaning that A_1 is the mutant allele and then statements (ii) and (iii) can be interpreted as saying the mutant allele cannot invade the current system.

Example 2. *Let $u_{11} = 1$, $u_{12} = \frac{1}{2}$ and $u_{22} = 0$. By Theorem 2b, there are no polymorphic genotypic equilibria. Since it is clear that both monomorphic populations are phenotypic equilbria, there are no genotypic equilibria. Since u_{12} is the average of u_{11} and u_{22}, the pure-strategy model is closely related to the discrete haploid model of Tao et al. (1997) who also considered fitness functions of the form e^{φ}. Specifically, if we assume individuals in the haploid species play one of the two possible pure strategies, the haploid dynamic is $p'_H = p_H e^{\varphi_1}/(p_H e^{\varphi_1} + (1 - p_H)e^{\varphi_2})$ where p_H is the frequency of the pure strategy R_1 in the haploid model and so, for our diploid dynamic (4), $\Delta p \equiv p' - p = \frac{1}{2}\Delta p_H$. In this sense, the diploid dynamic evolves at half the rate of the corresponding haploid dynamic.[16] The stability properties of equilibria of the two dynamics are identical except the value of $\gamma_{cr} > 0$ where bifurcations of an interior phenotypic equilibrium commence is smaller for the haploid model.*

We are more interested in comparing the long-run behavior for the two diploid models. If $\zeta \leqq 0$ or $\zeta \geqq 1$, all interior trajectories of both dynamics evolve monotonically to the unique boundary phenotypic equilibrium that corresponds to an ESS. Similarly, if $0 < \zeta < 1$ and $\gamma < 0$, both boundary phenotypic equilibria correspond to ESSs and evolution is monotonic to one of these. With respect to the bifurcation diagram of Fig. 4 when $0 < \zeta < 1$ and $\gamma > 0$, it is clear that both models have the same value of γ_{cr} given by (10). Furthermore, it is apparent that chaotic behavior and stable trajectories of period three emerge in this example for the mixed-strategy model (at $\gamma \simeq 35$) before similar behavior for the pure-strategy model.
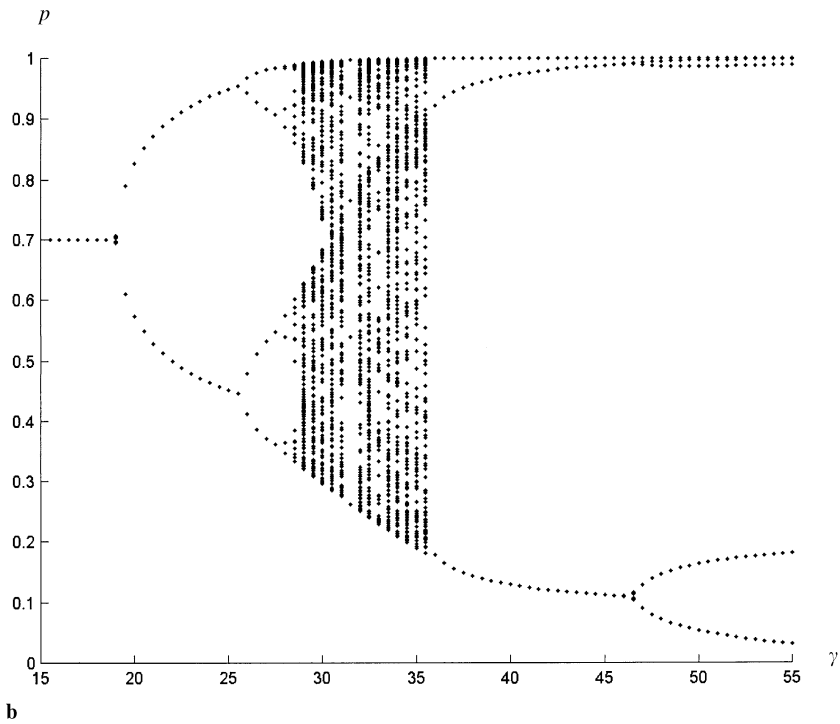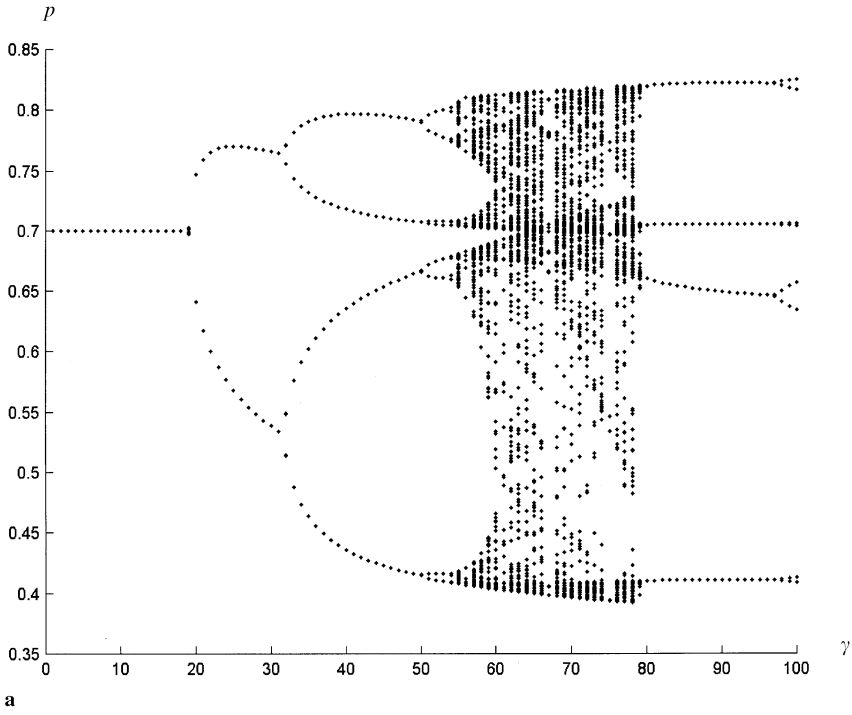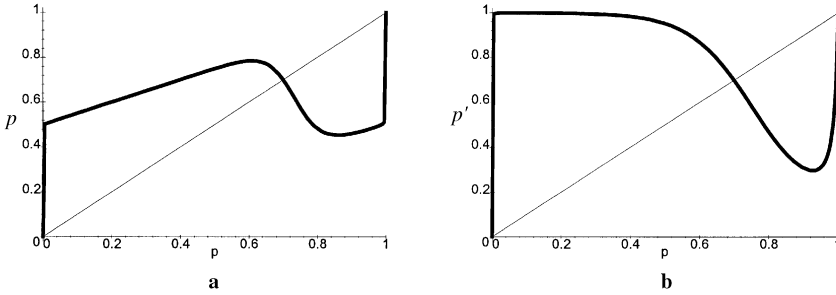
Fig. 4. The bifurcation diagram for Example 2 for **a** the pure-strategy model and **b** the mixed-strategy model. Here $\zeta = 0.7$ which has $p_1^* = 0.7$ as the only interior phenotypic equilibrium. There are no genotypic equilibria.

[16] The exact relationship between these discrete dynamic trajectories is quite complex. However, the corresponding continuous-time dynamic trajectories are identical up to a factor of 2.

a

b

Fig. 5. The graphs of p' versus p for $\gamma = 30$ in Example 2 for **a** the pure-strategy model and **b** the mixed-strategy model. Combined with the previous bifurcation diagram, we see that trajectories in **a** evolve to a cycle of period two contained in the interval $p \in [0.45, 0.8]$ whereas in **b** more complex dynamic behavior emerges in the interval $p \in [0.3, 1]$.

4.1. Polymorphic genotypic equilibria for the pure-strategy model

By Theorem 2b, we can assume in this section (and in Sect. 4.2) that $u_{12} > u_{11} > u_{22}$.[17] The other situations where there is over- or under-dominance can be treated symmetrically.

From (12), if $0 < \hat{p} < 1$, then $\hat{p} = \frac{u_{12} - u_{12}}{(u_{12} - u_{11}) + (u_{12} - u_{12})}$ and so $x(\hat{p})$ is a global extremum of the map $p \to x(p)$ as in Example 1. In particular, there is at most one polymorphic genotypic equilibrium. This property of the pure-strategy model is identical with Lessard's (1984) model.

For the local stability of the genotypic equilibrium, we have

$$\left.\frac{dp'}{dp}\right|_{p=\hat{p}} = 1 + \hat{p}\,\frac{(u_{11} - u_{12})(1 - \exp\{\gamma[x(\hat{p}) - \zeta]\})}{x(\hat{p}) + [1 - x(\hat{p})]\exp\{\gamma[x(\hat{p}) - \zeta]\}}. \tag{14}$$

Straightforward calculations show that $\frac{dp'}{dp}|_{p=\hat{p}} > -1$. Thus, there are no period doubling bifurcation near $\hat{p}$. Since $u_{12} > \max\{u_{11}, u_{22}\}$, $\frac{dp'}{dp}|_{p=\hat{p}} < 1$ if and only if $\gamma(\hat{x} - \zeta) < 0$ if and only if the effective fitness of allele A_1 is less than that of allele A_2 if the frequency of allele A_1 is greater than $\hat{p}$.

These results are included in Theorem 3 below. Furthermore, Theorems 3 and 1 combine to show that if p^* is an interior phenotypic equilibrium, then the genotypic equilibrium $\hat{p}$ (if one exists) is stable if and only if $x(p^*)$ is not an ESS. In other words, for the pure-strategy model, interior phenotypic equilibria corresponding to an ESS cannot

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[17] The case $u_{12} > u_{11} = u_{22}$ has already been discussed (see Example 1).

coexist with stable polymorphic genotypic equilibria. In particular, by Theorem 1b, it is not possible to have stable interior phenotypic equilibria and stable polymorphic genotypic equilibria in the same pure-strategy model. We will see in the following section that this latter possibility does arise in the mixed-strategy model.

4.2. Polymorphic genotypic equilibria for the mixed-strategy model

Recall that we have assumed $u_{12} > u_{11} > u_{22}$. Let $z_1 \equiv \frac{1 - e^{\gamma b(x - \zeta)}}{1 - e^{\gamma a(x - \zeta)}}$ and $z_2 \equiv \frac{p}{1 - p}$ where $a \equiv u_{12} - u_{11}$ and $b \equiv u_{12} - u_{22}$ satisfy $b > a > 0$. Although z_1 is not initially defined at $x(p) = \zeta$, it can be continued analytically there by setting this value to be b/a. From (13), the condition for a polymorphic genotypic equilibrium[18] p, can be rewritten as $x(p) \neq \zeta$ and

$$z_1 = z_2. \tag{15}$$

We are thus interested in those values of p where z_1 and z_2 intersect.

Define p_{max} as the interior solution of $dx/dp = 0$.[19] Then $x(p_{max})$ is the maximum of $x(p)$ and $p_{max} > \frac{1}{2}$. It is also true that p_{max} is an extreme point of $z_1(p)$ since $\frac{dz_1}{dx} > 0$ for all $x \in (0, 1)$. There are no polymorphic genotypic equilibria in $p \in (0, \frac{1}{2}]$ since $z_1 > z_2$ for all such p and so we only need to consider the possibility that eqn (15) has solutions in $(\frac{1}{2}, 1)$.

Let us start by assuming $\gamma > 0$. Then $x(p_{max})$ is a maximum of $z_1(p)$. If there are interior phenotypic equilibria[20] (i.e., if $u_{22} \leqq \zeta < x(p_{max})$), let p_1^* and p_2^* be the two possible solutions of $\zeta = p^2 u_{11} + 2p(1 - p)_{12} + (1 - p)^2 u_{22}$, and $p_1^* < p_{max} < p_2^*$. From the properties of the functions z_1 and z_2, eqn (15) must have exactly one solution in (p_{max}, p_2^*) (if $\zeta \leqq u_{11}$, then this solution must be in $(p_{max}, 1)$). Furthermore, if $p_1^* \leqq \frac{1}{2}$ (i.e. $\zeta \leqq x(\frac{1}{2})$), then this solution must be the only polymorphic genotypic equilibrium. On the other hand, if $p_1^* > \frac{1}{2}$ (i.e. $\zeta > x(\frac{1}{2})$), there must also exist solutions of eqn (15) in $(\frac{1}{2}, p_1^*)$ when γ is sufficiently large.[21]

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[18] Note that we often denote a polymorhic genotypic equilibria as p in this section as opposed to our more usual notation $\hat{p}$.

[19] p_{max} is the polymorphic genotypic equilibrium of the pure-strategy model which, since $u_{11} \neq u_{22}$, is not a polymorphic genotypic equilibrium of the mixed-strategy model.

[20] In the special case $\zeta = x(p_{max})$, although p_{max} is a solution of eqn (15), according to Definition 1, p_{max} is the interior phenotypic equilibrium and so there is no polymorphic genotypic equilibrium $p > p_{max}$. On the other hand, from the above discussions, when γ is sufficiently large, there must exist solutions of eqn (15) in $(\frac{1}{2}, p_{max})$.

[21] This follows from $z_1(\frac{1}{2}) > z_2(\frac{1}{2})$, $\lim_{p \to p_1^*} z_1 > z_2(p_1^*)$, $\frac{\partial z_1}{\partial \gamma} < 0$, and $\lim_{\gamma \to \infty} z_1 = 1$ for all $p \in (\frac{1}{2}, p_1^*)$.

Now suppose there are no interior phenotypic equilibria. When $\zeta > x(p_{max})$, there must exist solutions of eqn (15) in $(\frac{1}{2}, p_{max})$ since $\gamma > 0$, $z_1(\frac{1}{2}) > z_2(\frac{1}{2})$ and $z_1 < z_2$ for all $p \in [p_{max}, 1]$. When $\zeta \leqq u_{22}$, eqn (15) has only one solution and it must be in $(p_{max}, 1)$ since $\gamma > 0$, $z_1 > z_2$ for all $p \in [\frac{1}{2}, p_{max}]$, $z_1(1) < \lim_{p \to 1} z_2$, $\frac{dz_1}{dp} < 0$ and $\frac{dz_2}{dp} > 0$ for all $p \in (p_{max}, 1)$.

To summarize, when $\gamma > 0$, there is at most one polymorphic genotypic equilibrium in $(p_{max}, 1)$ and this occurs if and only if $\zeta < x(p_{max})$. In addition, there may be other polymorphic genotypic equilibria which must all occur in $(\frac{1}{2}, p_{max})$. When $\zeta > x(p_{max})$, exactly one such equilibrium is guaranteed to occur. When $\zeta \leqq x(\frac{1}{2})$, none occur. Finally, when $x(\frac{1}{2}) < \zeta < x(p_{max})$, there are no such equilibria for low levels of heterogeneity advantage but one or more[22] when γ becomes sufficiently large. For the sake of completeness, let us note that the description of polymorphic genotypic equilibria when $\gamma < 0$ is analogous to this summary except the roles of the intervals $(p_{max}, 1)$ and $(\frac{1}{2}, p_{max})$ are interchanged.

The stability of a polymorphic genotypic equilibrium p is given by the following theorem. In particular, part (a) asserts that no period doubling bifurcations occur at p.

Theorem 3. *Suppose $\hat{p}$ is a polymorphic genotypic equilibrium of the pure-strategy model or of the mixed-strategy model. Then*

(a) $\frac{dp'}{dp}\big|_{p=\hat{p}} > -1$.

(b) *$\hat{p}$ is stable[23] if and only if the effective fitness of allele A_1 is less than that of allele A_2 if the frequency of A_1 is slightly higher than at equilibrium.*

Proof. The proof for the pure-strategy model is given in Sect. 4.1. Assume $\hat{p}$ is a polymorphic genotypic equilibrium of the mixed-strategy model.

(a) From (6) and (7), with $a \equiv u_{12} - u_{11}$ and $b \equiv u_{12} - u_{22}$, we have

$$\frac{dp'}{dp} = 1 + \frac{p(1-p)}{\Phi_1}\left(\frac{d\Phi_1}{dp} - \frac{d\Phi_2}{dp}\right) \tag{16}$$

$$\frac{d\Phi_1}{dp} = -1 + e^{\gamma a(x-\zeta)} + pe^{\gamma a(x-\zeta)}\gamma a \frac{dx}{dp}$$

$$\frac{d\Phi_2}{dp} = 1 - e^{\gamma b(x-\zeta)} + (1-p)e^{\gamma b(x-\zeta)}\gamma b \frac{dx}{dp}.$$

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[22] In fact, it can be shown analytically by the same method used in Example 3 that there are exactly two when γ becomes sufficiently large.

[23] We ignore the degenerate case $\frac{dp'}{dp}\big|_{p=\hat{p}} = 1$ here since this is a fold bifurcation.

Since

$$\frac{d\Phi_1}{dp} - \frac{d\Phi_2}{dp} = -2 + e^{\gamma a(x-\zeta)} + e^{\gamma b(x-\zeta)}$$

$$+ \gamma \frac{dx}{dp}[pae^{\gamma a(x-\zeta)} - (1-p)be^{\gamma b(x-\zeta)}], \quad \frac{dp'}{dp} > -1$$

if and only if $p(1-p)(\frac{d\Phi_1}{dp} - \frac{d\Phi_2}{dp}) > -2\Phi_1$ if and only if

$$0 < 2(1-p)^2 + p(3-p)e^{\gamma a(x-\zeta)} + p(1-p)e^{\gamma b(x-\zeta)}$$

$$+ \gamma p(1-p)\frac{dx}{dp}[pae^{\gamma a(x-\zeta)} - (1-p)be^{\gamma b(x-\zeta)}].$$

Since $z_1 = z_2$ at p,

$$pae^{\gamma a(x-\zeta)} - (1-p)be^{\gamma b(x-\zeta)}$$

$$= (1-p)ae^{\gamma a(x-\zeta)}\left[\frac{p}{1-p} - \frac{be^{\gamma b(x-\zeta)}}{ae^{\gamma a(x-\zeta)}}\right]$$

$$= (1-p)ae^{\gamma a(x-\zeta)}\left[\frac{1 - e^{\gamma b(x-\zeta)}}{1 - e^{\gamma a(x-\zeta)}} - \frac{be^{\gamma b(x-\zeta)}}{ae^{\gamma a(x-\zeta)}}\right].$$

Since for all $x \neq \zeta$, we have

$$(b-a)e^{\gamma(a+b)(x-\zeta)} - be^{\gamma b(x-\zeta)} + ae^{\gamma a(x-\zeta)} > 0,$$

$\frac{1 - e^{\gamma b(x-\zeta)}}{1 - e^{\gamma a(x-\zeta)}} - \frac{be^{\gamma b(x-\zeta)}}{ae^{\gamma a(x-\zeta)}} < 0$ and $\gamma(x-\zeta) > 0$ have opposite sign. Thus, at any polymorphic genotypic equilibria, we have

$$\gamma \frac{dx}{dp}[pae^{\gamma a(x-\zeta)} - (1-p)be^{\gamma b(x-\zeta)}] > 0.$$

and so $\frac{dp'}{dp}|_{p=\hat{p}} > -1$.

(b) By part (a), and (16), $|\frac{dp'}{dp}|_{p=\hat{p}}| < 1$ if and only if $\frac{d\Phi_1}{dp} - \frac{d\Phi_2}{dp} < 0$. The result follows from the fact $\Phi_1 < \Phi_2$ if and only if the effective fitness of allele A_1 is less than that of allele A_2. It is interesting to note that any $\hat{p} \in (p_{max}, 1)$ is unstable if $\gamma > 0$ and that any $\hat{p} \in (\frac{1}{2}, p_{max})$ is stable if $\gamma < 0$. □

**Example 3.** *Let $u_{11} = \frac{1}{2}, u_{12} = 1$ and $u_{22} = 0$. Then*

$$x = \frac{1}{2}p^2 + 2p(1-p) \quad and \quad \frac{dx}{dp} = 0 \quad when \ p = \frac{2}{3}.$$

For interior phenotypic equilibria, we solve $\zeta = \frac{1}{2}p^2 + 2p(1-p)$ *for p.
Thus,* $p^*_{1,2} = \frac{2 \mp \sqrt{4 - 6\zeta}}{3}$ *whenever these solutions are frequencies between
0 and 1. It is straightforward to classify the following cases.*

(1) $p^*_1 \in (0, \frac{2}{3})$ *if and only if* $\zeta \in (0, \frac{2}{3})$.
(2) $p^*_2 \in (\frac{2}{3}, 1)$ *if and only if* $\zeta \in (\frac{1}{2}, \frac{2}{3})$.
(3) $p^*_1 = p^*_2 = \frac{2}{3}$ *if and only if* $\zeta = \frac{2}{3}$.
(4) *If* $\zeta \notin (0, \frac{2}{3})$, *then there are no interior phenotypic equilibria.*

*Finally, from Theorem 1b, when interior phenotypic equilibria exist, there
is a* $\gamma_{cr} > 0$ *such that the interior phenotypic equilibria are stable if and
only if* $0 < \gamma < \gamma_{cr}$.

*For the pure-strategy model, there is a polymorphic genotypic equilib-
rium at* $\hat{p} = \frac{2}{3}$ *except in the degenerate case that* $\zeta = \frac{2}{3}$. *From Sect. 4.1,
$\hat{p} = \frac{2}{3}$ is stable if and only if* $\gamma(\frac{2}{3} - \zeta) < 0$ *since* $x(\hat{p}) = \frac{2}{3}$.
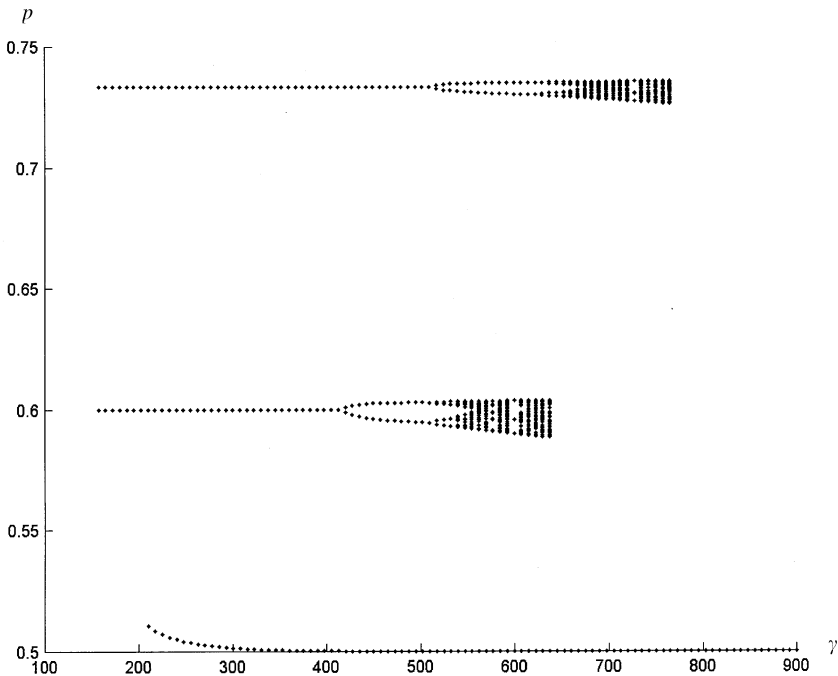
Fig. 6. The bifurcation diagram for Example 3 when $150 < \gamma < 900$ for the mixed-
strategy model with $\zeta \simeq 0.66$. For certain values of γ (say $200 < \gamma < 420$), stable
interior phenotypic equilibria coexist with a stable polymorphic genotypic equilib-
rium. As γ increases further, the complex dynamic behavior near the interior
phenotypic equilibria disappears (at $\gamma \simeq 640$ for p^*_1 and $\gamma \simeq 770$ for p^*_2) and almost all
interior trajectories approach $\hat{p}_3 \simeq 0.5$.

The mixed-strategy model has the same phenotypic equilibria and stability properties. The difference is in the polymorphic genotypic equilibria. From above, $p_{\max} = \frac{2}{3}$ and $x(p_{\max}) = \frac{2}{3}$. Let us assume $\gamma > 0$.

If $\zeta \in (0, \frac{2}{3})$, then there is one polymorphic genotypic equilibrium satisfying $\hat{p}_1 > \frac{2}{3}$ which must be unstable since $(\Phi_1(p) - \Phi_2(p))\gamma(p - \hat{p}_1) \geqq 0$ for all $p \in (\frac{2}{3}, p_2^*)$ with equality only at $p = \hat{p}_1$. This is the only
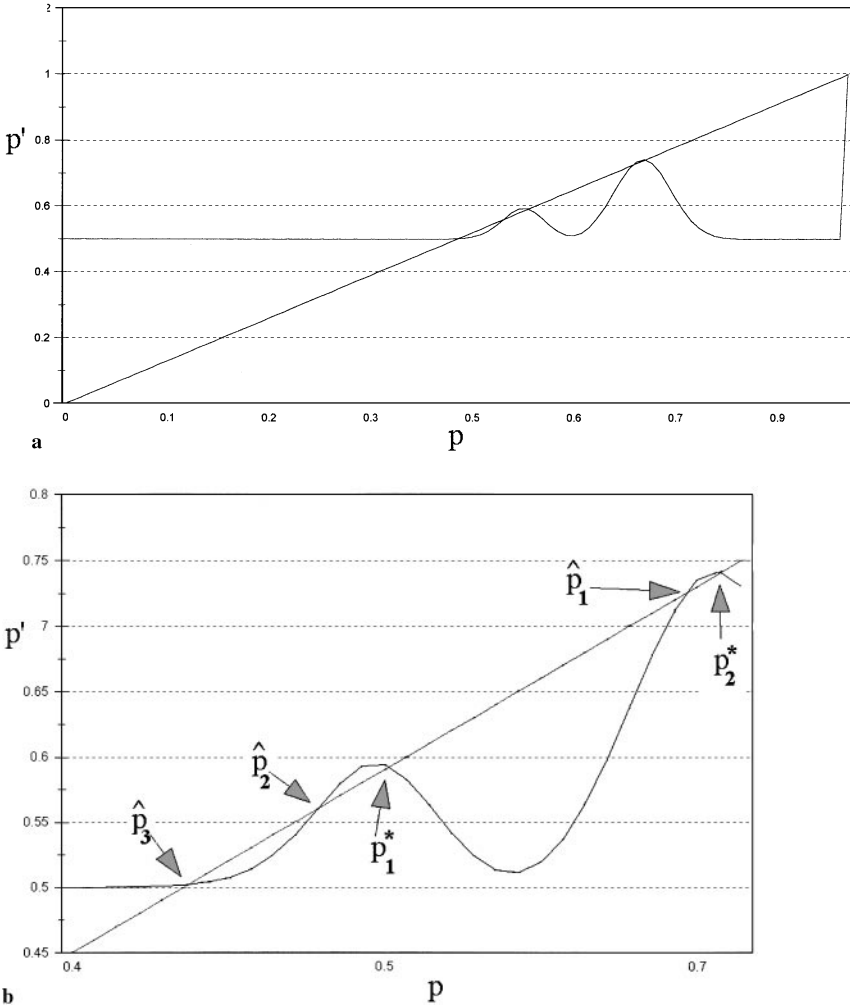
Fig. 7a, b. The graph of p' versus p for $\gamma = 300$ in the mixed-strategy model of Example 3. The two interior phenotypic equilibria p_1^* and p_2^* and the three polymorphic genotypic equilibria $\hat{p}_1, \hat{p}_2, \hat{p}_3$ are ordered $\frac{1}{2} < \hat{p}_3 < \hat{p}_2 < p_1^* < \frac{2}{3} < \hat{p}_1 < p_2^* < 1$. Both p_1^* and p_2^* are stable but have small basins of attraction. On the other hand, the other stable equilibrium, $\hat{p}_3$, has a large basin of attraction including the entire interval $(0, \hat{p}_2)$. **b** enlarges the critical region around these five equilibria.

polymorphic genotypic equilibrium if $p_1^* \in (0, 1/2]$ or if γ is sufficiently small. On the other hand, if $p_1^* \in (\frac{1}{2}, \frac{2}{3})$ and γ is sufficiently large, then there are exactly two polymorphic genotypic equilibria satisfying $\frac{1}{2} < \hat{p}_3 < \hat{p}_2 < p_1^* < \frac{2}{3}$. To see this, note that, with our choices of u_{ij}, $\Phi_1 = (1 - p) + p \exp\{\frac{\gamma}{2}(x - \zeta)\}$ and $\Phi_2 = p + (1 - p) \exp\{\gamma(x - \zeta)\}$ and this implies $z_1 = 1 + \exp\{\frac{\gamma}{2}(x - \zeta)\}$. Moreover, $\hat{p}_3$ is stable and $\hat{p}_2$ is unstable since $(\Phi_1(p) - \Phi_2(p))\gamma(p - \hat{p}_3)(p - \hat{p}_2) \geqq 0$ for $p \in (\frac{1}{2}, \frac{2}{3})$. Since $p = \frac{z_1}{1 + z_1}$ at a polymorphic genotypic equilibrium and $\frac{z_1}{1 + z_1}$ as a function of p changes concavity at most once for $p \in (\frac{1}{2}, p_1^*)$, the result follows.

5. Conclusion

As stated in the Introduction, the main purpose of this paper is to compare our two models of nonlinear frequency-dependent selection to results for linear fitness models when the population has two phenotypes. There is also a substantial literature on linear frequency-dependent selection at a single two-allele locus when there are three phenotypes that begins in the early 1970's (e.g. Cockerham et al., 1972) before the advent of evolutionary game theory. In these latter models, the frequency-dependent viability of genotype $A_i A_j$ can be written in matrix form as

$$\begin{bmatrix} F_{A_1 A_1}(p) \\ F_{A_1 A_2}(p) \\ F_{A_2 A_2}(p) \end{bmatrix} = \begin{bmatrix} W_{11} & W_{12} & W_{13} \\ W_{21} & W_{22} & W_{23} \\ W_{31} & W_{32} & W_{33} \end{bmatrix} \begin{bmatrix} p^2 \\ 2p(1 - p) \\ (1 - p)^2 \end{bmatrix}$$

and so genotypic fitness is a linear function of genotypic population frequencies. This is equivalent to (2) where the 2×2 payoff matrix there is replaced by the 3×3 matrix W (for three pure strategies) that has entries W_{kl}. Also, in this model, each individual with genotype $A_i A_j$ uses its corresponding pure strategy (e.g. all $A_1 A_1$ individuals use the first pure strategy). The connection with evolutionary game theory (specifically, with the ESS structure of W) has been largely ignored in this literature.

The most interesting aspect for our purposes is that these three phenotype linear fitness models display qualitatively the same type of dynamic behavior as our two phenotype exponential fitness models (e.g. Altenberg, 1991; Gavrilets and Hastings, 1995). Thus, ESS theory predicts the stability of frequency-dependent models only for two phenotype linear fitness functions where Lessard (1984) emphasized that the evolutionary attractive states are either ESS's (corresponding to stable phenotypic equilibria) of the matrix game or else extrema of

the population mean strategy that are locally as close as possible to the ESS (corresponding to stable genotypic equilibria). However, we have seen that these ESS and extremum criteria are also important for our two phenotype exponential fitness models – especially for boundary phenotypic equilibria and monomorphic genotypic equilibria. Although stability at interior phenotypic equilibria is not determined exclusively by ESS conditions, the stability at such equilibria is the same for both our models.

In contrast, Sect. 4 shows our models are substantially different when there are polymorphic genotypic equilibria. The pure-strategy model can have at most one such equilibrium which again must be an extremum of the population mean strategy. In particular, a stable interior phenotypic equilibrium and stable polymorphic genotypic equilibrium cannot coexist in the same pure-strategy example. On the other hand, multiple polymorphic genotypic equilibria can exist in the mixed-strategy model, some of which can be stable at the same time as a stable interior phenotypic equilibrium exists. These various possibilities are illustrated in Example 3 at the end of Sect. 4.

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