Mathematical Biology

Mathieu Lemire · Sabin Lessard

Equilibrium structure and stability in a frequency-dependent, two-population diploid model

Abstract. We investigate the equilibrium structure for an evolutionary genetic model in discrete time involving two monoecious populations subject to intraspecific and interspecific random pairwise interactions. A characterization for local stability of an equilibrium is found, related to the proximity of this equilibrium with evolutionarily stable strategies (ESS). This extends to a multi-population framework a principle initially proposed for single populations, which states that the mean population strategy at a locally stable equilibrium is as close as possible to an ESS.

1. Introduction

Within the framework of single populations undergoing frequency-dependent selection, a great amount of work have been done introducing Mendelian inheritance and dynamical properties to the static concept of an evolutionarily stable strategy (ESS), an optimality principle based on phenotypic fitness differences.

For instance, for a variety of locally adaptive models, where two alternative strategies are available to players, Eshel (1982) has shown that a stable allelic equilibrium corresponds to a fixation state or to a mixed strategy which is an ESS of a restricted game (restricted to the attainable set of mean strategies, or *ASMS* [Hines, 1984; Cressman, 1988], imposed by genetic considerations). Moreover, for diploid populations, Lessard (1984) has shown global convergence, over successive equilibria following the introduction of mutant alleles if necessary, to an equilibrium point corresponding to an ESS at least in the case of linear fitnesses, therefore excluding the possibilities of periodic solutions or chaos. However, relaxing the assumption of linear fitnesses, Tao et al. (1999) considered fitnesses in an exponential form, and found examples of chaotic behavior. Nevertheless, Lessard's (1984) result can be viewed as precursory for what is now called the long-term theory of evolution (Weissing, 1996; Hammerstein, 1996; Eshel, 1996) where the emphasis

M. Lemire, S. Lessard: Département de Mathématiques et de Statistique, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec, Canada H3C 3J7. e-mail: `lessards@dms.umontreal.ca`

is on a "final stop" for the process of evolution, an equilibrium which is immune, ideally at least, to the invasion of *any* conceivable mutant allele, enlightening the distinct roles of internal and external stability.

A definition of a two-population ESS has been proposed by Cressman (1992, 1996), motivated by the necessity of an evolutionary principle for two-population dynamical model, that would extend the ESS concept for single populations (Maynard Smith and Price, 1973; Maynard Smith, 1974; Vickers and Cannings, 1987; see also Hines, 1987; Lessard, 1990). It is through Roughgarden's (1979) coevolution model, that combines evolution in gene frequencies with population growth, that the extension has been developed.

Suppose that two populations, say $\mathscr{P}_1$ and $\mathscr{P}_2$, are subject to intraspecific and interspecific random pairwise interactions. Every individual can choose either one of two pure strategies, or a mixture of both, with probabilities represented by $(x, 1 - x)$, a strategy vector for an individual in $\mathscr{P}_1$, or $(y, 1 - y)$, a strategy vector for an individual in $\mathscr{P}_2$. Denote by (x, y) the mean strategy used in both populations.

Let $\phi_i(x, y)$ and $\psi_i(x, y)$ be the expected fitnesses of individuals in $\mathscr{P}_1$ and $\mathscr{P}_2$, respectively, using the pure strategy i $(i = 1, 2)$. Then a two-population ESS has been defined (Cressman (1992, 1996); reworded in the two-phenotype context used hereafter) as a strategy vector (x^*, y^*) for which we have

$$x^*\phi_1(x, y) + (1 - x^*)\phi_2(x, y) > x\phi_1(x, y) + (1 - x)\phi_2(x, y)$$

or

$$y^*\psi_1(x, y) + (1 - y^*)\psi_2(x, y) > y\psi_1(x, y) + (1 - y)\psi_2(x, y), \qquad (1)$$

for any other strategy vector (x, y) at least close enough to (x^*, y^*). This definition could provide an extension to the well documented models for *Hawk* and *Dove* behaviors with asymmetries in payoff functions (Maynard Smith and Parker, 1976; Selten, 1980; Eshel and Sansone, 1995; Crowley, 2000, and references therein). In a pairwise contest and with probability x (respectively y), an individual from $\mathscr{P}_1$ (respectively $\mathscr{P}_2$) would behave accordingly to what has been defined as a *Hawk* behavior, that is with an escalation of aggressiveness until injury or else the opponent retreats. With complementary probability $1 - x$ (respectively $1 - y$), that individual behaves as a *Dove* during the contest, and only displays without getting involved in an aggressive fight over the fitness-related coveted ressource.

The local stability of an interior equilibrium corresponding to a two-population ESS has been further analyzed in continuous time by Tao (1998), when two pure strategies (phenotypes) are available and the mixed strategy used by any player is genetically determined at a single locus where two alleles are segregating.

In this paper, we consider the corresponding model in discrete time, and we propose a characterization of a locally stable equilibrium, through an analysis of the whole equilibrium structure of the dynamics involved.

2. Dynamical equations

Two populations, $\mathscr{P}_1$ and $\mathscr{P}_2$, are subject to intraspecific and interspecific random pairwise interactions. We suppose the sizes of both populations infinite, but in equal

proportion, although a different ratio could be used; such a ratio would only change the elements of the fitness matrices below. Introducing genetics, we suppose that the mixed strategy adopted by an individual is determined at a single locus where two alleles, A_1 and A_2, are segregating. For convenience, we use the same notation for the alleles in both populations, although these are not necessarily the same. Mating is only allowed within each population.

The mixed strategy associated with the genotype $A_i A_j$ for an individual in $\mathscr{P}_1$ is entirely described by the probability P_{ij}. This is the probability for the individual to choose the pure strategy 1, or, say, Hawk. The individual chooses the pure strategy 2, Dove, with the complementary probability $1 - P_{ij}$. Similarly, the mixed strategy of an individual in $\mathscr{P}_2$ with genotype $A_i A_j$ is described by the probability Q_{ij}, the probability of adopting the Hawk bahavior, $1 - Q_{ij}$ being the probability of adopting the Dove behavior.

If we let p and q represent the frequency of allele A_1 in $\mathscr{P}_1$ and $\mathscr{P}_2$, respectively, and if we assume discrete, nonoverlapping generations with random mating within each population, then the mean population strategies in $\mathscr{P}_1$ and $\mathscr{P}_2$, respectively, are

$$
\begin{aligned}
x &= x(p) = p^2 P_{11} + 2p(1-p)P_{12} + (1-p)^2 P_{22}, \\
y &= y(q) = q^2 Q_{11} + 2q(1-q)Q_{12} + (1-q)^2 Q_{22}.
\end{aligned}
$$

These are the frequencies of Hawk in $\mathscr{P}_1$ and $\mathscr{P}_2$, respectively.

The fitness of an individual will depend on its own strategy and on the strategy of the individual interacting with it. Thus it depends on the state of the system at any time. Given pairwise interactions between individuals of two populations, $\mathscr{P}_1$ and $\mathscr{P}_2$, each individual can interact either with an individual from the same population or with an individual from the other population. We denote by a_{ij} the expected fitness of a $\mathscr{P}_1$-individual using the pure strategy i when interacting with a $\mathscr{P}_1$-individual using the pure strategy j. We denote by b_{ij}, c_{ij} and d_{ij} the corresponding fitnesses, when the interacting individuals are from the populations $\mathscr{P}_1$ versus $\mathscr{P}_2$, $\mathscr{P}_2$ versus $\mathscr{P}_1$, and $\mathscr{P}_2$ versus $\mathscr{P}_2$, respectively. With two pure strategies, Hawk and Dove, we have the fitness matrices

$$
F_{11} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \qquad F_{12} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix},
$$

$$
F_{21} = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}, \qquad F_{22} = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}.
$$

Let ϕ_i and ψ_i be the expected fitnesses of the individuals in populations $\mathscr{P}_1$ and $\mathscr{P}_2$, respectively, using the pure strategy i. The populations being in equal proportion and pairwise interactions being random, we have

$$
\phi_i = \phi_i(x, y) = [x a_{i1} + (1-x)a_{i2} + y b_{i1} + (1-y)b_{i2}]/2,
$$

and

$$
\psi_i = \psi_i(x, y) = [x c_{i1} + (1-x)c_{i2} + y d_{i1} + (1-y)d_{i2}]/2.
$$

The fitness of a $\mathscr{P}_1$-individual having genotype $A_i A_j$ is

$$v_{ij} = P_{ij}\phi_1 + (1 - P_{ij})\phi_2,$$

and the corresponding fitness for a $\mathscr{P}_2$-individual is

$$w_{ij} = Q_{ij}\psi_1 + (1 - Q_{ij})\psi_2.$$

With these fitnesses, the recurrence equations for the frequency of A_1 in $\mathscr{P}_1$ and $\mathscr{P}_2$ from one generation to the next are respectively

$$p' = \frac{p^2 v_{11} + p(1 - p)v_{12}}{\bar{v}},$$

$$q' = \frac{q^2 w_{11} + q(1 - q)w_{12}}{\bar{w}},$$

where

$$\begin{aligned}
\bar{v} &= p^2 v_{11} + 2p(1 - p)v_{12} + (1 - p)^2 v_{22} \\
&= x\phi_1 + (1 - x)\phi_2, \\
\bar{w} &= q^2 w_{11} + 2q(1 - q)w_{12} + (1 - q)^2 w_{22} \\
&= y\psi_1 + (1 - y)\psi_2.
\end{aligned}$$

Let

$$\begin{aligned}
\mu_1 &= pP_{11} + (1 - p)P_{12}, \\
\mu_2 &= pP_{12} + (1 - p)P_{22},
\end{aligned}$$

be the marginal strategies of alleles A_1 and A_2, respectively, in $\mathscr{P}_1$ and

$$\begin{aligned}
\nu_1 &= qQ_{11} + (1 - q)Q_{12}, \\
\nu_2 &= qQ_{12} + (1 - q)Q_{22},
\end{aligned}$$

be the corresponding marginal strategies in $\mathscr{P}_2$. Then we have

$$\begin{aligned}
p' - p &= p(1 - p)(\mu_1 - \mu_2)(\phi_1 - \phi_2)/\bar{v}, \\
q' - q &= q(1 - q)(\nu_1 - \nu_2)(\psi_1 - \psi_2)/\bar{w}.
\end{aligned} \tag{2}$$

The differences $\phi_1 - \phi_2$ and $\psi_1 - \psi_2$ can be expressed as

$$\begin{aligned}
\phi_1 - \phi_2 &= \alpha_{11}x + \alpha_{12}y - \beta_1, \\
\psi_1 - \psi_2 &= \alpha_{21}x + \alpha_{22}y - \beta_2,
\end{aligned}$$

where the parameters are defined as

$$\begin{aligned}
\alpha_{11} &= (a_{11} - a_{12} - a_{21} + a_{22})/2, \\
\alpha_{12} &= (b_{11} - b_{12} - b_{21} + b_{22})/2, \\
\alpha_{21} &= (c_{11} - c_{12} - c_{21} + c_{22})/2, \\
\alpha_{22} &= (d_{11} - d_{12} - d_{21} + d_{22})/2, \\
\beta_1 &= (a_{22} - a_{12} + b_{22} - b_{12})/2, \\
\beta_2 &= (c_{22} - c_{12} + d_{22} - d_{12})/2.
\end{aligned}$$

In the next generation, x' can be expressed as

$$x' = (p' - p)^2 (P_{11} - 2P_{12} + P_{22}) + 2(p' - p)(\mu_1 - \mu_2) + x,$$

so that, using (2), we have

$$x' - x = \frac{p(1 - p)(\mu_1 - \mu_2)^2 (\phi_1 - \phi_2)}{\bar{v}}$$
$$\times \left\{ 2 + \frac{p(1 - p)(P_{11} - 2P_{12} + P_{22})(\phi_1 - \phi_2)}{\bar{v}} \right\},$$

and a similar equation for the difference $y' - y$. The expression in brackets being positive (see Appendix), the direction taken by the mean population strategy x solely depends on the sign of $\phi_1 - \phi_2$. On the other hand, the direction taken by y only depends on the difference $\psi_1 - \psi_2$. Thus we are in the presence of a *locally adaptive* model (Eshel, 1982).

For a given strategy y in population $\mathscr{P}_2$, let $\Gamma_\phi(y)$ be the strategy in population $\mathscr{P}_1$ for which both pure strategies have equal fitnesses ($\phi_1 = \phi_2$). We have

$$\Gamma_\phi(y) = \frac{-\alpha_{12}y + \beta_1}{\alpha_{11}}.$$

Similarly, for a given strategy x in population $\mathscr{P}_1$, we denote by $\Gamma_\psi(x)$ the strategy in population $\mathscr{P}_2$ for which we have $\psi_1 = \psi_2$. We get

$$\Gamma_\psi(x) = \frac{-\alpha_{21}x + \beta_2}{\alpha_{22}}.$$

We will simply refer to the lines Γ_ϕ and Γ_ψ to represent the regions in the strategy space where $\phi_1 = \phi_2$ and $\psi_1 = \psi_2$, respectively.

Throughout this paper, to avoid degenerate situations, we assume that all the α_{ij} are different from 0, all the P_{ij} distinct, and all the Q_{ij} distinct.

3. Equilibrium points

An equilibrium for the system (2) satisfies either

$$p = 0 \text{ or } 1, \text{ or } \mu_1 = \mu_2, \text{ or } \phi_1 = \phi_2,$$

and either

$$q = 0 \text{ or } 1, \text{ or } \nu_1 = \nu_2, \text{ or } \psi_1 = \psi_2$$

(see Table 1). When $p = 0$ or 1, we have *fixation* in the $\mathscr{P}_1$-population, and similarly, when $q = 0$ or 1, fixation in the $\mathscr{P}_2$-population. When we have both, we have *double fixation* in the two populations.

When $\mu_1 = \mu_2$, the marginal allelic strategies are the same in $\mathscr{P}_1$ and then the equilibrium is said to be a *genetic equilibrium* with respect to the $\mathscr{P}_1$-population. This occurs when $p = \hat{p}$ in (0, 1), where

$$\hat{p} = \frac{P_{22} - P_{12}}{P_{11} - 2P_{12} + P_{22}}$$

Table 1. List of all possible equilibria.

		Genotypic		Phenotypic
		$p = 0, p = 1$	$p = \hat{p}$	$\phi_1 - \phi_2 = 0$
Geno-typic	$q = 0,$ $q = 1$	Double fixation $(0, 0), (0, 1)$ $(1, 0), (1, 1)$	Singly-Genetic $(\hat{p}, 0), (\hat{p}, 1)$	Singly-Phenotypic $(\bar{p}, 0), (\bar{p}, 1)$
	$q = \hat{q}$	Singly-Genetic $(0, \hat{q}), (1, \hat{q})$	Doubly-Genetic $(\hat{p}, \hat{q})$	Genetic-Phenotypic $(\bar{p}, \hat{q})$
Pheno-typic	$\psi_1 - \psi_2 = 0$	Singly-Phenotypic $(0, \bar{q}), (1, \bar{q})$	Genetic-Phenotypic $(\hat{p}, \bar{q})$	Doubly-Phenotypic (p^*, q^*)

(when $P_{11} - 2P_{12} + P_{22} \neq 0$). Such a $\hat{p}$ corresponds to a minimum or maximum point for the parabola $x = x(p)$ in $(0, 1)$. Note that $\hat{p}$ is in $(0, 1)$ only when we are in the presence of *overdominance* or *underdominance* (that is, when P_{12} is higher or lower, respectively, than both P_{11} and P_{22}). Similarly, we have a genetic equilibrium with respect to the $\mathscr{P}_2$-population when $\nu_1 = \nu_2$, that is, when $q = \hat{q}$ in $(0, 1)$, where

$$\hat{q} = \frac{Q_{22} - Q_{12}}{Q_{11} - 2Q_{12} + Q_{22}},$$

(when $Q_{11} - 2Q_{12} + Q_{22} \neq 0$). Such a $\hat{q}$ corresponds to a minimum or a maximum point for the parabola $y = y(q)$ in $(0, 1)$, and exists only when there is overdominance or underdominance.

A fixation state or a genetic equilibrium is said to be a *genotypic equilibrium*, since the genotypic frequencies at those equilibria do not change regardless of any phenotypic selection that might be taking place (Lessard, 1984).

On the other hand, when $\phi_1 = \phi_2$ or $\psi_1 = \psi_2$, the expected fitnesses of the two pure strategies are the same in $\mathscr{P}_1$ or $\mathscr{P}_2$, respectively, and then the equilibrium is said to be a *phenotypic equilibrium* with respect to $\mathscr{P}_1$ or $\mathscr{P}_2$, respectively.

In order to avoid unnecessary complication in the notation, we simply denote by $\bar{p}$, the allelic frequency value in $\mathscr{P}_1$ for which we have $\phi_1 = \phi_2$, regardless of the allelic frequency in $\mathscr{P}_2$ ($\bar{p}$ is actually a function of the allelic frequency in $\mathscr{P}_2$, but the notation used should not cause any confusion). Similarly, $\bar{q}$ is the allelic frequency in $\mathscr{P}_2$ for which we have $\psi_1 = \psi_2$.

An equilibrium is said to be a *singly-genetic equilibrium* or a *singly-phenotypic equilibrium* if it is genetic or phenotypic, respectively, with respect to one population while there is fixation in the other. It is said to be a *doubly-genetic equilibrium* or a *doubly-phenotypic equilibrium* if it is genetic or phenotypic, respectively, with respect to both populations. Finally it is said to be a *genetic-phenotypic equilibrium* if it is genetic with respect to one population and phenotypic with respect to the other.

In the pq-plane, the regions bounded by the lines $p = \hat{p}$ and $q = \hat{q}$, if they exist, along with the lines corresponding to the fixation states, are invariant with respect to the dynamics (2), since a trajectory starting in any one of these regions

always remains in it. Indeed, we have

$$
\begin{aligned}
\bar{v}(p' - \hat{p}) &= p(1 - p)(\mu_1 - \mu_2)(\phi_1 - \phi_2) + \bar{v}(p - \hat{p}) \\
&= (p - \hat{p})\{p(1 - p)(P_{11} - 2P_{12} + P_{22})(\phi_1 - \phi_2) + \bar{v}\} \\
&= (p - \hat{p})\{[p(1 - p)(P_{11} - 2P_{12} + P_{22}) + x](\phi_1 - \phi_2) + \phi_2\} \\
&= (p - \hat{p})\{[pP_{11} + (1 - p)P_{12}](\phi_1 - \phi_2) + \phi_2\}.
\end{aligned}
$$

Since the expression in brackets is always positive, the sign of $p' - \hat{p}$ is the same as the sign of $p - \hat{p}$. Therefore, we have up to four invariant regions in the pq-plane.

An equivalent notation ($\hat{x}$, $\hat{y}$, $\bar{x}$, $\bar{y}$, x^* and y^*) is used to represent the strategies used in each population when the frequencies are at genetic or phenotypic equilibria.

To avoid degenerate situations, we suppose that an equilibrium cannot be of two types. It is an equilibrium due to either equality in the expected strategy fitnesses or equality in the marginal allelic strategies or fixation, in both populations. Otherwise, the local stability analysis done by linearizing the transformation given in (2) fails since then the Jacobian matrix of the transformation exhibits an eigenvalue of modulus 1. A finer criterion, using a second order approximation, would thus be needed. We refer to Lessard and Karlin (1982), along with Morris et al. (1987), for such a criterion and its applications.

4. Existence of a two-population ESS

Rewriting definition (1), an equivalent condition for a point (x^*, y^*) to be a two-population ESS is that, for any other point (x, y) at least sufficiently close to it, we have either

$$
(x - x^*)(\phi_1 - \phi_2) < 0
$$

or

$$
(y - y^*)(\psi_1 - \psi_2) < 0. \tag{3}
$$

Let (x^*, y^*) be an *interior* point of the xy-plane (actually, of the $[0, 1] \times [0, 1]$ square). To be a two-population ESS, (x^*, y^*) must lie at the intersection of the lines Γ_ϕ and Γ_ψ. Solving, we get the values

$$
\begin{aligned}
x^* &= \frac{\alpha_{22}\beta_1 - \alpha_{12}\beta_2}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}, \\
y^* &= \frac{\alpha_{11}\beta_2 - \alpha_{21}\beta_1}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}.
\end{aligned}
$$

Using these values, we have

$$
\begin{aligned}
\phi_1 - \phi_2 &= \alpha_{11}(x - x^*) + \alpha_{12}(y - y^*), \\
\psi_1 - \psi_2 &= \alpha_{21}(x - x^*) + \alpha_{22}(y - y^*).
\end{aligned}
$$

Letting $s = x - x^*$ and $t = y - y^*$, condition (3) becomes

$$
s(\alpha_{11}s + \alpha_{12}t) < 0
$$

or

$$t(\alpha_{21}s + \alpha_{22}t) < 0,$$

for (s, t) at least sufficiently close but unequal to $(0, 0)$ (actually, for *all* $(s, t) \neq (0, 0)$, since the game is linear). As pointed out by Tao (1998), referring to Hofbauer and Sigmund (1988), at least one of the two inequalities is satisfied if and only if the matrix

$$-\begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix}$$

is a P-matrix, that is, if and only if it satisfies

$$\begin{aligned} \alpha_{11} &< 0, \\ \alpha_{22} &< 0, \\ \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} &> 0. \end{aligned} \tag{4}$$

In the classical Hawk-Dove model with asymmetries in payoffs, commonly labelled as Owner-Intruder conflicts, or more generally in the classes of bimatrix games (see, e.g., Hofbauer and Sigmund, 1988), both matrices F_{11} and F_{22} are the zero matrices, and then $\alpha_{11} = \alpha_{22} = 0$. Thus, no mixed (interior) strategy vector can be evolutionarily stable. Such a result is true for all bimatrix games (Selten, 1980).

Figure 1 shows the four possibilities for the lines Γ_ϕ and Γ_ψ, based on the conditions above, along with the signs of $\phi_1(x, y) - \phi_2(x, y)$ and $\psi_1(x, y) - \psi_2(x, y)$ in each region. Please note that Figure 1 is only an illustration of the possible slopes of Γ_ϕ and Γ_ψ : either their slopes are of different signs, or else the slope of Γ_ϕ is greater than the slope of Γ_ψ in absolute value. Since both α_{11} and α_{22} are nonzero, these slopes are neither null nor undetermined. Since $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}$ is different from 0, the lines Γ_ϕ and Γ_ψ are never parallel.

In the remaining of this paper, we assume the existence of an interior two-population ESS; the lines Γ_ϕ and Γ_ψ do have an intersection in the interior of the xy-plane, and conditions (4) are satisfied. Note however that the results in section 6 remain true even when an interior ESS does not exist but conditions (4) are satisfied.

Let the mean strategy used in $\mathscr{P}_2$ be fixed at some value $\tilde{y}$, and let the mean strategy used in $\mathscr{P}_1$ be $\Gamma_\phi(\tilde{y})$, the corresponding point on the line Γ_ϕ. Since (see Figure 1) $\phi_1(x, \tilde{y}) - \phi_2(x, \tilde{y}) > 0$ when $x < \Gamma_\phi(\tilde{y})$, and $\phi_1(x, \tilde{y}) - \phi_2(x, \tilde{y}) < 0$ when $x > \Gamma_\phi(\tilde{y})$, we have

$$[x - \Gamma_\phi(\tilde{y})][\phi_1(x, \tilde{y}) - \phi_2(x, \tilde{y})] < 0,$$

or equivalently

$$\Gamma_\phi(\tilde{y})\phi_1(x, \tilde{y}) + [1 - \Gamma_\phi(\tilde{y})]\phi_2(x, \tilde{y}) > x\phi_1(x, \tilde{y}) + [1 - x]\phi_2(x, \tilde{y}).$$

This indicates that the fitness of an individual in $\mathscr{P}_1$ playing $\Gamma_\phi(\tilde{y})$ is greater than the fitness of an individual in $\mathscr{P}_1$ playing any other strategy x when the population is at $(x, \tilde{y})$. We can then interpret $\Gamma_\phi(\tilde{y})$ as an ESS in $\mathscr{P}_1$ when the mean strategy used in $\mathscr{P}_2$ is fixed at $\tilde{y}$. Similarly, $\Gamma_\psi(\tilde{x})$ is an ESS in $\mathscr{P}_2$ when the mean strategy used in $\mathscr{P}_1$ is fixed at $\tilde{x}$.
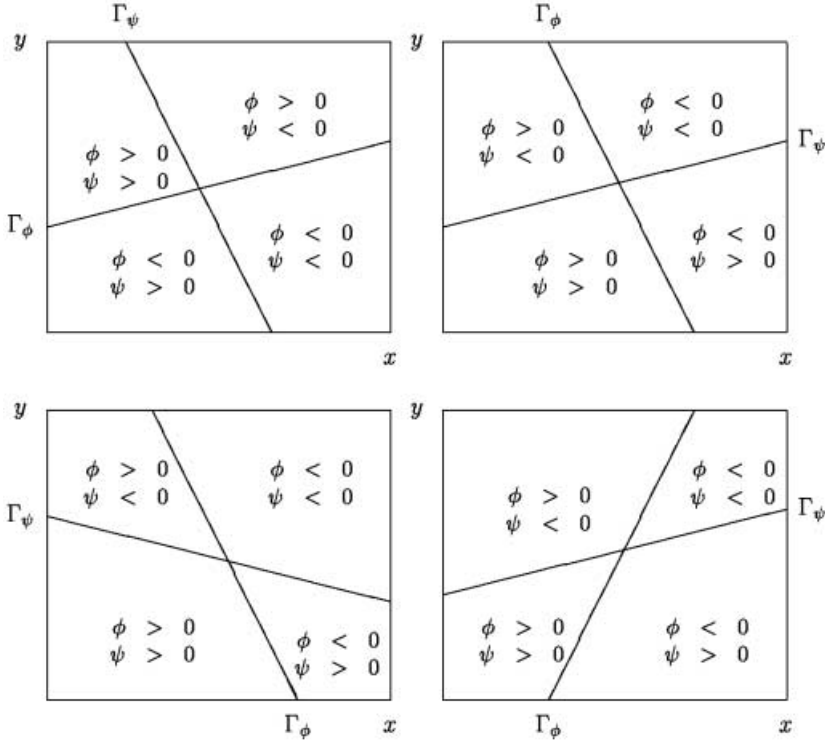
Fig. 1. The four possibilities for the lines Γ_ϕ and Γ_ψ, as imposed by conditions (4), along with the signs of $\phi = \phi_1 - \phi_2$ and $\psi = \psi_1 - \psi_2$.

5. Local stability of the ESS

Let (p^*, q^*) be a doubly-phenotypic equilibrium, for which the corresponding strategy vector (x^*, y^*) is a two-population ESS.

We investigate the local stability of this equilibrium using a first order approximation of the recurrence equations (2). The Jacobian matrix is given by

$$\left. \begin{pmatrix} \dfrac{\partial p'}{\partial p} & \dfrac{\partial p'}{\partial q} \\[2ex] \dfrac{\partial q'}{\partial p} & \dfrac{\partial q'}{\partial q} \end{pmatrix} \right|_{(p^*, q^*)},$$

where (omitting the superscript *)

$$\left. \frac{\partial p'}{\partial p} \right|_{(p^*, q^*)} = 1 + \frac{2p(1-p)(\mu_1 - \mu_2)^2}{\bar{v}} \alpha_{11},$$

$$\left. \frac{\partial p'}{\partial q} \right|_{(p^*, q^*)} = \frac{2p(1-p)(\mu_1 - \mu_2)(\nu_1 - \nu_2)}{\bar{v}} \alpha_{12},$$

$$\frac{\partial q'}{\partial p}\bigg|_{(p^*,q^*)} = \frac{2q(1-q)(\mu_1-\mu_2)(\nu_1-\nu_2)}{\bar{w}}\alpha_{21},$$

$$\frac{\partial q'}{\partial q}\bigg|_{(p^*,q^*)} = 1 + \frac{2q(1-q)(\nu_1-\nu_2)^2}{\bar{w}}\alpha_{22}.$$

This matrix admits the two eigenvalues

$$\lambda^{\pm} = 1 + B \pm \sqrt{A},$$

where

$$A = B^2 - 4C,$$
$$B = \frac{p(1-p)(\mu_1-\mu_2)^2}{\bar{v}}\alpha_{11} + \frac{q(1-q)(\nu_1-\nu_2)^2}{\bar{w}}\alpha_{22},$$
$$C = \frac{p(1-p)q(1-q)(\mu_1-\mu_2)^2(\nu_1-\nu_2)^2}{\bar{v}\bar{w}}(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}).$$

Note that in the situation where $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}$ is large enough, it is quite possible that both eigenvalues be complex. Suppose first that they are real, that is, suppose $A > 0$. Since $B < 0$ and $0 < \sqrt{A} < -B$, we have

$$\lambda^{+} = 1 + B + \sqrt{A} \begin{cases} < 1 \\ > 1 + B \end{cases}$$

and

$$\lambda^{-} = 1 + B - \sqrt{A} \begin{cases} < 1 \\ > 1 + 2B \end{cases}.$$

At this point, we need the following Lemma. The proof is relegated to the Appendix.

Lemma 1. *At the equilibrium* (p^*, q^*),

$$\frac{p^*(1-p^*)(\mu_1-\mu_2)^2}{\bar{v}}\alpha_{11} > -\frac{1}{2},$$
$$\frac{q^*(1-q^*)(\nu_1-\nu_2)^2}{\bar{w}}\alpha_{22} > -\frac{1}{2}.$$

Then, using these inequalities, both λ^{+} and λ^{-} are greater than -1. Therefore the doubly-phenotypic equilibrium (p^*, q^*) is locally stable.

On the other hand, if $A < 0$, then the two eigenvalues are complex, with modulus satisfying

$$0 \le |\lambda|^2 = (1 + B)^2 - A$$
$$= 1 + 2(B + 2C).$$

If $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}$ is large enough, it is quite possible that $B + 2C > 0$, which would lead to instability of (p^*, q^*). Yet, sufficient conditions for local stability

can be deduced. First, if $\alpha_{12}\alpha_{21} > 0$, the equilibrium is locally stable. Indeed, let us write, for convenience,

$$-\frac{1}{2} < a = \frac{p^*(1-p^*)(\mu_1 - \mu_2)^2}{\bar{v}}\alpha_{11} < 0,$$

$$-\frac{1}{2} < b = \frac{q^*(1-q^*)(\nu_1 - \nu_2)^2}{\bar{w}}\alpha_{22} < 0.$$

Then

$$B + 2C = a + b + 2ab\left(1 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}\right)$$

$$= a(1+b) + b(1+a) - 2ab\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}$$

$$< 0.$$

Moreover, if $\alpha_{12}\alpha_{21} < 0$ but $-\alpha_{12}\alpha_{21} < \alpha_{11}\alpha_{22}$, then

$$1 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}} < 2.$$

Suppose $a \le b$ (or otherwise interchange a and b in the following). Since $-2a < 1$, we have $4ab < -2b$ and then

$$B + 2C = a + b + 2ab\left(1 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}\right)$$

$$< a + b + 4ab$$

$$< a - b$$

$$\le 0.$$

Thus (p^*, q^*) is locally stable.

Therefore, it is in the case $-\alpha_{12}\alpha_{21}$ positive and large enough that instability happens. It is a situation where there is interspecific heterogeneity: when interspecific competition occurs, a member from one population receives higher payoff if both players use the same behavior, or pure strategy, while the member from the other population receives higher payoff if both members behave differently.

Otherwise, the allelic equilibrium corresponding to a two-population ESS is locally stable.

6. Local stability of the other equilibria

In this section, we study the local stability of all equilibria other than a doubly-phenotypic equilibrium corresponding to an ESS, and find a characterization of such locally stable equilibria. Then we analyze the equilibrium structure of the whole system and we show that in any invariant region for the dynamics (2), one and only one equilibrium can be locally stable, except maybe when the ESS itself is unstable. When the ESS is unstable, a cyclic behavior in the trajectories of (2) has been numerically observed (see Figure 3 below).

We first present a Lemma where conditions for local stability are stated. We restrict ourself to only a particular representative of each class of equilibria, but similar conditions hold for the other equilibria. The proof is relegated to the Appendix.

Lemma 2. *Consider system* (2) *and suppose conditions* (4) *satisfied.*

1. *The double fixation* $(0, 0)$ *is locally stable if and only if*

$$P_{12} < P_{22} < \Gamma_\phi(Q_{22}) \ \ or \ \ P_{12} > P_{22} > \Gamma_\phi(Q_{22})$$

   and

$$Q_{12} < Q_{22} < \Gamma_\psi(P_{22}) \ \ or \ \ Q_{12} > Q_{22} > \Gamma_\psi(P_{22});$$

2. *the singly-genetic equilibrium* $(\hat{p}, 0)$ *is locally stable if and only if*

$$\Gamma_\phi(Q_{22}) < \hat{x} \ if \ underdominance \ in \ \mathscr{P}_1$$
$$\Gamma_\phi(Q_{22}) > \hat{x} \ if \ overdominance \ in \ \mathscr{P}_1$$

   and

$$Q_{12} < Q_{22} < \Gamma_\psi(\hat{x}) \ \ or \ \ Q_{12} > Q_{22} > \Gamma_\psi(\hat{x});$$

3. *the singly-phenotypic equilibrium* $(\bar{p}, 0)$ *is locally stable if and only if*

$$Q_{12} < Q_{22} < \Gamma_\psi(\bar{x}) \ \ or \ \ Q_{12} > Q_{22} > \Gamma_\psi(\bar{x});$$

4. *the doubly-genetic equilibrium* $(\hat{p}, \hat{q})$ *is locally stable if and only if*

$$\Gamma_\phi(\hat{y}) < \hat{x} \ if \ underdominance \ in \ \mathscr{P}_1$$
$$\Gamma_\phi(\hat{y}) > \hat{x} \ if \ overdominance \ in \ \mathscr{P}_1$$

   and

$$\Gamma_\psi(\hat{x}) < \hat{y} \ if \ underdominance \ in \ \mathscr{P}_2$$
$$\Gamma_\psi(\hat{x}) > \hat{y} \ if \ overdominance \ in \ \mathscr{P}_2;$$

5. *the genetic-phenotypic equilibrium* $(\hat{p}, \bar{q})$ *is locally stable if and only if*

$$\Gamma_\phi(\bar{y}) < \hat{x} \ if \ underdominance \ in \ \mathscr{P}_1$$
$$\Gamma_\phi(\bar{y}) > \hat{x} \ if \ overdominance \ in \ \mathscr{P}_1.$$

The following corollary is a characterization of a locally stable equilibrium. The proof follows from the conditions cited above. Corollary 1 generalizes, to the multi-population framework, a note by Maynard Smith (1981) where it is argued that for a single sexual population, a locally stable equilibrium is an equilibrium for which the mean population strategy is as close as possible to an ESS, in any invariant region.
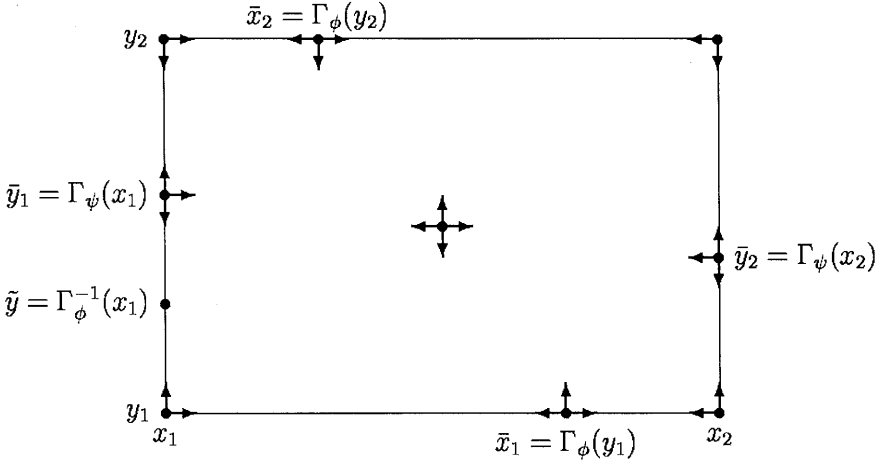
Fig. 2. Region $\mathscr{R}$ in the xy-plane corresponding to some invariant region in the pq-plane.

Corollary 1. *An equilibrium $(\tilde{p}, \tilde{q})$ with the corresponding two-population mean strategy $(\tilde{x}, \tilde{y})$ that is not a two-population ESS is locally stable if and only if a perturbation in the gene frequencies in one population moves the mean strategy of that population away from $\Gamma_\phi(\tilde{y})$, if the perturbation is in $\mathscr{P}_1$, and away from $\Gamma_\psi(\tilde{x})$, if the perturbation is in $\mathscr{P}_2$.*

Result 1. *In any invariant region, one and only one equilibrium is locally stable.*

(Of course, we exclude the case where the ESS itself is unstable. Otherwise a cyclic behavior of the system is observed, but nevertheless such a cycle is still restrained to one invariant region where no other equilibrium is stable. See Figure 3 for an illustration.)

Proof. The proof is only a matter of tracing the lines Γ_ϕ and Γ_ψ in the xy-plane, and verifying whether or not conditions given in Corollary 1 apply. Figure 2 illustrates a region $\mathscr{R}$ in the xy-plane corresponding to an invariant region of the pq-plane bounded in part by the lines $p = \hat{p}$ and $q = \hat{q}$ when they exist. It gives the directions of the two-population strategy following a perturbation in the gene frequencies in one of the two populations. Points at the corners correspond to doubly-genotypic equilibria (with both components representing fixation states and/or genetic equilibria), while points on the edges correspond to genotypic-phenotypic equilibria, if they exist. The interior point corresponds to an ESS, if it exists.

By Corollary 1, two equilibria on the same edge cannot be simultaneously stable, since at least one of the two would be brought closer to a one-population ESS following a perturbation in the gene frequency in the appropriate population. Then if we take any two equilibria not on a same edge of $\mathscr{R}$ and suppose these both locally stable, and if we trace the lines Γ_ϕ and Γ_ψ satisfying the conditions of Corollary 1, we would find an arrangement of those lines that does not satisfy any of the four possibilities of Figure 1. Thus, only one equilibrium can be locally stable in any invariant region.

Now, let us look at the existence of a locally stable equilibrium in any invariant region. If both Γ_ϕ and Γ_ψ intersect in the interior of $\mathcal{R}$, then a doubly-phenotypic equilibrium exists in the invariant region, which is locally stable (or leads to an observed cyclic behavior). Suppose from now on that they do not intersect in $\mathcal{R}$.

Assume that there exists at least one genotypic-phenotypic equilibrium (either singly-phenotypic or genetic-phenotypic). Suppose that Γ_ϕ crosses both the lower and upper edge of $\mathcal{R}$, at $(\bar{x}_1, y_1)$ and $(\bar{x}_2, y_2)$, respectively. Both equilibria are genotypic with respect to $\mathcal{P}_2$ and phenotypic with respect to $\mathcal{P}_1$. Since both Γ_ϕ and Γ_ψ do not intersect in $\mathcal{R}$, we must have

$$\text{either } \Gamma_\psi(\bar{x}_1) < y_1 \text{ or } \Gamma_\psi(\bar{x}_2) > y_2,$$

and therefore one is locally stable.

On the other hand, suppose without loss of generality that Γ_ϕ only crosses the lower edge of $\mathcal{R}$ at $(\bar{x}_1, y_1)$, and crosses, say, the left edge at $(x_1, \tilde{y}_1)$. If $\Gamma_\psi(\bar{x}_1) < y_1$, the equilibrium $(\bar{x}_1, y_1)$ is locally stable. On the other hand, if $\Gamma_\psi(\bar{x}_1) > y_1$, we must have

$$\Gamma_\psi(x_1) > \tilde{y}_1,$$

since otherwise both lines would intersect in $\mathcal{R}$. If Γ_ψ also intersects the left edge at $(x_1, \bar{y}_1)$, we have a phenotypic-genotypic equilibrium which is locally stable, since then $\Gamma_\phi(\bar{y}_1) < x_1$. If not, then (x_1, y_2) is locally stable. Indeed, we would have $\bar{x}_2 = \Gamma_\phi(y_2) < x_1$ and $\bar{y}_1 = \Gamma_\psi(x_1) > y_2$. Symmetry holds whenever there exists any phenotypic-genotypic equilibrium.

Finally, if no phenotypic-genotypic equilibrium exists, then one of the four corners is locally stable. It has coordinates x_1 or x_2, depending on whether Γ_ϕ has positive or negative slope, respectively, and y_1 or y_2, if Γ_ψ has positive or negative slope, respectively.

7. Numerical examples

In this section we give two examples to illustrate our results.

Example 1. Figure 3 shows both the xy-plane along with the pq-plane (actually illustrated as a qp-plane), with Γ_ϕ and Γ_ψ which are lines in the xy-plane, hyperbolas or ellipses in the qp-plane. The parabolas $x(p)$ and $y(q)$ help determine the direction of the mean strategy following a perturbation in the gene frequency in one population. The set of parameters used is

$$F_{11} = \begin{pmatrix} .634 & .009 \\ .727 & .076 \end{pmatrix}, \quad F_{12} = \begin{pmatrix} .565 & .372 \\ .064 & .884 \end{pmatrix},$$

$$F_{21} = \begin{pmatrix} .372 & .565 \\ .884 & .064 \end{pmatrix}, \quad F_{22} = \begin{pmatrix} .080 & .867 \\ .009 & .758 \end{pmatrix},$$

with $P_{11} = Q_{11} = .4$, $P_{12} = Q_{12} = .1$ and $P_{22} = Q_{22} = .8$. With these, the two-population ESS $(x^*, y^*) = (0.580, 0.586)$, corresponding to the unique doubly-phenotypic equilibrium $(q^*, p^*) = (0.174, 0.180)$ in the qp-plane, is unstable. Any trajectory starting in the interior of the invariant region bounded by $p = 0$, $p = \hat{p}$,
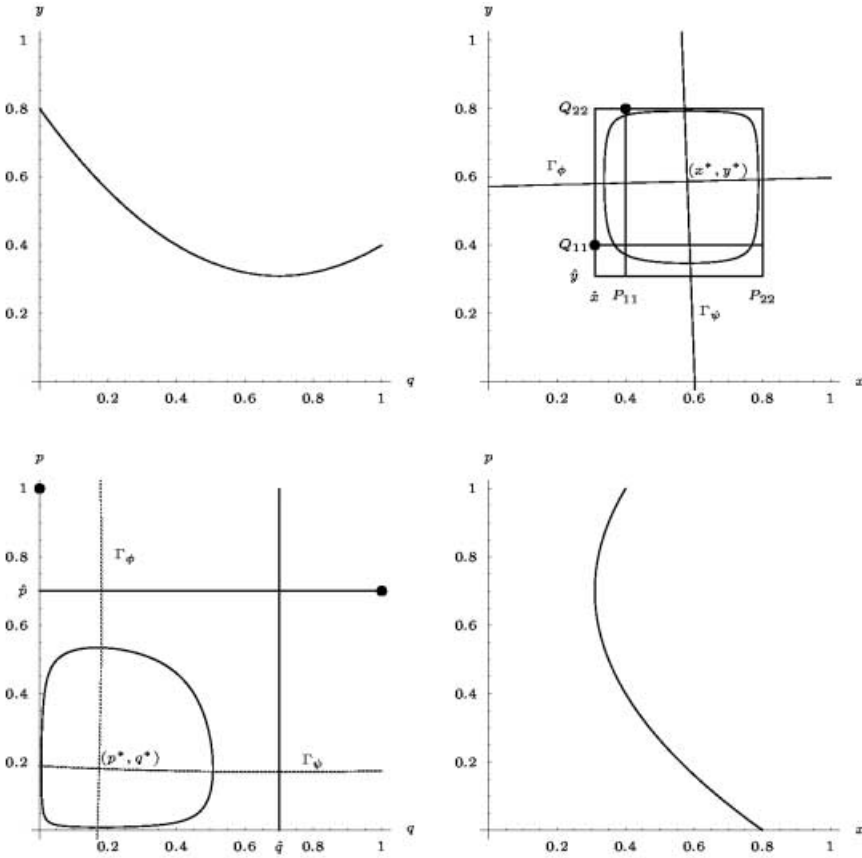
Fig. 3. The xy-plane and qp-plane with four invariant regions bounded by the lines $p = \hat{p}$ and $q = \hat{q}$. Bold dots indicate locally stable equilibria.

$q = 0$ and $q = \hat{q}$, evolves to the periodic orbit shown in Figure 3. Moreover, there exist two locally stable equilibria, $(\hat{x}, Q_{11})$ and (P_{11}, Q_{22}) (or respectively $(0, 1)$ and $(1, \hat{p})$ in the qp-plane) in agreement with the caracterization of Corollary 1.

Example 2. This example is inspired from Maynard Smith and Parker's (1976) model of an asymmetric game involving two pure strategies, Hawk and Dove, where two types of players differ in their fighting abilities for the control of some ressource.

Let V_1 be the value of the ressource in terms of increase in fitness for members of $\mathscr{P}_1$ and V_2 be the corresponding value for members of $\mathscr{P}_2$. The cost of losing a fight by being injured is denoted by D_i for members of population $\mathscr{P}_i$ ($i = 1, 2$). Suppose that in an intraspecific contest, two contestants behaving according to the same pure strategy have equal chance of winning the ressource. We might suppose a different probability when it comes to interspecific competition. A Dove always
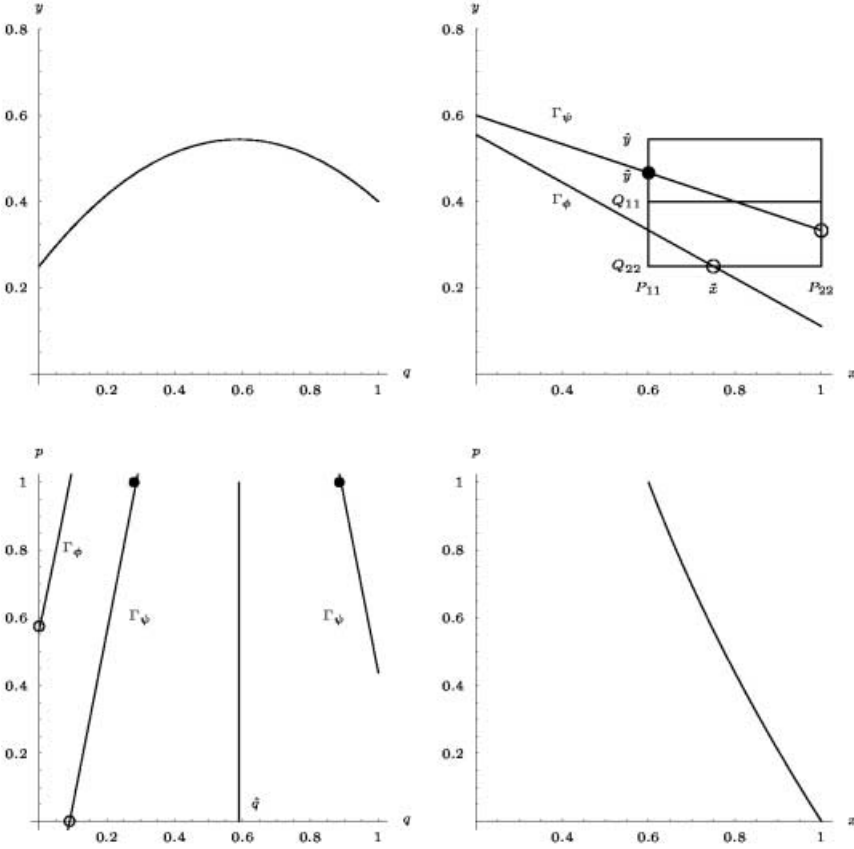
Fig. 4. Equilibrium structure for Example 2.

retreats when opposed with a Hawk. Take the fitness matrices

$$F_{11} = \begin{pmatrix} (V_1 - D_1)/2 & V_1 \\ 0 & V_1/2 \end{pmatrix}, \qquad F_{12} = \begin{pmatrix} V_1 h - D_1(1-h) & V_1 \\ 0 & V_1 d \end{pmatrix},$$

$$F_{21} = \begin{pmatrix} V_2(1-h) - D_2 h & V_2 \\ 0 & V_2(1-d) \end{pmatrix}, \qquad F_{22} = \begin{pmatrix} (V_2 - D_2)/2 & V_2 \\ 0 & V_2/2 \end{pmatrix},$$

where h, respectively d, is the probability that a Hawk, respectively a Dove, from $\mathscr{P}_1$ wins a contest against a Hawk, respectively a Dove, from $\mathscr{P}_2$. Note that the payoffs must all be positive when studying the discrete dynamics of the game. One could add a same constant to all the above matrices without changing the equilibrium structure.

Numerically, Figure 4 represents the structure of this game, with $V_1 = 6$, $V_2 = 2$, $C_1 = 10$, $C_2 = 6$, $h = .25$ and $d = .25$. The strategies used are $P_{11} = .6$, $P_{12} = .75$, $P_{22} = 1$, $Q_{11} = .4$, $Q_{12} = .75$ and $Q_{22} = .25$. Bold dots indicate a locally stable phenotypic-genotypic equilibrium; small circles are the unstable

phenotypic-genotypic equilibria. Note that although in these three states one of the two populations is at a phenotypic equilibrium, hence at a (single-population) ESS, two of those are unstable because a shift in the mean strategy in one population, through a perturbation in the gene frequency, would initially bring that population closer to its ESS. Moreover, the vertical distance between the point $(\tilde{x}, Q_{22})$ with the line Γ_ψ, measuring the actual distance between the state in population $\mathscr{P}_2$, namely Q_{22}, with its ESS, namely $\Gamma_\psi(\tilde{x})$, is actually smaller than the distance between the point $(P_{11}, \tilde{y})$ with the line Γ_ϕ, which is the distance between the state in population $\mathscr{P}_1$, namely P_{11}, with its ESS, namely $\Gamma_\phi(\tilde{y})$. So the key in determining whether or not an equilibrium is locally stable does not rely on the simultaneous minimization of distances from evolutionarily stable strategies in the single-population context, but rather on the statement of Corollary 1.

8. Conclusion

In this paper we have been concerned with the equilibrium structure of a dynamical system involving two diploid populations undergoing intra- and interspecific random pairwise interactions. We have used a definition proposed by Cressman (1992, 1996) relating the concept of an evolutionarily stable strategy with the coevolution of two populations. but called it a *two-population* ESS instead of a *two-species* ESS as originally. We believe that this terminology is more appropriate since the concept can be extended to populations within a single species. We have not considered *restricted* games (as in Eshel, 1982); ESS could have been defined within the set of attainable strategies, but would have then failed to satisfy the ESS conditions for the "whole" game. Our main objective has been to find a characterization for local stability of an equilibrium in relation with the existence of a two-population ESS, having in mind the limitation of the dynamics within an invariant region imposed by genetic constraints such as over- and underdominance.

As shown by Corollary 1, local stability of an equilibrium can be predicted from the simultaneous "proximity" of each mean population strategy with the corresponding single-population ESS that prevails. Actually, a shift of the mean population strategy in one population toward a single-population ESS, following a perturbation on gene frequencies in that population, proved to be sufficient to predict instability of the equilibrium. Note that we do not use the terminology "proximity" in a common sense. There are situations where two genotypic-phenotypic equilibria coexist within the same invariant region, one being locally stable and the other unstable, while the unstable one is actually *closer* (in the common sense) to both corresponding single-population ESSs.

However, with the dynamical properties enlightened in this paper, Maynard Smith's (1981) claim that a locally stable equilibrium has a mean strategy as close as possible (with genetic constraints in mind) to an ESS, extends to the framework of two populations.

A. Conditions for local stability

We find sufficient conditions for local stability of any equilibrium, by means of a linear approximation of the dynamical system (2). Under the assumptions made throughout this paper, these are necessary conditions as well; the only situation where the eigenvalues above could have modulus 1 is when the equilibrium is of two types (being simultaneously phenotypic and genotypic, or being a fixation state while being genetic), or else if the P_{ij}'s or the Q_{ij}'s are not all unequal.

   Using a first order approximation, we seek conditions under which the leading eigenvalue of the Jacobian matrix

$$\begin{pmatrix} \dfrac{\partial p'}{\partial p} & \dfrac{\partial p'}{\partial q} \\[2mm] \dfrac{\partial q'}{\partial p} & \dfrac{\partial q'}{\partial q} \end{pmatrix},$$

(where all elements are evaluated at the equilibrium under investigation) is less than 1 in modulus. Except at an equilibrium (p^*, q^*) corresponding to an ESS, at least one of $\partial p'/\partial q$ or $\partial q'/\partial p$ is 0 when evaluated at the equilibrium. Indeed, at any other equilibrium, at least one of $p' - p$ or $q' - q$ is identically 0, independently of q or p, respectively. Then, the eigenvalues of the Jacobian matrix are simply the elements on the diagonal.

   For simplicity, we only seek conditions for which $\partial p'/\partial p$ is less than 1 in modulus, since equivalent conditions can be found from those below for the second eigenvalue $\partial q'/\partial q$. We use $\tilde{q}$ for an arbitrary component of an equilibrium, and $\tilde{y}$ for its corresponding strategy.

   Starting with an equilibrium $(0, \tilde{q})$, with corresponding strategy vector $(P_{22}, \tilde{y})$, we find conditions for which we have

$$-1 < \left. \frac{\partial p'}{\partial p} \right|_{(0,\tilde{q})} < 1.$$

The eigenvalue is

$$\left. \frac{\partial p'}{\partial p} \right|_{(0,\tilde{q})} = \left. \frac{(P_{12} - P_{22})(\phi_1 - \phi_2)}{\bar{v}} \right|_{(0,\tilde{q})} + 1,$$

where

$$\bar{v}|_{(0,\tilde{q})} = [P_{22}(\phi_1 - \phi_2) + \phi_2]_{(0,\tilde{q})} .$$

Simplifying, it can easily be seen that the eigenvalue is positive. Now $\phi_1 - \phi_2 > 0$ if $(P_{22}, \tilde{y})$ lies to the left of Γ_ϕ, and $\phi_1 - \phi_2 < 0$ if $(P_{22}, \tilde{y})$ lies to the right of Γ_ϕ. So the eigenvalue is less than 1 if either

$$P_{12} < P_{22} \text{ and } P_{22} < \Gamma_\phi(\tilde{y})$$

or

$$P_{12} > P_{22} \text{ and } P_{22} > \Gamma_\phi(\tilde{y}).$$

For an equilibrium in the form $(\hat{p}, \tilde{q})$, we have

$$\left.\frac{\partial p'}{\partial p}\right|_{(\hat{p},\tilde{q})} = \left.\frac{\hat{p}(1-\hat{p})(P_{11}-2P_{12}+P_{22})(\phi_1-\phi_2)}{\bar{v}}\right|_{(\hat{p},\tilde{q})} + 1$$

where, once evaluated at $(\hat{p}, \tilde{q})$, $\bar{v} = \hat{x}(\phi_1 - \phi_2) + \phi_2$. We have

$$\hat{p}(1-\hat{p})(P_{11}-2P_{12}+P_{22})(\phi_1-\phi_2) + \bar{v}$$
$$= \{\hat{p}P_{11}+(1-\hat{p})P_{22}\}(\phi_1-\phi_2) + \phi_2,$$

which is positive, since the expression in brackets is between 0 and 1. Then, the eigenvalue is positive. For it to be less than 1, we need $\phi_1 - \phi_2 < 0$ at $(\hat{p}, \tilde{q})$ when there is underdominance in $\mathscr{P}_1$, since $P_{11} - 2P_{12} + P_{22} > 0$. That is, we need

$$\Gamma_\phi(\tilde{y}) < \hat{x}.$$

On the other hand, when there is overdominance ($P_{11} - 2P_{12} + P_{22} < 0$), we need $\phi_1 - \phi_2 > 0$, or equivalently

$$\Gamma_\phi(\tilde{y}) > \hat{x}.$$

Finally, for an equilibrium $(\bar{p}, \tilde{q})$, the eigenvalue is

$$\left.\frac{\partial p'}{\partial p}\right|_{(\bar{p},\tilde{q})} = \left.\frac{2\bar{p}(1-\bar{p})(\mu_1-\mu_2)^2\alpha_{11}}{\bar{v}}\right|_{(\bar{p},\tilde{q})} + 1,$$

which is less than 1 since we suppose α_{11} negative. It is also positive, as shown in the next Appendix.

B. Proof of Lemma 1

Here we show the required inequality

$$\left.\frac{p(1-p)(\mu_1-\mu_2)^2\alpha_{11}}{\bar{v}}\right|_{(p^*,q^*)} > -\frac{1}{2}. \tag{5}$$

where (p^*, q^*) is a doubly-phenotypic equilibrium for which the strategy vector (x^*, y^*) is a two-population ESS. Let the allele frequencies in $\mathscr{P}_2$ be *fixed* at q^*. Write

$$\phi_1 = x\left(\frac{a_{11}+k_1}{2}\right) + (1-x)\left(\frac{a_{12}+k_1}{2}\right),$$
$$\phi_2 = x\left(\frac{a_{21}+k_2}{2}\right) + (1-x)\left(\frac{a_{22}+k_2}{2}\right),$$

where

$$k_1 = y^*b_{11}+(1-y^*)b_{12},$$
$$k_2 = y^*b_{21}+(1-y^*)b_{22}.$$

Then the recurrence equation

$$p' - p = \frac{p(1-p)(\mu_1 - \mu_2)(\phi_1 - \phi_2)}{\bar{v}}, \tag{6}$$

is the classical dynamics involved in a single-population model of evolutionarily stability, with two strategies and two alleles, with payoff matrix

$$\begin{pmatrix} \dfrac{a_{11} + k_1}{2} & \dfrac{a_{12} + k_1}{2} \\[2ex] \dfrac{a_{21} + k_2}{2} & \dfrac{a_{22} + k_2}{2} \end{pmatrix}.$$

In the single-population context, Lessard (1984) has shown that $|\phi_1 - \phi_2|$ is a strict Lyapounov function. Moreover (Hofbauer and Sigmund, 1988), $\phi_1 - \phi_2$ does not change its sign. This, in turn, implies that near enough the phenotypic equilibrium p^*, the difference $p' - p$ in (6) does not change its sign, or, equivalently, that

$$\left. \frac{dp'}{dp} \right|_{p*} = 1 + \left. \frac{2p(1-p)(\mu_1 - \mu_2)^2 \alpha_{11}}{\bar{v}} \right|_{(p^*, q^*)} > 0.$$

Hence, (5) is true.

References

1. Cressman, R.: Frequency-dependent viability selection (a single-locus, multi-phenotype model), J. theor. Biol., **130**, 147–165 (1988)
2. Cressman, R.: "The Stability Concept of Evolutionary Game Theory (A Dynamic Approach)," Lecture Notes in Biomathematics, Vol. 94, Springer-Verlag, Berlin Heidelberg New York (1992)
3. Cressman, R.: Frequency-dependent stability for two-species interactions, Theor. Pop. Biol., **49**, 189–210 (1996)
4. Crowley, P.H.: Hawks, Doves and mixed-symmetry games, J. theor. Biol., **204**, 543–563 (2000)
5. Eshel, I.: Evolutionarily stable strategies and viability selection in Mendelian populations, Theor. Pop. Biol., **22**, 204–217 (1982)
6. Eshel, I.: On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution, J. Math. Biol., **34**, 485–510 (1996)
7. Eshel, I., Sansone, E.: Owner-intruder conflict, Grafen effect and self-assessment. The Bourgeois principle re-examined, J. theor. Biol., **177**, 341–356 (1995)
8. Hammerstein, P.: Darwinian adaptation, population genetics and the streetcar theory of evolution, J. Math. Biol., **34**, 511–532 (1996)
9. Hines, W.G.S.: Evolutionarily stable strategies: a review of basic theory, Theor. Pop. Biol., **31**, 195–272 (1987)
10. Hines, W.G.S., Bishop, D.T.: Can and will a sexual diploid population attain an evolutionary stable strategy?, J. theor. Biol., **111**, 667–686 (1984)
11. Hofbauer, J., Sigmund, K.: "The Theory of Evolution and Dynamical Systems," Cambridge University Press, Cambridge (1988)

12. Lessard, S.: Evolutionary dynamics in frequency dependent two-phenotype models, Theor. Pop. Biol., **25**, 210–234 (1984)
13. Lessard, S.: Evolutionary stability: one concept, several meanings, Theor. Pop. Biol., **37**, 159–170 (1990)
14. Lessard, S., Karlin, S.: A criterion for stability-instability at fixation states involving an eigenvalue one with applications in population genetics, Theor. Pop. Biol., **22**, 108–126 (1982)
15. Maynard Smith, J.: The theory of games and the evolution of animal conflicts, J. theor. Biol., **47**, 209–221 (1974)
16. Maynard Smith, J.: Will a sexual population evolve to an ESS?, Am. Nat., **117**, 1015–1018 (1981)
17. Maynard Smith, J., Parker, G.A.: The logic of asymmetric contests, Anim. Behav., **24**, 159–175 (1976)
18. Maynard Smith, J., Price, G.R.: The logic of animal conflict, Nature., **246**, 15–18 (1973)
19. Morris, M., Matessi, C., Karlin, S.: Models of intergenerational kin altruism, Am. Nat., **130**, 544–569 (1987)
20. Roughgarden, J.: "Theory of Population Genetics and Evolutionary Ecology: An Introduction," Macmillan Co., New York (1979)
21. Selten, R.: A note on evolutionarily stable strategies in asymmetric animal conflicts, J. theor. Biol., **84**, 93–101 (1980)
22. Tao, Y.: Frequency-dependent selection: a two-phenotype, two-allele, single-locus, two-species diploid model, J. theor. Biol., **191**, 289–294 (1998)
23. Tao, Y., Cressman, R., Brooks, B.: Nonlinear frequency-dependent selection at a single locus with two alleles and two phenotypes, J. Math. Biol., **39**, 283–308 (1999)
24. Vickers, G.T., Cannings, C.: On the definition of an evolutionarily stable strategy, J. theor. Biol., **129**, 349–353 (1987)
25. Weissing, F.J.: Genetic versus phenotypic models of selection: can genetics be neglected in a long-term perspective?, J. Math. Biol., **34**, 533–555 (1996)