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Frequency-Dependent Selection: a Two-Phenotype, Two-Allele, Single-Locus,Two-Species Diploid Model

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The two-species matrix games developed by Cressman (1996, *Theoretical Population Biology* **49,** 189–210) are extended to interacting diploid populations. In this paper, a simple two-phenotype, two-allele, single-locus, two-species diploid model is investigated. The main focus of the paper is to illustrate the local stability of all interior positive equilibrium points of the two-species diploid model and the evolutionary significance of the stability. Results show that (i) in the two-species diploid model, three possible types of interior positive equilibrium points can exist, phenotypic equilibrium point, genetic equilibrium point and PG equilibrium point; (ii) if the phenotypic equilibrium point is a two-species ESS, then it must be locally asymptotically stable; (iii) at the genetic equilibrium point, if there are heterozygote advantages in both species, then the genetic equilibrium point is locally asymptotically stable; (iv) at the PG equilibrium point, one species exhibiting phenotypic equilibrium and the other genetic equilibrium, if the genetic equilibrium corresponds to heterozygote advantage and the phenotypic equilibrium is a single-species ESS, then the PG equilibrium point must be locally asymptotically stable.

1. Introduction

Cressman (1996) presented the two-species frequency-dependent model. In this model, evolutionary game theory is extended to models of two-species interactions where fitnesses are based on individual characteristics (strategies) rather than on a population dynamic that assumes homogeneous species. His main purpose is to investigate the application of the ESS solution concept to dynamic stability when fitnesses are given by random interactions between individuals as opposed to viability selection. For the two-species frequency-dependent model, Cressman (1996) defined the concept of two-species ESS that asserts that, if any system near the ESS, at least one of the species is better off if it evolves towards ESS.

The simplest two-species frequency-dependent model is the two-species matrix game model. In this model, Cressman (1996) assumes that: (1) the number of the possible phenotypes (also called pure strategies) is finite in both species; (2) the strategies are passed on to offspring through asexual inheritance; (3) the intra- and interspecific interactions between a pair of individuals are completely random; (4) the density effects are ignored and the proportion of the two species is fixed. Obviously, Cressman's two-species matrix game model can also be considered to be a natural extension of the classic matrix game models. Cressman's (1996) result shows that a polymorphic two-species ESS is globally asymptotically stable in the two-species matrix game model.

Clearly, Cressman's (1996) two-species matrix game model concerns the coevolution of two species (Roughgarden, 1979). From Roughgarden's (1979) definition, we know that "coevolution" is the term applied to the simultaneous evolution of interacting populations. In this paper, the two-species matrix game will be extended to the diploid model that

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assumes that the two species are Mendelian populations. The main purpose of this paper is to investigate the relationship between phenotypic evolution and genetic evolution in the two-species system. In Section 3, the necessary and sufficient conditions for the two-species ESS in the simplest two-phenotype, two-species haploid model will first be discussed. In Section 4, the dynamic properties of the two-species diploid model and the biological significance of these dynamic properties will be-analysed.

2. Basic Assumptions and Basic Models

In this paper, the following basic assumptions are made:

(i) there are two interacting populations, which can be called species 1 and species 2;

(ii) the generations of species 1 and species 2 are continuous and overlapping;

(iii) the intra- and interspecific interactions between individuals are random pairwise contests, and the proportion of species 1 to species 2 is 1:1 (Cressman, 1996);

(iv) let R_1 and R_2 denote the two pure strategies in species 1 and S_1 and S_2 denote the two pure strategies in species 2. For convenience, the individuals of species 1 and species 2 can be called the R-strategists and S-strategists, respectively. From Maynard Smith's (1982) definition for the symmetric and asymmetric contests, we know that the pay-off matrices of the symmetric contests between a pair of R-strategists and between a pair of S-strategists are given by $\mathbf{A} = [a_{ij}]_{i,j=1,2}$ and $\mathbf{D} = [d_{ij}]_{i,j=1,2}$, respectively, where a_{ij} is the pay-off value of the R_i-strategist when the R_i-strategist plays against the R_j-strategist for all $i, j = 1, 2$, and d_{ij} is the pay-off value of the S_i-strategist when the S_i-strategist plays against the S_j-strategist for all $i, j = 1, 2$. The pay-off matrices of the asymmetric pairwise contests between R-strategists and S-strategists are given by $\mathbf{B} = [b_{ij}]_{i,j=1,2}$ and $\mathbf{C} = [c_{ij}]_{i,j=1,2}$, respectively, where b_{ij} is the pay-off value of the R_i-strategist when the R_i-strategist plays against the S_j-strategist for all $i, j = 1, 2$, and c_{ij} is the pay-off value of the S_i-strategist when the S_i-strategist plays against the R_j-strategist for all $i, j = 1, 2$ (Cressman, 1996).

In order to obtain the necessary and sufficient conditions for the two-species ESS developed by Cressman (1996), we first establish the two-species haploid model. In this model, species 1 and species 2 are assumed to be haploid populations. Let $x(t)$ and $1 - x(t)$ be the frequencies of the pure strategies R_1 and R_2 in species 1 at time t, and $y(t)$ and $1 - y(t)$ be the frequencies of the pure strategies S_1 and S_2 in species 2 at time t. Let $\varphi_i[x(t), y(t)]$ and $\psi_i[x(t), y(t)]$ be the expected pay-off values of the pure strategies R_i and S_i at time t for all $i, j = 1, 2$. Then from the basic assumptions, we must have

$$\begin{aligned}\varphi_i[x(t), y(t)] &= \{x(t)a_{i1} + [1 - x(t)]a_{i2} \\ &\qquad + y(t)b_{i1} + [1 - y(t)]b_{i2}\}/2, \\ \psi_i[x(t), y(t)] &= \{x(t)c_{i1} + [1 - x(t)]c_{i2} + \\ &\qquad y(t)d_{i1} + [1 - y(t)]d_{i2}\}/2. \qquad (1)\end{aligned}$$

Thus the average pay-off values of species 1 and species 2 at time t are given by

$$\begin{aligned}\bar{\varphi}(t) &= x(t)\varphi_1[x(t), y(t)] + [1 - x(t)]\varphi_2[x(t), y(t)], \\ \bar{\psi}(t) &= y(t)\psi_1[x(t), y(t)] + [1 - y(t)]\psi_2[x(t), y(t)]. \qquad (2)\end{aligned}$$

From eqn (1) and eqn (2), the evolutionary dynamics of the frequency of the pure strategy R_1 in species 1 and the frequency of the pure strategy S_1 inspecies 2 can be written as

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= x[\varphi_1(x, y) - \bar{\varphi}] \\ &= x(1 - x)[\varphi_1(x, y) - \varphi_2(x, y)] \\ &= x(1 - x)(\alpha_{11}x + \alpha_{12}y - \beta_1) \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= y[\psi_1(x, y) - \bar{\psi}] \\ &= y(1 - y)[\psi_1(x, y) - \psi_2(x, y)] \\ &= y(1 - y)(\alpha_{21}x + \alpha_{22}y - \beta_2), \qquad (3)\end{aligned}$$

where

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

(Hofbauer & Sigmund, 1988; Cressman, 1992). Equation (3) is the standard frequency-dependent model based on pay-off differences. In Section 3, it will be used to determine the conditions of the two-species ESS.

For the two-species diploid model, we need to assume that species 1 and species 2 are diploid populations, and that mating is completely random in both populations. A further assumption is that selection is only viability selection in this diploid model (Lessard, 1984). Let the phenotypes of individuals in species 1 be determined by an autosomal locus with alleles A_1 and A_2. In species 1, the phenotype of individuals with genotype A_iA_j is given by $(P_{ij}, 1 - P_{ij})$, where P_{ij} is the probability of using pure strategy R_1 and $1 - P_{ij}$ is the complementary probability of using pure strategy R_2 for all $i, j = 1, 2$. Similarly, let the phenotypes of individuals in species 2 be determined by an autosomal locus with alleles B_1 and B_2. In species 2, the phenotype of individuals with genotype B_iB_j is given by $(Q_{ij}, 1 - Q_{ij})$, where Q_{ij} is the probability of using pure strategy S_1 and $1 - Q_{ij}$ is the complementary probability of using pure strategy S_2 for all $i, j = 1, 2$ (Lessard, 1984).

Let $p(t)$ and $1 - p(t)$ be the frequencies of alleles A_1 and A_2 in species 1 at time t, respectively, and $q(t)$ and $1 - q(t)$ be the frequencies of alleles B_1 and B_2 in species 2 at time t, respectively. Since the mating is completely random in both populations, which means that the population is approximately at any time in Hardy–Weinberg equilibrium (Hofbauer & Sigmund, 1988), the frequencies of genotypes A_1A_1, A_1A_2 and A_2A_2 in species 1 at time t are given by $p(t)^2$, $2p(t)[1 - p(t)]$ and $[1 - p(t)]^2$, respectively, and the frequencies of genotypes B_1B_1, B_1B_2 and B_2B_2 in species 2 at time t are given by $q(t)^2$, $2q(t)[1 - q(t)]$ and $[1 - q(t)]^2$, respectively. It is necessary to point out that the assumption of Hardy–Weinberg equilibrium is reasonable under weak selection (Crow & Kimura, 1970). Thus the relationships between the frequency of allele A_1 and the frequency of pure strategy R_1, and between the frequency of allele B_1 and the frequency of pure strategy S_1 at any time t can be written as

$$x(t) = p(t)^2P_{11} + 2p(t)[1 - p(t)]P_{12} + [1 - p(t)]^2P_{22}$$

$$y(t) = q(t)^2Q_{11} + 2q(t)[1 - q(t)]Q_{12} + [1 - q(t)]^2Q_{22}. \tag{4}$$

Let $f_{A_iA_j}(t)$ and $F_{B_iB_j}(t)$ be the fitnesses of genotypes A_iA_j and B_iB_j for all $i, j = 1, 2$ at time t. Then from eqn (1), we have

$$f_{A_iA_j}(t) = P_{ij}\varphi_1[x(t), y(t)] + (1 - P_{ij})\varphi_2[x(t), y(t)]$$

$$F_{B_iB_j}(t) = Q_{ij}\psi_1[x(t), y(t) + (1 - Q_{ij})\psi_2[x(t), y(t)$$

$$\text{for all} \quad i, j = 1, 2. \tag{5}$$

In the two-species diploid model, let $\bar{f}(t)$ and $\bar{F}(t)$ be the mean finesses of species 1 and species 2 at any time t, then from eqn (2), we must have $\bar{f}(t) = \bar{\varphi}(t)$ and $\bar{F}(t) = \bar{\psi}(t)$.

From the continuous selection model (Hofbauer & Sigmund, 1988, p. 225), we know that the evolutionary dynamics of the gene frequencies in both populations can be written as

$$\frac{dp}{dt} = p(f_{A_1} - \bar{f}) = p(1 - p)(f_{A_1} - f_{A_2})$$

$$\frac{dq}{dt} = q(F_{B_1} - \bar{F}) = q(1 - q)(F_{B_1} - F_{B_2}), \tag{6}$$

where for all $i = 1, 2$

$$\begin{aligned} f_{A_i} &= pf_{A_iA_1} + (1 - p)f_{A_iA_2} \\ &= [pP_{i1} + (1 - p)P_{i2}]\varphi_1(x, y) \\ &\quad + \{1 - [pP_{i1} + (1 - p)P_{i2}]\}\varphi_2(x, y) \\ F_{B_i} &= qF_{B_iB_1} + (1 - q)F_{B_iB_2} \\ &= [qQ_{i1} + (1 - q)Q_{i2}]\psi_1(x, y \\ &\quad + \{1 - [qQ_{i1} + (1 - q)Q_{i2}]\}\psi_2(x, y). \end{aligned} \tag{7}$$

Let $\mu_{A_i} = pP_{i1} + (1 - p)P_{i2}$ and $v_{B_i} = qQ_{i1} + (1 - q)Q_{i2}$ for all $i = 1, 2$ (Lessard, 1984), then from eqn (3), eqn(6) can be rewritten as

$$\frac{dp}{dt} = p(1 - p)(\mu_{A_1} - \mu_{A_2})(\alpha_{11}x + \alpha_{12}y - \beta_1)$$

$$\frac{dq}{dt} = q(1 - q)(v_{B_1} - v_{B_2})(\alpha_{21}x + \alpha_{22}y - \beta_2). \tag{8}$$

Equation (8) is a two-phenotype, two-allele, single-lcus, two-species diploid model

3. The Necessary and Sufficient Conditions for the Two-Species ESS

3.1. THE LOCAL STABILITY OF THE INTERIOR POSITIVE EQUILIBRIUM POINT FOR THE TWO-PHENOTYPE, TWO-SPECIES HAPLOID MODEL

Let (x^*, y^*) be the interior positive equilibriumpoint of eqn (3), then we must have

$$x^* = \frac{\beta_1\alpha_{22} - \beta_2\alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \in (0, 1)$$

$$y^* = \frac{\beta_2\alpha_{11} - \beta_1\alpha_{21}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \in (0, 1). \tag{9}$$

It is easy to obtain the Jacobian matrix of eqn (3) at (x^*, y^*), which is

$$\mathbf{J} = \begin{bmatrix} x^*(1 - x^*)\alpha_{11} & x^*(1 - x^*)\alpha_{12} \\ y^*(1 - y^*)\alpha_{21} & y^*(1 - y^*)\alpha_{22} \end{bmatrix}.$$

From the theory of differential equation, we know that (x^*, y^*) is locally asymptotically stable if and only if $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$ and $x^*(1 - x^*)\alpha_{11} + y^*(1 - y^*)\alpha_{22} < 0$.

3.2. THE CONDITIONS FOR A TWO-SPECIES ESS

In this section, the conditions for (x^*, y^*) to be a two-species ESS only are discussed. Since (x^*, y^*) is a unique interior equilibrium point of eqn (3), according to Cressman's (1996) definition, we know that (x^*, y^*) is a two-species ESS if, for all

$$(x, y) \neq (x^*, y^*) \text{ (where } x \in (0, 1) \text{ and } y \in (0, 1),$$

$$x^*\varphi_1(x, y) + (1 - x^*)\varphi_2(x, y) > x\varphi_1(x, y, + (1 - x)\varphi_2(x, y)$$

or

$$y^*\psi_1(x, y) + (1 - y^*)\psi_2(x, y) > y\psi_1(x, y, + (1 - y)\psi_2(x, y). \quad (10)$$

Let

$$\Phi(x, y) = (x^* - x)(\alpha_{11}x + \alpha_{12}y - \beta_1)$$

and

$$\Psi(x, y) = (y^* - y)(\alpha_{21}x + \alpha_{22}y - \beta_2),$$

then we have

$$\begin{bmatrix} \Phi(x, y) \\ \Psi(x, y) \end{bmatrix} = [x - x^* \; y - y^*] \cdot \begin{bmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{bmatrix} \begin{bmatrix} x^* - x \\ y^* - y \end{bmatrix}. \quad (11)$$

Inequality (10) is equivalent to $\Phi(x, y) > 0$ or $\Psi(x, y) > 0$ for all $(x, y) \neq (x^*, y^*)$. From Hofbauer & Sigmund (1988, p. 201), we know that $\Phi(x, y)$ or $\Psi(x, y)$ is positive for all $(x, y) \neq (x^*, y^*)$ if and only if $-[\alpha_{ij}]_{i,j=1,2}$ is a P-matrix. Thus the necessary and sufficient conditions for (x^*, y^*) to be a two-species ESS are:

(i) $\alpha_{11} < 0$ and $\alpha_{22} < 0$;
(ii) $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$.

It is necessary to point out that $\alpha_{11} < 0$ and $\alpha_{22} < 0$ are the single-species ESS conditions, respectively (Cressman, 1996). This means that if (x^*, y^*) is a two-species ESS, then when y is fixed at y^*, we must have $\Phi(x, y^*) = -\alpha_{11}(x^* - x)^2 > 0$ for all $x \neq x^*$, and similarly, when x is fixed at x^*, we also must have $\Psi(x^*, y) = -\alpha_{22}(y^* - y)^2 > 0$ for all $y \neq y^*$.

On the other hand, from the discussion in Section 3.1, if (x^*, y^*) is a two-species ESS, then it must be locally asymptotically stable in eqn (3). The more general results for the stability of the two-species ESS can be found in Cressman (1996).

4. The Analysis of the Two-Species Diploid Model

In this section, the local stability of all possible interior positive equilibrium points of the two-species diploid model are discussed. It is easy to note that in eqn (8), three possible types of interior positive equilibrium points can exist:

(i) if (x^*, y^*) satisfies eqn (9), then (x^*, y^*) can be called the *phenotypic equilibrium point* (Lessard, 1984; Hofbauer & Sigmund, 1988; Cressman, 1992);

(ii) if $(\hat{p}, \hat{q})$ satisfies $\mu_{A_1} - \mu_{A_2} = 0$ and $\nu_{B_1} - \nu_{B_2} = 0$, and $\hat{p} \in (0, 1)$ and $\hat{q} \in (0, 1)$, then $(\hat{p}, \hat{q})$ can be called the *genetic equilibrium point* (Lessard, 1984; Hofbauer & Sigmund, 1988; Cressman, 1992);

(iii) for $\hat{p} \in (0, 1)$ that satisfies $\mu_{A_1} - \mu_{A_2} = 0$, if there exists $\hat{y}$ that satisfies

$$\hat{y} = \frac{\beta_2 - \alpha_{21}x(\hat{p})}{\alpha_{22}} \in (0, 1), \quad (12)$$

where $x(\hat{p}) = \hat{p}^2P_{11} + 2\hat{p}(1 - \hat{p})P_{12} + (1 - \hat{p})^2P_{22}$, then $(\hat{p}, \hat{y})$ must be the interior positive equilibrium point of eqn (8). Similarly, for $\hat{q} \in (0, 1)$ that satisfies $\nu_{B_1} - \nu_{B_2} = 0$, if there exists $\hat{x}$ that satisfies

$$\hat{x} = \frac{\beta_1 - \alpha_{12}y(\hat{q})}{\alpha_{11}} \in (0, 1), \quad (13)$$

where $y(\hat{q}) = \hat{q}^2Q_{11} + 2\hat{q}(1 - \hat{q})Q_{12} + (1 - \hat{q})^2Q_{22}$, then $(\hat{x}, \hat{q})$ also must be the interior positive equilibrium point of eqn (8). At $(\hat{p}, \hat{y})$, or $(\hat{x}, \hat{q})$, one species is at the phenotypic equilibrium, but the other one is at the genetic equilibrium. For convenience, $(\hat{p}, \hat{y})$, or $(\hat{x}, \hat{q})$, are defined to be the *PG equilibrium point* of eqn (8).

4.1. THE LOCAL STABILITY OF THE PHENOTYPIC EQUILIBRIUM

The Jacobian matrix of eqn (8) at (x^*, y^*) is given by

$$\mathbf{J} = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix},$$

where

$$J_{11} = 2p(1 - p)(\mu_{A_1} - \mu_{A_2})^2\alpha_{11}|_{(x^*, y^*)}$$

$$J_{12} = 2p(1 - p)(\mu_{A_1} - \mu_{A_2})(\nu_{B_1} - \nu_{B_2})\alpha_{12}|_{(x^*, y^*)}$$

$$J_{21} = 2q(1 - q)(\mu_{A_1} - \mu_{A_2})(\nu_{B_1} - \nu_{B_2})\alpha_{21}|_{(x^*, y^*)}$$

$$J_{22} = 2q(1 - q)(\nu_{B_1} - \nu_{B_2})^2\alpha_{22}|_{(x^*, y^*)}.$$

Obviously, (x^*, y^*) is locally asymptotically stable if and only if

$$\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$$

$$[p(1 - p)(\mu_{A_1} - \mu_{A_2})^2\alpha_{11} + q(1 - q)(\nu_{B_1} - \nu_{B_2})^2\alpha_{22}]|_{(x^*, y^*)} < 0. \quad (14)$$

From Section 3, we obtain that if the phenotypic equilibrium point (x^*, y^*), of eqn (8) is a two-species ESS, then it must be locally asymptotically stable.

Inequality (14) shows that other phenotypic equilibria can be asymptotically stable in eqn (8), but we also have to note that any non-ESS phenotypic equilibrium will be unstable for some single-species diploid models (Maynard Smith, 1982; Lessard, 1984;Hofbauer & Sigmund, 1988; Cressman, 1992).

4.2. THE LOCAL STABILITY OF THE GENETIC EQUILIBRIUM

Since we have $\partial(\mathrm{d}p/\mathrm{d}t)/\partial q = 0$ and $\partial(\mathrm{d}q/\mathrm{d}t)/\partial p = 0$ at $(\hat{p}, \hat{q})$, the eigenvalues of the Jacobian matrix of eqn(8) at $(\hat{p}, \hat{q})$ can be given by

$$\begin{aligned}\lambda_1 &= \hat{p}(1-\hat{p})(P_{11} - 2P_{12} + P_{22})[\alpha_{11}x(\hat{p}) + \alpha_{12}y(\hat{q}) - \beta_1] \\ &= -\hat{p}(1-\hat{p})\{2f_{A_1A_2}[x(\hat{p}), y(\hat{q})] \\ &\quad - f_{A_1A_1}[x(\hat{p}), y(\hat{q})] - f_{A_2A_2}[x(\hat{p}), y(\hat{q})]\} \\ \lambda_2 &= \hat{q}(1-\hat{q})(Q_{11} - 2Q_{12} + Q_{22})[\alpha_{21}x(\hat{p}) + \alpha_{22}y(\hat{q}) - \beta_2] \\ &= -\hat{q}(1-\hat{q})\{2F_{B_1B_2}[x(\hat{p}), y(\hat{q})] \\ &\quad - F_{B_1B_1}[x(\hat{p}), y(\hat{q}) - F_{B_2B_2}[x(\hat{p}), y(\hat{q})]\}. \qquad (15)\end{aligned}$$

Equation (15) shows that:

(i) at $(\hat{p}, \hat{q})$, if there are heterozygote advantages in both species, then $(\hat{p}, \hat{q})$ must be locally asymptotically stable;

(ii) at $(\hat{p}, \hat{q})$, if only one species has heterozygote advantage, but the other one has not, then $(\hat{p}, \hat{q})$ is an unstable saddle point;

(iii) at $(\hat{p}, \hat{q})$, if there are not heterozygote advantages in both species, then $(\hat{p}, \hat{q})$ must be completely unstable.

4.3. THE LOCAL STABILITY OF THE PG EQUILIBRIUM POINTS

Since the PG equilibrium points $(\hat{p}, \hat{y})$ and $(\hat{x}, \hat{q})$ have identical properties on the stability, here we only need to discuss the local stability of $(\hat{p}, \hat{y})$.

At $(\hat{p}, \hat{y})$, we still have $\partial(\mathrm{d}p/\mathrm{d}t)/\partial q = 0$ and $\partial(\mathrm{d}q/\mathrm{d}t)/\partial p = 0$. Thus the eigenvalues of the Jacobian matrix of eqn (8) at $(\hat{p}, \hat{y})$ can be given by

$$\begin{aligned}\lambda_1 &= p(1-p)(P_{11} - 2P_{12} + P_{22})(\alpha_{11}x + \alpha_{12}y - \beta_1)\big|_{(\hat{p},\hat{y})} \\ &= -p(1-p)[2f_{A_1A_2}(x,y) - f_{A_1A_1}(x,y) - f_{A_2A_2}(x,y)]\big|_{(\hat{p},\hat{y})} \\ \lambda_2 &= 2q(1-q)(v_{B_1} - v_{B_2})^2\alpha_{22}\big|_{(\hat{p},\hat{y})}. \qquad (16)\end{aligned}$$

Equation (16) shows that:

(i) if the genetic equilibrium corresponds to heterozygote advantages and the phenotypic equilibrium is a single-species ESS (Cressman, 1996), then the PG equilibrium point must be locally asymptotically stable;

(ii) if the genetic equilibrium corresponds to heterozygote advantages, but the phenotypic equilibrium is not a single-species ESS, or if the phenotypic equilibrium is a single-species ESS, but the genetic equilibrium does not correspond to heterozygote advantages, then the PG equilibrium point is an unstable saddle point;

(iii) if the genetic equilibrium does not correspond to heterozygote advantage and the phenotypic equilibrium is not a single-species ESS, then the PG equilibrium point must be completely unstable.

Summarizing the results of Sections 4.1, 4.2 and 4.3, we can note that the results of Sections 4.1 and 4.2 are very similar to Lessard's (1984) results in the single-species two-phenotype model [see also Hofbauer & Sigmund (1988) and Cressman (1992)]. The result of Section 4.3 should be considered to be a new result since the PG equilibrium points defined by the author only exist in the two-species diploid model.

5. Conclusion

Cressman (1996) first developed the two-species matrix games model. This model should be considered to be a basic theoretical framework for the coevolution of the multi-interacting species. The concept of the two-species ESS developed by Cressman (1996) is very important for understanding the evolution of the interspecific relationship. In this paper, Cressman's (1996) two-species haploid model has been extended to the diploid model. A simple two-phenotype, two-allele, single-locus, two-species diploid model has been investigated. In this model, it has been assumed that the two interacting populations are Mendelian populations. In Section 3, the necessary and sufficient conditions have been given for a two-species ESS in the two-phenotype, two-species haploid model, which are $\alpha_{11} < 0$, $\alpha_{22} < 0$ and $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$. In Section 4, the local stability of the interior positive equilibrium point of the two-species diploid model has been analysed. The results show that:

(i) in the two-species diploid model, three possible types of interior positive equilibrium points can exist. These are phenotypic equilibrium points, genetic equilibrium points and PG equilibrium points;

(ii) at a phenotypic equilibrium point, if the phenotypic equilibrium point is a two-species ESS, then it must be locally asymptotically stable;

(iii) at a genetic equilibrium point, if there are heterozygote advantages in both species, then the genetic equilibrium point must be locally asymptotically stable;

(iv) at a PG equilibrium point, one species exhibiting phenotypic equilibrium and the other one genetic equilibrium, if the genetic equilibrium corresponds to heterozygote advantage and the phenotypic equilibrium is a single-species ESS (Cressman, 1996), then the PG equilibrium point must be locally asymptotically stable.

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REFERENCES

Cressman, R. (1992). The stability concept of evolutionary game theory (a dynamic approach). *Lecture Note in Biomathematics*, Vol. 94. Berlin: Springer-Verlag.

Cressman, R. (1996). Frequency-dependent selection for two-species interactions. *Theor. Pop. Biol.* **49,** 189–210.

Crow, J. F. & Kimura, A. (1970). *An Introduction to Population Genetics Theory*. New York: Harper & Row.

Hofbauer, J. & Sigmund, K. (1988). *The Theory of Evolution and Dynamical Systems*. Cambridge: Cambridge University Press.

Lessard, S. (1984). Evolutionary dynamics in frequency dependent two-phenotype models. *Theor. Pop. Biol.* **25,** 210–234.

Maynard-Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Roughgarden, J. (1979). *Theory of Population Genetics and Evolutionary Ecology: an Introduction*. New York: Macmillan.