

PERSISTENCE AND EXTINCTION IN A PREDATOR-PREY MODEL CONSISTING OF NINE PREY GENOTYPES

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Abstract

A predator-prey model in which the prey population is subdivided into nine genotypes corresponding to a two-locus, two-allele problem is considered. Sufficient conditions are given which lead to extinction of all the prey allele types except one, as well as conditions which guarantee the persistence of all the allele types.

1. Introduction

In Freedman and Waltman [5, 6] and Freedman, So and Waltman [7], the authors considered a predator-prey model in which the prey population consists of three genotypes corresponding to a one-locus, two-allele problem. In this paper, we extend that model to the case when the prey population is subdivided into nine genotypes corresponding to a two-locus, two-allele problem. Let A and a denote the two allele types at the first (prey) locus and let B and b denote the two allele types at the second locus. Since we shall not distinguish between the genotypes AB/ab and Ab/aB (they will be combined and denoted by $AaBa$), we denote the number of prey of the genotype $AABB$ (resp. $AABb$, $AAbb$, $AaBB$, $AaBb$, $Aabb$, $aaBB$, $aaBb$, $aabb$) by x_{11} (resp. x_{12} , x_{13} , x_{21} , x_{22} , x_{23} , x_{31} , x_{32} , x_{33}). Also, let y denote the number of

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predators. The model we wish to consider is of the form:

$$\begin{aligned}
 \dot{x}_{11} &= (u_1^2/x^2)B(x) - (x_{11}/x)[D(x) + yP_{11}(x)] \\
 \dot{x}_{12} &= (2u_1u_2/x_2)B(x) - (x_{12}/x)[D(x) + yP_{12}(x)] \\
 \dot{x}_{13} &= (u_2^2/x^2)B(x) - (x_{13}/x)[D(x) + yP_{13}(x)] \\
 \dot{x}_{21} &= (2u_1u_3/x^2)B(x) - (x_{21}/x)[D(x) + yP_{21}(x)] \\
 \dot{x}_{22} &= (2(u_1u_4 + u_2u_3)/x_2)B(x) - (x_{22}/x)[D(x) + yP_{22}(x)] \\
 \dot{x}_{23} &= (2u_2u_4/x^2)B(x) - (x_{23}/x)[D(x) + yP_{23}(x)] \\
 \dot{x}_{31} &= (u_3^2/x^2)B(x) - (x_{31}/x)[D(x) + yP_{31}(x)] \\
 \dot{x}_{32} &= (2u_3u_4/x^2)B(x) - (x_{32}/x)[D(x) + yP_{32}(x)] \\
 \dot{x}_{33} &= (u_4^2/x^2)B(x) - (x_{33}/x)[D(x) + yP_{33}(x)] \\
 \dot{y} &= y \left[-s + k \sum_{i,j=1}^3 \frac{x_{ij}}{x} P_{ij}(x) \right]
 \end{aligned}
 \tag{1.1}$$

$$x_{ij}(0) \geq 0 \quad (i, j = 1, 2, 3), \quad y(0) \geq 0,$$

where $\dot{} = \frac{d}{dt}$ and $s, k > 0$. Here u_1 (resp. u_2, u_3 and u_4) is the number of prey of the gamete type AB (resp. Ab, aB and ab); that is,

$$\begin{aligned}
 u_1 &= x_{11} + x_{12}/2 + x_{21}/2 + x_{22}/4 \\
 u_2 &= x_{13} + x_{12}/2 + x_{23}/2 + x_{22}/4 \\
 u_3 &= x_{31} + x_{21}/2 + x_{32}/2 + x_{22}/4 \\
 u_4 &= x_{33} + x_{23}/2 + x_{32}/2 + x_{22}/4,
 \end{aligned}
 \tag{1.2}$$

and x is the total prey population, that is:

$$x = \sum_{i,j=1}^3 x_{ij} = \sum_{i=1}^4 u_i. \tag{1.3}$$

$B(x)/x$ (resp. $D(x)/x$) is the natural, intrinsic birth (resp. death) rate of the entire prey population. The constant s is the death rate of the predator in the absence of prey. $P_{ij}(x)$ ($i, j = 1, 2, 3$) is the predator functional response on the prey genotype x_{ij} . The constant k is the conversion factor from prey biomass to predator biomass. $B(x), D(x)$, and $P_{ij}(x)$ ($i, j = 1, 2, 3$) are assumed to satisfy (H1)–(H6) of So and Freedman [10], namely,

- (H1) $B, D, P_{ij} : [0, \infty) \rightarrow [0, \infty)$ ($i, j = 1, 2, 3$) are smooth (C^2);
- (H2) $B(0) = D(0) = P_{ij}(0)$ ($i, j = 1, 2, 3$);
- (H3) $B'(x) > 0, D'(x) > 0, P'_{ij}(x) > 0$ ($i, j = 1, 2, 3$) for all $x \in [0, \infty)$;
- (H4) $B'(0) > D'(0)$;
- (H5) there exists a unique $K > 0$ (carrying capacity of prey) such that $B(K) = D(K)$; and,
- (H6) $B'(K) < D'(K)$ where $' = d/dx$.

The derivation of (1.1) is similar to that given in So [9]. Let f be the common fertility of the nine prey genotypes. The total number of gametes in the gamete pool is given by $fu_1 + fu_2 + fu_3 + fu_4 = fx$. By the assumption of random union of gametes, the proportion of $AABB$ genotypes produced is $(fu_1/fx)(fu_1/fx) = u_1^2/x^2$. This accounts for the coefficients of $B(x)$ in the first equation of (1.1). The other coefficients are derived similarly.

The main purpose of this paper is to obtain conditions under which system (1.1) exhibits uniform persistence (that is, there exists $\eta > 0$ such that $\liminf_{t \rightarrow +\infty} x_{ij}(t) \geq \eta$ ($i, j = 1, 2, 3$) and $\liminf_{t \rightarrow +\infty} y(t) \geq \eta$ for all solutions $(x_{11}(t), \dots, x_{33}(t), y(t))$ of (1.1) with $x_{ij}(0) > 0$ ($i, j = 1, 2, 3$) and $y(0) > 0$), as well as conditions which lead to the extinction of all the prey gamete types except one. In the process, we show that if the predator is absent then the prey genotypes converge to Hardy-Weinberg proportions. Also a comparison between the two-locus model (1.1) and the previously studied one-locus model will be discussed.

The remainder of the paper is organized as follows. In the next section we introduce the necessary notations and summarize some elementary facts about (1.1). In Section 3, the case when the predator is absent will be considered. Section 4 deals with the extinction cases, while the persistent cases are considered in Section 5. We finish with a discussion and comparison of our results for the two-locus model (1.1) with those for the one-locus model in Section 6.

2. Preliminaries

We first introduce some notations which will be useful later. Let $\mathbb{R}_+^n = \{(z_1, \dots, z_n) \in \mathbb{R}^n : z_i \geq 0 (i = 1, \dots, n)\}$ denote the non-negative cone in \mathbb{R}^n . For a set $S \subset \mathbb{R}^n$, $\text{cl}(S)$ denotes its closure, $\overset{\circ}{S}$ denotes its interior and $\partial(S)$ denotes its boundary. In particular, $\overset{\circ}{\mathbb{R}}_+^n$ denotes the positive cone in \mathbb{R}^n . Let H_{z_i} denote the non-negative z_i axis in \mathbb{R}^n , i.e., $H_{z_i} = \{(0, \dots, 0, z_i, 0, \dots, 0) \in \mathbb{R}^n : z_i \geq 0\}$. Similarly, H_{z_i, z_j} denotes the cone spanned by the non-negative z_i and z_j axes in \mathbb{R}^n , i.e.,

$$H_{z_i, z_j} = \{(0, \dots, 0, z_i, 0, \dots, 0, z_j, 0, \dots, 0) \in \mathbb{R}^n : z_i, z_j \geq 0\},$$

etc.

System (1.1) is not defined when $(X, y) \equiv (x_{11}, \dots, x_{33}, y) = (0, \dots, 0, y)$. When $(X, y) = (0, \dots, 0, y)$, we define (1.1) to be

$$\dot{x}_{ij} = 0, \quad \dot{y} = -sy. \quad (2.1)$$

It is easily seen that with the extended definition (2.1), the right hand side (RHS) of (1.1) is locally Lipschitz on \mathbb{R}_+^{10} and is C^2 on $\overset{\circ}{\mathbb{R}}_+^{10}$. Thus (1.1) defines a continuous semiflow on \mathbb{R}_+^{10} which becomes a smooth (C^2) local flow when restricted to $\overset{\circ}{\mathbb{R}}_+^{10}$. Moreover, it is \mathcal{A} -dissipative with

$$\mathcal{A} = \{(x_{11}, \dots, x_{33}, y) \in \mathbb{R}_+^{10} : x \leq K \text{ and } kx + y \leq \frac{k}{s}(M + sK)\}, \quad (2.2)$$

where $M = \max\{B(x) - D(x) : x \in [0, K]\}$. That is, for all solutions $(X(t), y(t)) \equiv (x_{11}(t), \dots, x_{33}(t), y(t))$ of (1.1), $\text{dist}(\mathcal{A}, (X(t), y(t))) \rightarrow 0$ as $t \rightarrow +\infty$ where $\text{dist}(\cdot, \cdot)$ denotes the Euclidean distance (cf. p. 472–474 of So and Freedman [10]). Hence, solutions of (1.1) are bounded for all positive time. Further, $H_{x_{11}}, H_{x_{13}}, H_{x_{31}}, H_{x_{33}}, H_y, H_{x_{11}, y}, H_{x_{13}, y}, H_{x_{31}, y}, H_{x_{33}, y}$ are invariant and $H_{x_{11}, x_{12}, x_{13}}, H_{x_{11}, x_{21}, x_{31}}, H_{x_{13}, x_{23}, x_{33}}, H_{x_{31}, x_{32}, x_{33}}, H_{x_{11}, x_{12}, x_{13}, y}, H_{x_{11}, x_{21}, x_{31}, y}, H_{x_{13}, x_{23}, x_{33}, y}, H_{x_{31}, x_{32}, x_{33}, y}$, and $H_{x_{11}, \dots, x_{33}}$ are positively invariant. The vector field $F_{(1.1)}$ defined by the RHS of (1.1) points into $\overset{\circ}{\mathbb{R}}_+^{10}$ on $\partial(\mathbb{R}_+^{10}) \setminus \nu$, where

$$\begin{aligned} \nu = & H_{x_{11}, x_{12}, x_{13}, y} \cup H_{x_{11}, x_{21}, x_{31}, y} \cup H_{x_{13}, x_{23}, x_{33}, y} \\ & \cup H_{x_{31}, x_{32}, x_{33}, y} \cup H_{x_{11}, \dots, x_{33}}. \end{aligned} \quad (2.3)$$

Thus, no point in $\partial(\mathbb{R}_+^{10}) \setminus \nu$ can lie in the omega limit set of any point in $\overset{\circ}{\mathbb{R}}_+^{10}$.

We will now list some of the equilibrium points of (1.1) and discuss their stability. More discussions will be given in later sections. By (2.1), $E_0 = (0, \dots, 0, 0)$ is an equilibrium point of (1.1). System (1.1) when restricted to the invariant set $H_{x_{ij}, y}$ ($i, j = 1, 3$) is the usual generalized Gauss predator-prey model (c.f. Chapter 4 of Freedman [4]). Thus $H_{x_{ij}, y}$ ($i, j = 1, 3$) contains a positive equilibrium point if and only if $b_{ij} > 0$ ($i, j = 1, 3$), where

$$b_{ij} = -s + kP_{ij}(K) \quad (i, j = 1, 3). \quad (2.4)$$

Also, these equilibrium points are unique, by (H3). Let us denote them by E_i ($i = 1, \dots, 4$). That is, let $E_1 = (\bar{x}_{11}, 0, \dots, 0, \bar{y}_{11})$, $E_2 = (0, 0, \bar{x}_{13}, 0, \dots, 0, \bar{y}_{13})$, $E_3 = (0, \dots, 0, \bar{x}_{31}, 0, 0, \bar{y}_{31})$, and $E_4 = (0, \dots, 0, \bar{x}_{33}, \bar{y}_{33})$ where $\bar{x}_{ij}, \bar{y}_{ij} > 0$ ($i, j = 1, 3$). System (1.1) when restricted to the positively invariant set $H_{x_{11}, x_{21}, x_{31}, y}$ (resp. $H_{x_{11}, x_{12}, x_{13}, y}, H_{x_{13}, x_{23}, x_{33}, y}$, and $H_{x_{31}, x_{32}, x_{33}, y}$) is the one-locus, two-allele model, considered in Freedman and Waltman [5,6] and Freedman, So and Waltman [7], whose global dynamics is known when there is an ordering of the predator functional responses. In particular, we point out Theorem 3.1 of Freedman, So and Waltman [7], which will be used repeatedly in Sections 4 and 5. The positively invariant sets $H_{x_{11}, x_{21}, x_{31}, y}, H_{x_{11}, x_{12}, x_{13}, y}, H_{x_{13}, x_{23}, x_{33}, y}$, and $H_{x_{31}, x_{32}, x_{33}, y}$ may or may not contain equilibrium points. Some conditions are known which guarantee the existence or non-existence of these equilibrium points (see Freeman, So and Waltman [7]).

However, we will not use these criteria in what follows. Finally, it will be shown in Corollary 3.3 that $H_{x_{11}, \dots, x_{33}}$ contains a two-dimensional set of equilibrium points.

E_0 is unstable and in fact we have the following proposition.

PROPOSITION 2.1. *For all $(\hat{X}, \hat{y}) \equiv (\hat{x}_{11}, \dots, \hat{x}_{33}, \hat{y}) \in \mathring{\mathbb{R}}_+^{10}$, we have, $E_0 \notin \omega(\hat{X}, \hat{y})$, the omega limit set of the point (\hat{X}, \hat{y}) .*

PROOF. First we observe that since the flow on \mathring{H}_y is given by $\dot{y} = -sy$ whose negative orbits are all unbounded, $(0, \dots, 0, y^*) \notin \omega(\hat{X}, \hat{y})$ for any $y^* > 0$. Next, for (X, y) near E_0 , we have

$$\dot{x} \geq B(x) - D(x) - yP(x) \geq k_1x \quad \text{for some } k_1 > 0$$

and

$$\dot{y} \leq y(-s + kP(x)) \leq -k_2y \quad \text{for some } k_2 > 0,$$

where $P(x) = \max\{P_{ij}(x) : 0 \leq x \leq K, i, j = 1, 2, 3\}$. Therefore $\{E_0\}$ is an isolated invariant set and its stable set, $W^s(E_0)$, is H_y . According to Theorem 4.1 of Butler and Waltman [1], if $E_0 \in \omega(\hat{X}, \hat{y})$ then $W^s(E_0) \cap \omega(\hat{X}, \hat{y})$ contains a point other than E_0 , which is a contradiction. (See also Lemma 1 of Freedman and So [10].)

TABLE 1. $M(E_1)$ is given by

	x_{11}	y	x_{12}	x_{13}	x_{21}	x_{22}	x_{23}	x_{32}	x_{32}	x_{33}
x_{11}	?	-ve	?	?	?	?	?	?	?	?
y	+ve	0	?	?	?	?	?	?	?	?
x_{12}	0	0	?	+ve	0	+ve	+ve	0	0	0
x_{13}	0	0	0	-ve	0	0	0	0	0	0
x_{21}	0	0	0	0	?	+ve	0	+ve	+ve	0
x_{22}	0	0	0	0	0	?	+ve	0	+ve	+ve
x_{23}	0	0	0	0	0	0	-ve	0	0	0
x_{31}	0	0	0	0	0	0	0	-ve	0	0
x_{32}	0	0	0	0	0	0	0	0	-ve	0
x_{33}	0	0	0	0	0	0	0	0	0	-ve

where +ve (resp. -ve, 0, ?) means that the entry is positive (resp. is negative, zero, has indeterminate sign).

The stability of $E_i (i = 1, 2, 3, 4)$ is governed by the signs of the real parts of the eigenvalues of the variational matrix $M(E_i)$ ($i = 1, 2, 3, 4$) of (1.1) evaluated at E_i ($i = 1, 2, 3, 4$). For illustration we present $M(E_1)$ in Table 1. Note that y is moved from the 10th to the 2nd position.

The nonzero entries of $M(E_1)$ are given by:

$$M_{11,11}(E_1) = B'(\bar{x}_{11}) - D'(\bar{x}_{11}) - \bar{y}_{11}P'_{11}(\bar{x}_{11})$$

$$M_{11,y}(E_1) = -P_{11}(\bar{x}_{11}) < 0$$

$$M_{11,12}(E_1) = M_{11,21}(E_1) = B'(\bar{x}_{11}) - D'(\bar{x}_{11}) - \bar{y}_{11}P'_{11}(\bar{x}_{11})$$

$$M_{11,22}(E_1) = -B(\bar{x}_{11})/(2\bar{x}_{11}) + B'(\bar{x}_{11}) - D'(\bar{x}_{11}) - \bar{y}_{11}P'_{11}(\bar{x}_{11})$$

$$M_{11,ij}(E_1) = -B(\bar{x}_{11})/\bar{x}_{11} + B'(\bar{x}_{11})D'(\bar{x}_{11}) - \bar{y}_{11}P'_{11}(\bar{x}_{11})$$

for $(i, j) = (1, 3), (2, 3), (3, 1), (3, 2)$ and (3.3)

$$M_{y,11}(E_1) = k\bar{y}_{11}P'_{11}(\bar{x}_{11}) > 0$$

$$M_{y,ij}(E_1) = (k\bar{y}_{11}/\bar{x}_{11})[\bar{x}_{11}P'_{11}(\bar{x}_{11}) + P_{ij}(\bar{x}_{11}) - P_{11}(\bar{x}_{11})],$$

for $(i, j) \neq (1, 1)$

$$M_{12,12}(E_1) = \frac{1}{\bar{x}_{11}} [B(\bar{x}_{11}) - D(\bar{x}_{11}) - \bar{y}_{11}P_{12}(\bar{x}_{11})] = \frac{\bar{y}_{11}}{\bar{x}_{11}} \left[\frac{s}{k} - P_{12}(\bar{x}_{11}) \right]$$

$$M_{12,13}(E_1) = B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{12,22}(E_1) = B(\bar{x}_{11})/(2\bar{x}_{11}) > 0$$

$$M_{12,23}(E_1) = B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{13,13}(E_1) = - [D(\bar{x}_{11}) + \bar{y}_{11}P_{13}(\bar{x}_{11})]/\bar{x}_{11} < 0$$

$$M_{21,21}(E_1) = \frac{1}{\bar{x}_{11}} [B(\bar{x}_{11}) - D(\bar{x}_{11}) - \bar{y}_{11}P_{21}(\bar{x}_{11})] = \frac{\bar{y}_{11}}{\bar{x}_{11}} \left[\frac{s}{k} - P_{21}(\bar{x}_{11}) \right]$$

$$M_{21,22}(E_1) = B(\bar{x}_{11})/(2\bar{x}_{11}) > 0$$

$$M_{21,31}(E_1) = B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{21,32}(E_1) = B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{22,22}(E_1) = \frac{1}{\bar{x}_{11}} \left[\frac{1}{2}B(\bar{x}_{11}) - D(\bar{x}_{11}) - \bar{y}_{11}P_{22}(\bar{x}_{11}) \right]$$

$$= \frac{1}{\bar{x}_{11}} \left[\bar{y}_{11} \left(\frac{s}{k} - P_{22}(\bar{x}_{11}) \right) - \frac{1}{2}B(\bar{x}_{11}) \right]$$

$$M_{22,23}(E_1) = B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{22,32}(E_1) = B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{22,23}(E_1) = 2B(\bar{x}_{11})/\bar{x}_{11} > 0$$

$$M_{23,23}(E_1) = - [D(\bar{x}_{11}) + \bar{y}_{11}P_{23}(\bar{x}_{11})]/\bar{x}_{11} < 0$$

$$M_{31,31}(E_1) = - [D(\bar{x}_{11}) + \bar{y}_{11}P_{31}(\bar{x}_{11})]/\bar{x}_{11} < 0$$

$$M_{32,32}(E_1) = - [D(\bar{x}_{11}) + \bar{y}_{11}P_{32}(\bar{x}_{11})]/\bar{x}_{11} < 0$$

$$M_{33,33}(E_1) = - [D(\bar{x}_{11}) + \bar{y}_{11}P_{33}(\bar{x}_{11})]/\bar{x}_{11} < 0.$$

Therefore $M(E_1)$ has five negative eigenvalues: $M_{13,13}(E_1), M_{23,23}(E_1), M_{31,31}(E_1), M_{32,32}(E_1), M_{33,33}(E_1)$; three real eigenvalues with indeterminate signs: $M_{12,12}(E_1), M_{21,21}(E_1), M_{22,22}(E_1)$; and the sign of the real parts of the two remaining eigenvalues (corresponding to eigenvectors lying on the x_{11} - y plane) is the same as that of the sign of $M_{11,11}(E_1)$.

In order to apply Theorem 3.1 and Theorem 4.1 of Butler and Waltman [1] to show persistence in the latter sections, we need to know the stable set of a boundary equilibrium point, for example, the E_i 's. The following proposition is a very useful result, which allows us to show that the intersection of the stable manifold of a hyperbolic boundary equilibrium point with the positive cone $\mathring{\mathbb{R}}_+^n$, is empty, by knowing only one unstable eigen-direction.

PROPOSITION 2.2. *Consider $\dot{x} = f(x)$ ($x \in \mathbb{R}^n$). Assume that f is C^2 and that $\mathring{\mathbb{R}}_+^n$ is positively invariant. Let $E \in \partial(\mathring{\mathbb{R}}_+^n)$ be a hyperbolic equilibrium point. Denote the stable (resp. unstable) manifold of E by $W^s(E)$ (resp. $W^u(E)$). If $W^u(E) \cap (\mathbb{R}^n \setminus \mathring{\mathbb{R}}_+^n) \neq \emptyset$, then $W^s(E) \cap \mathring{\mathbb{R}}_+^n = \emptyset$.*

PROOF. Suppose not; that is, suppose $W^s(E) \cap \mathring{\mathbb{R}}_+^n \neq \emptyset$. If we can show that for fixed $p_1 \in W^s(E)$ and $p_2 \in W^u(E)$ where $p_1, p_2 \neq E$ and for arbitrary $\varepsilon > 0$, there exists a point p and a time $t > 0$ such that p is ε close to p_1 and $\pi(p, t)$ is ε close to p_2 , then this will contradict the positive invariance of $\mathring{\mathbb{R}}_+^n$. Since this can be reduced to a local question, by Hartman-Grobman's theorem, it suffices to establish the following.

Consider the system $\dot{x} = Ax, \dot{y} = By$ where $x \in \mathbb{R}^m, y \in \mathbb{R}^n$, and all the eigenvalues of A have negative real parts and all the eigenvalues of B have positive real parts. Fix $p_1 = (x^*, 0)$ and $p_2 = (0, y^*) \in \mathbb{R}^{m+n}$ with $x^* \neq 0$ and $y^* \neq 0$. Then there exists $(x_N, y_N) \in \mathbb{R}^{m+n}$ and $t_N > 0$ such that $(x_N, y_N) \rightarrow (x^*, 0)$ and $\pi((x_N, y_N), t_N) \rightarrow (0, y^*)$ as $N \rightarrow \infty$.

For a proof of the above statement, let $t_N = N, x_N = x^*$ and $y_N = e^{-t_N B} y^*$. Then clearly $x_N \rightarrow x^*$ and $y_N \rightarrow 0$ as $N \rightarrow \infty$, since all eigenvalues of B have positive real parts. Furthermore, we have,

$$\pi((x_N, y_N), t_N) = (e^{t_N A} x_N, e^{t_N B} y_N) = (e^{t_N A} x^*, y^*) \rightarrow (0, y^*)$$

as $N \rightarrow \infty$.

3. The case of no predators

In this section we shall consider the global dynamics of (1.1) when the predator y is absent. For the sake of future reference, let us refer to the

resulting system with nine equations as (NP). As in Section 2, we define the RHS of (NP) as the zero vector $(0, \dots, 0) \in \mathbb{R}^9$ when $X \equiv (x_{11}, \dots, x_{33}) = (0, \dots, 0)$. Then the RHS of (NP) will be a locally Lipschitz vector field $F_{(NP)}$ and (NP) defines a continuous semi-flow on \mathbb{R}_+^9 which becomes a smooth (C^2) local flow when restricted to $\overset{\circ}{\mathbb{R}}_+^9$. Since

$$\dot{x} = B(x) - D(x), \tag{3.1}$$

we have

$$\lim_{t \rightarrow \infty} x(t) = K \quad \text{for all } x(0) > 0. \tag{3.2}$$

Let σ denote the simplex

$$\sigma = \left\{ X \equiv (x_{11}, \dots, x_{33}) \in \mathbb{R}_+^9 : \sum_{i,j=1}^3 x_{ij} = K \right\}. \tag{3.3}$$

Then σ is positively invariant and is globally stable over $\mathbb{R}_+^9 \setminus \{(0, \dots, 0)\}$. $(0, \dots, 0)$ is a repelling equilibrium point. $H_{x_{11}}, H_{x_{13}}, H_{x_{31}}$ and $H_{x_{33}}$ are invariant and $H_{x_{11}, x_{12}, x_{13}}, H_{x_{11}, x_{21}, x_{31}}, H_{x_{13}, x_{23}, x_{33}}$ and $H_{x_{31}, x_{32}, x_{33}}$ are positively invariant. The vector field $F_{(NP)}$ points into \mathbb{R}_+^9 on $\partial(\mathbb{R}_+^9) \setminus (H_{x_{11}, x_{12}, x_{13}} \cup H_{x_{11}, x_{21}, x_{31}} \cup H_{x_{13}, x_{23}, x_{33}} \cup H_{x_{31}, x_{32}, x_{33}})$.

Clearly, by (3.2), all equilibrium points of (NP) other than $(0, \dots, 0)$ lie in σ . The following proposition and its first corollary describe the set of equilibrium points of (NP), which will be referred to as the Hardy-Weinberg manifold of (NP).

PROPOSITION 3.1. Define $H: \overset{\circ}{\mathbb{R}}_+^2 \rightarrow \sigma$ by

$$H(c_1, c_2) = (H_{11}(c_1, c_2), \dots, H_{33}(c_1, c_2)) \text{ for } (c_1, c_2) \in \overset{\circ}{\mathbb{R}}_+^2$$

where

$$\begin{aligned} H_{11}(c_1, c_2) &= c_1^2 c_2^2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{12}(c_1, c_2) &= 2c_1^2 c_2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{13}(c_1, c_2) &= c_1^2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{21}(c_1, c_2) &= 2c_1 c_2^2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{22}(c_1, c_2) &= 4c_1 c_2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{23}(c_1, c_2) &= 2c_1 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{31}(c_1, c_2) &= c_2^2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{32}(c_1, c_2) &= 2c_2 K / [(1 + c_1)^2 (1 + c_2)^2] \\ H_{33}(c_1, c_2) &= K / [(1 + c_1)^2 (1 + c_2)^2]. \end{aligned} \tag{3.4}$$

Then $H(\overset{\circ}{\mathbb{R}}_+^2)$, the image of $\overset{\circ}{\mathbb{R}}_+^2$ under H , is the set of all equilibrium points of (NP) in $\overset{\circ}{\mathbb{R}}_+^9$.

PROOF. First we show that all points of the form $H(c_1, c_2)$ where $(c_1, c_2) \in \overset{\circ}{\mathbb{R}}_+^2$ are equilibrium points of (NP). Let $H(c_1, c_2) = X^* \equiv (x_{11}^*, \dots, x_{33}^*)$. Clearly $X^* \in \overset{\circ}{\mathbb{R}}_+^9$. Define, as in (1.2),

$$\begin{aligned} u_1^* &= x_{11}^* + x_{12}^*/2 + x_{21}^*/2 + x_{22}^*/4 \\ u_2^* &= x_{13}^* + x_{12}^*/2 + x_{23}^*/2 + x_{22}^*/4 \\ u_3^* &= x_{31}^* + x_{21}^*/2 + x_{32}^*/2 + x_{22}^*/4 \\ u_4^* &= x_{33}^* + x_{23}^*/2 + x_{32}^*/2 + x_{22}^*/4 \end{aligned} \tag{3.5}$$

and

$$x^* = x_{11}^* + \dots + x_{33}^*.$$

Then

$$\begin{aligned} u_1^* &= c_1 c_2 K / [(1 + c_1)(1 + c_2)], & u_2^* &= c_1 K / [(1 + c_1)(1 + c_2)], \\ u_3^* &= c_2 K / [(1 + c_1)(1 + c_2)], & u_4^* &= K / [(1 + c_1)(1 + c_2)] \end{aligned} \tag{3.6}$$

and $x^* = K$. Therefore the first component $F_{(\text{NP})11}$ of the RHS of (NP) when evaluated at X^* is given by

$$(u_1^{*2}/x^{*2})B(x^*) - (x_{11}^*/x^*)D(x^*) = (u_1^{*2} - x_{11}^*K)B(K)/K^2 = 0.$$

Similarly, one shows that the other components of the RHS of (NP) are all equal to 0 and hence X^* is an equilibrium point.

Next, we show that every interior equilibrium point of (NP) is of the form $H(c_1, c_2)$ for some $(c_1, c_2) \in \overset{\circ}{\mathbb{R}}_+^2$. Let $X^* = (x_{11}^*, \dots, x_{33}^*)$ be an equilibrium point (NP) with $x_{ij}^* > 0 (i, j = 1, 2, 3)$. Define $u_1^*, u_2^*, u_3^*, u_4^*$ and x^* as in (3.5). Clearly $x^* = K$. Also define

$$d_{ij} = x_{ij}^*/x_{33}^* \quad (i, j = 1, 2, 3) \tag{3.7}$$

and

$$r_i = u_i^*/x_{33}^* \quad (i = 1, \dots, 4). \tag{3.8}$$

Then

$$r_1^2 x_{33}^* = d_{11}K \tag{i}$$

$$2r_1 r_2 x_{33}^* = d_{12}K \tag{ii}$$

$$r_2^2 x_{33}^* = d_{13}K \tag{iii}$$

$$2r_1 r_3 x_{33}^* = d_{21}K \tag{iv}$$

$$(2r_1 r_4 + 2r_2 r_3) x_{33}^* = d_{22}K \tag{v}$$

$$2r_2 r_4 x_{33}^* = d_{23}K \tag{vi}$$

$$r_3^2 x_{33}^* = d_{31}K \tag{vii}$$

$$2r_3 r_4 x_{33}^* = d_{32}K \tag{viii}$$

$$r_4^2 x_{33}^* = d_{33}K = K. \tag{ix}$$

Define $c_1, c_2 > 0$ by $c_1 = x_{23}^*/(2x_{33}^*)$ and $c_2 = x_{32}^*/(2x_{33}^*)$. Then $2c_1 = d_{23}$ and $2c_2 = d_{32}$. Moreover, (ii)/(i): $2r_2/r_1 = d_{12}/d_{11}$ and (ii)/(iii): $2r_1/r_2 = d_{12}/d_{13}$ give $d_{12}^2 = 4d_{11}d_{13}$. (viii)/(vii): $2r_4/r_3 = d_{32}/d_{31}$ and (viii)/(ix): $2r_3/r_4 = d_{32}/d_{33} = d_{32}$ give $d_{31} = c_2^2$. (iv)/(i): $2r_3/r_1 = d_{21}/d_{11}$ and (iv)/(vii): $2r_1/r_3 = d_{21}/d_{31}$ give $d_{21} = 2c_2\sqrt{d_{11}}$. (vi)/(iii): $2r_4/r_2 = d_{23}/d_{13}$ and (vi)/(ix): $2r_2/r_4 = d_{23}d_{33} = d_{23}$ give $d_{13} = c_1^2$. Thus, $d_{12} = 2c_1\sqrt{d_{11}}$. Since $r_2/r_1 = c_1/\sqrt{d_{11}}$, $r_3/r_1 = c_2/\sqrt{d_{11}}$, $r_4/r_1 = 1/\sqrt{d_{11}}$, and (v)/(i): $2r_4/r_1 + 2r_2r_3/r_1^2 = d_{22}/d_{11}$, therefore $d_{22} = 2c_1c_2 + 2\sqrt{d_{11}}$. Substituting all of the above into the equation $x^* = K$, we get

$$(d_{11} + 2c_1\sqrt{d_{11}} + c_1^2 + 2c_2\sqrt{d_{11}} + 2c_1c_2 + 2\sqrt{d_{11}} + 2c_1 + c_2^2 + 2c_2 + 1)x_{33}^* = K$$

which in turn implies that $x_{33}^* = K/(\sqrt{d_{11}} + c_1 + c_2 + 1)^2$. Now, substituting the latter into (i) and by noting $r_1 = d_{11} + d_{12}/2 + d_{21}/2 + d_{22}/4$, we have $d_{11} = c_1^2c_2^2$. From this, one can easily deduce that $X^* = H(c_1, c_2)$.

COROLLARY 3.2. $Cl(H(\mathbb{R}_+^{\circ 2})) = H(\mathbb{R}_+^2)$ is the set of equilibrium points of (NP) in $\mathbb{R}_+^9 \setminus \{(0, \dots, 0)\}$.

COROLLARY 3.3. $H(\mathbb{R}_+^1) \times \{0\}$ is the set of equilibrium points of (1.1) in $H_{x_{11}, \dots, x_{33}} \setminus \{(0, \dots, 0, 0)\}$.

The main result of this section is a complete description of the global dynamics of (NP): all solutions $X(t)$ of (NP) other than $X(t) \equiv 0$ converge to the Hardy-Weinberg manifold as $t \rightarrow +\infty$. In order to describe this result more precisely and to present its proof, we need to introduce some auxiliary

quantities. Define

$$\begin{aligned}x_{AA} &= x_{11} + x_{12} + x_{13} \\x_{Aa} &= x_{21} + x_{22} + x_{23}\end{aligned}\tag{3.9}$$

$$\begin{aligned}x_{aa} &= x_{31} + x_{32} + x_{33}, \\x_{BB} &= x_{11} + x_{21} + x_{31} \\x_{Bb} &= x_{12} + x_{22} + x_{32} \\x_{bb} &= x_{13} + x_{23} + x_{33},\end{aligned}\tag{3.10}$$

$$u_A = x_{AA} + x_{Aa}/2, \quad u_a = x_{aa} + x_{Aa}/2,\tag{3.11}$$

and

$$u_B = x_{BB} + x_{Bb}/2, \quad u_b = x_{bb} + x_{Bb}/2.\tag{3.12}$$

Clearly

$$\begin{aligned}u_A + u_a &= x_{AA} + x_{Aa} + x_{aa} = x \\u_B + u_b &= x_{BB} + x_{Bb} + x_{bb} = x,\end{aligned}\tag{3.13}$$

and

$$\begin{aligned}u_A &= u_1 + u_2, & u_a &= u_3 + u_4, \\u_B &= u_1 + u_3, & u_b &= u_2 + u_4.\end{aligned}\tag{3.14}$$

THEOREM 3.4. Define $c_1 = u_A(0)/u_a(0)$ and $c_2 = u_B(0)/u_b(0)$. Then

$$(x_{11}(t), \dots, x_{33}(t)) \rightarrow H(c_1, c_2)\tag{3.15}$$

as $t \rightarrow +\infty$, where $H(c_1, c_2)$ was given in (3.4).

Before we prove Theorem 3.4, we need a couple of lemmas describing the long term behaviour of the auxiliary quantities defined in (3.9)–(3.12), as well as that of the u_i 's.

LEMMA 3.5. Let $c_1 = u_A(0)/u_a(0)$ and $c_2 = u_B(0)/u_b(0)$. Then

$$(I) \quad u_A(t) = c_1 u_a(t), \quad u_B(t) = c_2 u_b(t) \quad \text{for all } t \geq 0,\tag{3.16}$$

$$(II) \quad (u_A(t), u_a(t)) \rightarrow (c_1 K/(1 + c_1), K/(1 + c_1))\tag{3.17}$$

$$(u_B(t), u_b(t)) \rightarrow (c_2 K/(1 + c_2), K/(1 + c_2))\tag{3.18}$$

as $t \rightarrow +\infty$, and,

$$(III) \quad (x_{AA}(t), x_{Aa}(t), x_{aa}(t)) \rightarrow \left(\frac{c_1^2 K}{(1+c_1)^2}, \frac{2c_1 K}{(1+c_2)^2}, \frac{K}{(1+c_1)^2} \right) \quad (3.19)$$

$$(x_{BB}(t), x_{Bb}(t), x_{bb}(t)) \rightarrow \left(\frac{c_2^2 K}{(1+c_2)^2}, \frac{2c_2 K}{(1+c_2)^2}, \frac{K}{(1+c_2)^2} \right) \quad (3.20)$$

as $t \rightarrow +\infty$.

PROOF. Clearly

$$\begin{aligned} \dot{x}_{AA} &= (u_A^2/x^2)B(x) - (x_{AA}/x)D(x) \\ \dot{x}_{Aa} &= (2u_A u_a/x^2)B(x) - (x_{Aa}/x)D(x) \\ \dot{x}_{aa} &= (u_a^2/x^2)B(x) - (x_{aa}/x)D(x) \end{aligned} \quad (3.21)$$

and

$$\begin{aligned} \dot{x}_{BB} &= (u_B^2/x^2)B(x) - (x_{BB}/x)D(x) \\ \dot{x}_{Bb} &= (2u_B u_b/x^2)B(x) - (x_{Bb}/x)D(x) \\ \dot{x}_{bb} &= (u_b^2/x^2)B(x) - (x_{bb}/x)D(x). \end{aligned} \quad (3.22)$$

Proceeding as in the one-locus case (c.f. p. 369 of Freedman and Waltman [5], and p. 231 of So [9]) one can easily show that (I) holds and that

$$\begin{aligned} x_{AA}(t) - c_1^2 x_{aa}(t) &\rightarrow 0, & x_{Aa}(t) - 2c_1 x_{aa}(t) &\rightarrow 0 \\ x_{BB}(t) - c_2^2 x_{bb}(t) &\rightarrow 0, & x_{Bb}(t) - 2c_2 x_{bb}(t) &\rightarrow 0, \end{aligned} \quad (3.23)$$

as $t \rightarrow +\infty$. (II) and (III) now follow from (3.2), (3.13) and (3.23).

REMARK. Lemma 3.5 and (3.14) show that

$$\begin{aligned} u_1(t) &= c_2 u_b(t) - u_a(t) + u_4(t) = c_1 u_a(t) - u_b(t) + u_4(t) \\ u_2(t) &= u_b(t) - u_4(t), & u_3(t) &= u_a(t) - u_4(t) \end{aligned} \quad (3.24)$$

for all $t \geq 0$, where $c_1 = u_A(0)/u_a(0)$ and $c_2 = u_B(0)/u_b(0)$.

LEMMA 3.6. Let $c_1 = u_A(0)/u_a(0)$ and $c_2 = u_B(0)/u_b(0)$. Then

$$(u_1(t), u_2(t), u_3(t), u_4(t)) \rightarrow \left(\frac{c_1 c_2 K}{(1+c_1)(1+c_2)}, \frac{c_1 K}{(1+c_1)(1+c_2)}, \frac{c_2 K}{(1+c_1)(1+c_2)}, \frac{K}{(1+c_1)(1+c_2)} \right) \quad (3.25)$$

as $t \rightarrow \infty$.

PROOF. The proof is divided into three steps.

Step 1: $u_i (i = 1, 2, 3, 4)$ satisfy the following system of differential equations.

$$\begin{aligned}
 \dot{u}_1 &= (u_1^2 + u_1u_2 + u_1u_3 + \frac{1}{2}u_1u_4 + \frac{1}{2}u_2u_3) \frac{B(x)}{x^2} - u_1 \frac{D(x)}{x} \\
 \dot{u}_2 &= (u_2^2 + u_1u_2 + u_2u_4 + \frac{1}{2}u_1u_4 + \frac{1}{2}u_2u_3) \frac{B(x)}{x^2} - u_2 \frac{D(x)}{x} \\
 \dot{u}_3 &= (u_3^2 + u_1u_3 + u_3u_4 + \frac{1}{2}u_1u_4 + \frac{1}{2}u_2u_3) \frac{B(x)}{x^2} - u_3 \frac{D(x)}{x} \\
 \dot{u}_4 &= (u_4^2 + u_2u_4 + u_3u_4 + \frac{1}{2}u_1u_4 + \frac{1}{2}u_2u_3) \frac{B(x)}{x^2} - u_4 \frac{D(x)}{x},
 \end{aligned}
 \tag{3.26}$$

where $x = u_1 + u_2 + u_3 + u_4$. This follows directly from (NP), (1.2) and (1.3).

Step 2:

$$\begin{aligned}
 &u_1(t) - c_2u_2(t) \\
 &= (u_1(0) - c_1u_2(0)) \exp \left[\int_0^t \left(\frac{(1 + c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)} \right) d\tau \right] \\
 &u_3(t) - c_2u_4(t) \\
 &= (u_3(0) - c_2u_4(0)) \exp \left[\int_0^t \left(\frac{(1 + c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)} \right) d\tau \right] \\
 &u_1(t) - c_1u_3(t) \\
 &= (u_1(0) - c_1u_3(0)) \exp \left[\int_0^t \left(\frac{(1 + c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)} \right) d\tau \right] \\
 &u_2(t) - c_1u_4(t) \\
 &= (u_2(0) - c_1u_4(0)) \exp \left[\int_0^t \left(\frac{(1 + c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)} \right) d\tau \right].
 \end{aligned}
 \tag{3.27}$$

This can be proved by writing down the linear differential equation that each of the functions on the LHS of (3.27) satisfies. For example, by (3.24) and (3.26)

$$\begin{aligned}
 \dot{u}_2 - c_1\dot{u}_4 &= (u_2 - c_1u_4) \left[(1 + c_2)u_bB(x)/(2x^2) - D(x)/x \right] \\
 &= (u_2 - c_1u_4) \left[(1 + c_1)u_aB(x)/(2x^2) - D(x)/x \right].
 \end{aligned}$$

Step 3:

$$\begin{aligned}
 u_1(t) - c_2u_2(t) &\rightarrow 0, & u_3(t) - c_2u_4(t) &\rightarrow 0, \\
 u_1(t) - c_1u_3(t) &\rightarrow 0, & u_2(t) - c_1u_4(t) &\rightarrow 0,
 \end{aligned}
 \tag{3.28}$$

as $t \rightarrow +\infty$. This can be proved by noting that (3.2), (3.7) and (3.18) imply

$$\frac{(1 + c_1)u_a(t)B(x(t))}{2x^2(t)} - \frac{D(x(t))}{x(t)} \rightarrow -\frac{B(K)}{2K} < 0$$

as $t \rightarrow \infty$. Therefore, the integral in (3.27) is divergent and consequently we have (3.28).

Using (3.28) and (1.3), it is then easy to see that (3.25) holds.

PROOF OF THEOREM 3.4. To show (3.15), it suffices to show

$$\begin{aligned} x_{11}(t) - c_1^2 c_2^2 x_{33}(t) &\rightarrow 0, \quad x_{12}(t) - 2c_1^2 c_2 x_{33}(t) \rightarrow 0, \quad x_{13}(t) - c_1^2 x_{33}(t) \rightarrow 0, \\ x_{21}(t) - 2c_1 c_2^2 x_{33}(t) &\rightarrow 0, \quad x_{22}(t) - 4c_1 c_2 x_{33}(t) \rightarrow 0, \quad x_{23}(t) - 2c_1 x_{33}(t) \rightarrow 0, \\ x_{31}(t) - c_2^2 x_{33}(t) &\rightarrow 0, \quad x_{32}(t) - 2c_2 x_{33}(t) \rightarrow 0 \end{aligned}$$

as $t \rightarrow +\infty$. We illustrate this by showing $z(t) \equiv x_{32}(t) - 2c_2 x_{33}(t) \rightarrow 0$ as $t \rightarrow +\infty$. Clearly $z(t)$ satisfies the linear differential equation

$$\dot{z}(t) + Q_1(t)z(t) = Q_2(t)$$

where $Q_1(t) = D(x(t))/x(t)$, $Q_2(t) = 2u_4(t)[u_3(t) - c_2 u_4(t)]B(x(t))/x^2(t)$. Solving this equation yields

$$z(t) = z(0) \exp \left[- \int_0^t Q_1(\tau) d\tau \right] + \int_0^t \exp \left[- \int_s^t Q_1(\tau) d\tau \right] Q_2(s) ds.$$

We shall show that both the first and the second term tend to 0 as t tends to $+\infty$.

Since $\lim_{t \rightarrow +\infty} Q_1(t) = D(K)/K$, by (3.2), $\int_0^{+\infty} Q_1(t) dt = +\infty$, and hence, $\lim_{t \rightarrow +\infty} \exp \left[- \int_0^t Q_1(\tau) d\tau \right] = 0$. On the other hand, by (3.27),

$$\begin{aligned} &\int_0^t \exp \left[- \int_s^t Q_1(\tau) d\tau \right] Q_2(s) ds \\ &= 2(u_3(0) - c_2 u_4(0)) \exp \left[- \int_0^t \frac{D(x(\tau))}{x(\tau)} d\tau \right] \\ &\quad \cdot \int_0^t u_4(s) \exp \left[\frac{1+c_1}{2} \int_0^s \frac{u_a(\tau)B(x(\tau))}{x^2(\tau)} d\tau \right] \frac{B(x(s))}{x^2(s)} ds. \end{aligned} \tag{3.29}$$

To show that the LHS of (3.29) tends to 0 as t tends to $+\infty$, it suffices, by L'Hospital's rule, to show that

$$\lim_{t \rightarrow +\infty} \frac{u_4(t) \exp \left[\frac{1+c_1}{2} \int_0^t \frac{u_a(\tau)B(x(\tau))}{x^2(\tau)} d\tau \right] \frac{B(x(t))}{x^2(t)}}{\exp \left[\int_0^t \frac{D(x(\tau))}{x(\tau)} d\tau \right] \frac{D(x(t))}{x(t)}} = 0. \tag{3.30}$$

Since $\lim_{t \rightarrow +\infty} u_4(t) = K/(1 + c_1)(1 + c_2) > 0$, $\lim_{t \rightarrow +\infty} B(x(t))/x(t) = B(K)/K > 0$, and, $\lim_{t \rightarrow +\infty} D(x(t))/x(t) = D(K)/K > 0$, it suffices to show

$$\lim_{t \rightarrow +\infty} \int_0^t \left[\frac{D(x(\tau))}{x(\tau)} - \frac{(1 + c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} \right] d\tau = +\infty.$$

But this follows from

$$\begin{aligned} \lim_{t \rightarrow +\infty} \left[\frac{D(x(t))}{x(t)} - \frac{(1 + c_1)u_a(t)B(x(t))}{2x^2(t)} \right] &= \frac{D(K)}{K} - \frac{1 + c_1}{2} \cdot \frac{K}{1 + c_1} \cdot \frac{B(K)}{K^2} \\ &= \frac{B(K)}{2K} > 0. \end{aligned}$$

In the following corollary we reformulate Theorem 3.4 in terms of proportions.

COROLLARY 3.7. *If $(x_{11}(t), \dots, x_{33}(t))$ is a solution of (NP) other than the trivial solution $(0, \dots, 0)$, then*

$$\begin{aligned} x_{11}(t) : x_{12}(t) : x_{13}(t) : x_{21}(t) : x_{22}(t) : x_{23}(t) : x_{31}(t) : x_{32}(t) : x_{33}(t) \\ \rightarrow c_1^2 c_2^2 : 2c_1^2 c_2 : c_1^2 : 2c_1 c_2^2 : 4c_1 c_2 : 2c_1 : c_2^2 : 2c_2 : 1 \end{aligned}$$

as $t \rightarrow +\infty$, where

$$c_1 = \frac{x_{11}(0) + x_{12}(0) + x_{13}(0) + \frac{1}{2}x_{21}(0) + \frac{1}{2}x_{22}(0) + \frac{1}{2}x_{23}(0)}{x_{31}(0) + x_{32}(0) + x_{33}(0) + \frac{1}{2}x_{21}(0) + \frac{1}{2}x_{22}(0) + \frac{1}{2}x_{23}(0)}$$

and

$$c_2 = \frac{x_{11}(0) + x_{21}(0) + x_{31}(0) + \frac{1}{2}x_{12}(0) + \frac{1}{2}x_{22}(0) + \frac{1}{2}x_{32}(0)}{x_{13}(0) + x_{23}(0) + x_{33}(0) + \frac{1}{2}x_{12}(0) + \frac{1}{2}x_{22}(0) + \frac{1}{2}x_{32}(0)}.$$

4. Conditions which lead to evolution of pure strains

In this section, conditions leading to the global stability of one of the boundary equilibrium points E_i ($i = 1, 2, 3, 4$) will be considered. First we describe a condition which guarantees the persistence of y .

PROPOSITION 4.1. *Let*

$$\begin{aligned} d(c_1, c_2) = -s + \frac{K}{(1 + c_1)^2(1 + c_2)^2} [c_1^2 c_2^2 P_{11}(K) + 2c_1^2 c_2 P_{12}(K) \\ + c_1^2 P_{13}(K) + 2c_1 c_2^2 P_{21}(K) + 4c_1 c_2 P_{22}(K) + 2c_1 P_{23}(K) \\ + c_2^2 P_{31}(K) + c_2 P_{32}(K) + P_{33}(K)]. \end{aligned} \tag{4.1}$$

If there exists $\zeta > 0$ such that

$$d(c_1, c_1) \geq \zeta \quad \text{for all } c_1, c_2 \geq 0, \tag{4.2}$$

then y is uniformly persistent, that is, there exists $\eta > 0$ such that $\lim_{t \rightarrow +\infty} y(t) \geq \eta$ for all $(x_{11}(0), \dots, x_{33}(0), y(0)) \in \mathbf{R}_+^{10}$.

PROOF. Let $(x_{11}, \dots, x_{33}, y) \in \mathring{\mathbb{R}}_+^{10}$. Since the acyclic condition is satisfied on $H_{x_{11}, \dots, x_{33}}$, by Butler, Freedman and Waltman [2, Section 3], it suffices to show that y is persistent. We note that $d(c_1, c_2)$ is the eigenvalue of the variational matrix, $M(E_{c_1, c_2})$, of (1.1) evaluated at the equilibrium point $E_{c_1, c_2} = (H(c_1, c_2), 0)$ corresponding to eigenvectors of $M(E_{c_1, c_2})$ which have a nonzero y component. Let ε be the set of all equilibrium points of (1.1) in $H_{x_{11}, \dots, x_{33}} \setminus \{(0, \dots, 0, 0)\}$, that is, $\varepsilon = \{E_{c_1, c_2} : c_1, c_2 \geq 0\}$. Then by center manifold theory, ε is an isolated invariant set. According to hypothesis (4.2), the stable set, $W^s(\varepsilon)$, of ε has an empty intersection with $\mathring{\mathbb{R}}_+^{10}$. By Theorem 4.1 of Butler and Waltman [1], in order for $\lim_{t \rightarrow +\infty} y(t) = 0$, the omega-limit set, $\omega(x_{11}(0), \dots, x_{33}(0), y(0))$, of the point $(x_{11}(0), \dots, x_{33}(0), y(0))$ must intersect $W^s(\varepsilon)$ at a point other than those in ε . Now $W^s(\varepsilon) \cap \mathring{\mathbb{R}}_+^{10} \subset H_{x_{11}, \dots, x_{33}}$, with the global dynamics on $H_{x_{11}, \dots, x_{33}}$ as given in Theorem 3.4, implies that $\omega(x_{11}(0), \dots, x_{33}(0), y(0))$ either contains E_0 or is unbounded. In either case, we have a contradiction (cf. Proposition 2.1).

Since the analysis for the rest of this section and the next requires a knowledge of the global dynamics of (1.1) on the boundary positively invariant set ν , we will make the following additional assumptions.

- (A1) The predator y persists. (By Proposition 4.1, it suffices to assume that $d(c_1, c_2) \geq \zeta > 0$ for all $c_1, c_2 \geq 0$.)
- (A2) E_1 (resp. E_2, E_3, E_4) exists and is globally exponentially stable on $\mathring{H}_{x_{11}, y}$, the positive $x_{11} - y$ cone (resp. $\mathring{H}_{x_{13}, y}, \mathring{H}_{x_{31}, y}, \mathring{H}_{x_{33}, y}$). (Some sufficient conditions for the global stability of a positive equilibrium point of generalised Gauss predator-prey systems were given in Hsu [8] and in Cheng, Hsu and Lin [3].)
- (A3) $E_i (i = 1, 2, 3, 4)$ are hyperbolic. (By looking at $M(E_i)$ (c.f. Table 1), one can easily show that it is equivalent to assume

$$\bar{y}_{ij} [s/k - P_{22}(\bar{x}_{ij})] \neq B(\bar{x}_{ij})/2 \quad \text{for } (i, j = 1, 3).$$

The following theorem provides conditions under which the equilibrium point E_1 is globally stable (on $\mathring{\mathbb{R}}_+^{10}$).

THEOREM 4.2. *Suppose (H1)–(H6) and (A1)–(A3) hold. If the P_{ij} ($i, j = 1, 2, 3$) are totally ordered:*

$$P_{11} \triangleleft P_{12} \triangleleft P_{13} \triangleleft P_{21} \triangleleft P_{22} \triangleleft P_{23} \triangleleft P_{31} \triangleleft P_{32} \triangleleft P_{33}$$

where $P_{ij} \triangleleft P_{hl}$ means that there exists $e > 0$ such that $P_{hl}(x) - P_{ij}(x) \geq ex$ for all $x \in [0, K]$, then E_1 is globally stable on $\mathring{\mathbb{R}}_+^{10}$.

PROOF. Let $(x_{11}, \dots, x_{33}, y) \in \overset{\circ}{\mathbb{R}}_+^{10}$. Denote the omega limit set of $(x_{11}, \dots, x_{33}, y)$ by $\omega \equiv \omega(x_{11}, \dots, x_{33}, y)$. The proof proceeds in two steps. In step 1, we will show that $\omega \subset \partial(\mathbb{R}_+^{10})$ and in step 2, we show that no point in $\partial(\mathbb{R}_+^{10})$ can lie in ω except E_1 . Therefore, $E_1 \in \omega$. Now, by assumption, E_1 is asymptotically stable and thus $\omega = \{E_1\}$. Hence, E_1 is globally stable.

Step 1. Using REDUCE (an algebraic manipulation computer language), one shows that

$$\frac{\dot{u}_a}{u_a} - \frac{\dot{u}_A}{u_A} \leq -\frac{y}{u_A u_a} [e_{33} x_{13} x_{33} + \text{non-negative terms}],$$

where e_{33} is a positive constant. Therefore as in the proof of Theorem 3.1 in Freedman, So and Waltman [7].

$$u_a(t) \leq \frac{u_a(0)}{u_A(0)} u_A(t) \exp \left[-\frac{e_{33}}{K^2} \int_0^t (x_{12} x_{33} y)(\tau) d\tau \right].$$

If the integral diverges, then $\lim_{t \rightarrow +\infty} u_a(t) = 0$ so that $\omega \cap \partial(\mathbb{R}_+^{10}) \neq \emptyset$. Otherwise, $z(t) \equiv (x_{12} x_{33} y)(t) \in L^1[0, +\infty)$. Since $\dot{z}(t)$ is bounded, we have, $\lim_{t \rightarrow +\infty} z(t) = 0$. Hence, $\lim_{t \rightarrow +\infty} x_{12}(t) = 0$ or $\lim_{t \rightarrow +\infty} x_{33}(t) = 0$ (since $\lim_{t \rightarrow +\infty} y(t) > 0$ by (A1)). This again implies $\omega \cap \partial(\mathbb{R}_+^{10}) \neq \emptyset$.

Step 2. It was pointed out in Section 2 that no point in $\partial(\mathbb{R}_+^{10}) \setminus \nu$ can lie in ω . Therefore, it suffices to consider only points in ν . By looking at the eigenvalues of the variational matrix $M(E_i)$ ($i = 1, 2, 3, 4$) (cf. Table 1), we see that the dimension (dim) of the unstable manifolds, $W^u(E_i)$, of E_i ($i = 1, 2, 3, 4$) satisfy $\dim W^u(E_1) = 0$, $\dim W^u(E_2) \geq 1$, $\dim W^u(E_3) \geq 1$ and $\dim W^u(E_4) \geq 2$. Therefore E_1 is asymptotically stable and $W^u(E_i)$ ($i = 2, 3, 4$) have a nonempty intersection with $\mathbb{R}^{10} \setminus \mathbb{R}_+^{10}$. Consequently, by Proposition 2.2, we see that $W^s(E_i) \cap \mathbb{R}_+^{10} \subset \partial(\mathbb{R}_+^{10})$. On the other hand the main result for the one-locus model (cf. Theorem 3.1 of Freedman, So and Waltman [7]) tells us that E_2 (resp. E_3, E_4) is globally stable on $\overset{\circ}{H}_{x_{13}, x_{23}, x_{33}, y}$ (resp. $\overset{\circ}{H}_{x_{31}, x_{32}, x_{33}, y}$, $\overset{\circ}{H}_{x_{33}, y}$). Thus, $W^s(E_2) \cap \mathbb{R}_+^{10} \subset H_{x_{13}, x_{23}, x_{33}, y}$, $W^s(E_3) \cap \mathbb{R}_+^{10} \subset H_{x_{31}, x_{32}, x_{33}, y}$ and $W^s(E_4) \cap \mathbb{R}_+^{10} \subset H_{x_{33}, y}$. Knowing the global dynamics on ν , it follows easily (using Theorem 4.1 of Butler and Waltman [1]) that E_1 is the only point in $\partial(\mathbb{R}_+^{10})$ that can lie in ω .

5. Some persistence results

In this section we consider conditions which lead to the uniform persistence of system (1.1). Due to the large number of possibilities, we shall restrict ourselves to the cases when Theorem 3.1 of Freedman, So and Waltman [7] applies; that is, the predator functional responses for the heterozygotes

are ordered between the homozygote ones. Under this restriction, the global dynamics of (1.1) on the boundary invariant set ν is known. By interchanging the roles of the allele type A and a , or B and b if necessary, there are three cases to consider.

CASE 1: $P_{11} \triangleleft P_{12} \triangleleft P_{13}, P_{11} \triangleleft P_{21} \triangleleft P_{31}, P_{13} \triangleleft P_{23} \triangleleft P_{33}, P_{31} \triangleleft P_{32} \triangleleft P_{33}.$

CASE 2: $P_{11} \triangleleft P_{12} \triangleleft P_{13}, P_{11} \triangleleft P_{21} \triangleleft P_{31}, P_{33} \triangleleft P_{23} \triangleleft P_{13}, P_{33} \triangleleft P_{32} \triangleleft P_{31}.$

CASE 3: $P_{11} \triangleleft P_{12} \triangleleft P_{13}, P_{11} \triangleleft P_{21} \triangleleft P_{31}, P_{13} \triangleleft P_{23} \triangleleft P_{33}, P_{33} \triangleleft P_{32} \triangleleft P_{31}.$

THEOREM 5.1. *Under the assumptions (H1)–(H6) and (A1)–(A3), system (1.1) is uniformly persistent if*

- (i) $\bar{y}_{11}(s/k - P_{22}(\bar{x}_{11})) - B(\bar{x}_{11})/2 > 0$ under Case 1 and Case 3, and
- (ii) $\bar{y}_{ii}(s/k - P_{22}(\bar{x}_{ii})) - B(\bar{x}_{ii})/2 > 0, i = 1, 3$ under Case 2.

PROOF. We only discuss Case 1. The other two cases are similar. Let $\Omega = cl(\cup_{p \in \nu} \omega(p))$ be the global attractor in ν . Then $\{\mathcal{M}_i\}_{i=0}^5$, where $\mathcal{M}_i = \{E_i\}, (i = 1, \dots, 5)$ and $\mathcal{M}_5 = \varepsilon$, is an acyclic isolated covering of Ω . According to Theorem 3.1 of Butler and Waltman [1], it suffices to show that $W^s(\mathcal{M}_i) \cap \mathring{R}_+^{10} = \emptyset (i = 1, \dots, 5)$. Firstly, $W^s(\mathcal{M}_5) \cap \mathring{R}_+^{10} = \emptyset$ follows from (A1). Secondly, $\dim W^u(E_4) \geq 2$ implies $W^u(E_4) \cap (\mathbb{R}^{10} \setminus \mathring{R}_+^{10}) \neq \emptyset$ and hence by Proposition 2.2, $W^s(E_4) \cap \mathring{R}_+^{10} = W^s(\mathcal{M}_4) \cap \mathring{R}_+^{10} = \emptyset$. Similarly, one can show that $W^s(\mathcal{M}_i) \cap \mathring{R}_+^{10} = \emptyset (i = 1, 2, 3)$, since $\dim W^u(E_i) \geq 1 (i = 1, 2, 3)$. Finally, $W^s(\mathcal{M}_0) \cap \mathring{R}_+^{10} = W^s(E^0) \cap \mathring{R}_+^{10} = \emptyset$ follows from Proposition 2.1.

6. Discussion

In Section 4, we demonstrated one case where all the prey allele types in system (1.1) become extinct except one. This is analogous to the previously studied one-locus model. In contrast to that, we also illustrated in Section 5 that there are cases for which, when considered as a one-locus problem, some prey allele types becomes extinct, whereas by making the predator functional

response P_{22} for the double heterozygote sufficiently small, we get persistence for all the prey allele types (as well as the predator).

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