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A STUDY ON SOME ONE- AND TWO- LOCI PREDATOR-PREY INTERACTION MODELS

BY

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ABSTRACT

Four continuous models of population genetics with nonlinear birth and death processes are considered. The first model is concerned with a one-locus, two-allele problem in which fertility / viability is incorporated. Global dynamics of this three population system is obtained. The second model is a predator-prey interaction model in which the prey population is subdivided into three genotypes and its dynamics is given by the first model. The trade-offs between the fertility / viability of the prey genotypes and their predation functional responses relating to questions of convergence to pure strains and persistence are discussed. The third and fourth models are the analogues of the first two models but for a two-locus, two-allele problem and with no fertility / viability differences. Global convergence to the Hardy-Weinberg manifold is shown for the third model. Some results relating to the question of convergence to pure strains as well as to the question of persistence are obtained for the fourth model.

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CHAPTER 1

INTRODUCTION

Population genetics is the study of how genetic principles apply to a population and is principally concerned with the genetic and phenotypic properties of the members of a population. Ecology, on the other hand, is more concerned with population size and distribution as well as population interactions such as competition, predation and mutualism. Even though these two areas of population biology are closely related, most mathematical studies tend to specialize more in one of these areas than another. The purpose of this dissertation is to study a number of mathematical models in which both the genetic and the ecological components are present.

The usual setting for problems in population genetics is with difference equations rather than differential equations. Difference equations in population ecology are appropriate for problems of non-overlapping generations. When organisms reproduce continuously the differential equation approach seems more appropriate. Since environmental factors act continuously, it seems more appropriate to integrate the genetic and ecological components in a continuous formulation. This is the approach undertaken in this thesis.

Even among continuous models, it is convenient, for our purpose, to classify them into three types. First, there are the pure genetic models, representatives of which are the ones studied in Hadeler-Liberman (1975), Butler-Freedman-Waltman (1982), and, Hadeler-Glas (1983). In these models, the birth and death rates are taken to be constants. In some cases the death rate is taken to be zero, and it is more natural to talk about frequency of a genotype rather than the number of organisms of that genotype, since the number of organisms grows unboundedly. It should be pointed out that many of the continuous models in population genetics are of this type. Among them two famous ones are the Fisher-Wright-Haldane model for one locus problems (see Crow-Kimura (1970), Akin-Hofbauer (1982), and, Losert-Akin (1983)) and the Kimura model for two loci problems (see Crow-Kimura (1970), Kimura (1958), and, Akin (1979, 1983)). The second class of models is the ones that incorporate nonlinear birth and death processes. Representatives of this class are: Freedman-Waltman (1978, 1982), and, Beck (1982). In this class of models the birth and the death functions are singled out, and the coefficient associated with the birth function determines the mating structure and selection. The third class of models is the ones that incorporate environmental effects, as well as nonlinear birth and death processes. Representatives of this class are: Freedman-Waltman (1978, 1982), Beck-Keener-Ricciardi (1982, 1984), and, Beck (1984).

The models (3.1) and (5.1) to be studied in this thesis belong to the second class and models (4.1) and (6.1) belong to the third class. These models attempt to extend the model studied in Freedman-Waltman (1978, 1982) to include fertility/viability differences and to two loci problems. It turns out that even for the case studied in Freedman-Waltman (1978, 1982), we are able to generalize and unify their results as one single theorem (Theorem 4.6).

The genetic component of all the models studied in the papers mentioned under class 2 and 3 can be derived from the models of Nagylaki-

Crow (1974). This derivation is carried out in Waltman (1984). The model (3.1) (one-locus, two-allele with fertility / viability differences) and (5.1) (two-locus, two-allele with equal fertility / viability) studied in this thesis are extensions of these models. A different derivation can also be found in Appendix 1 and 2. The main theme for models (3.1) and (5.1) is global convergence to equilibrium. The recent work of Akin mentioned previously shows that even though global convergence to equilibrium is to be expected for one locus problems, periodic solutions (through Hopf bifurcation) are possible in the two loci problems if selection and recombination are incorporated.

In model (4.1) (resp. (6.1)), an ecological component in the form of a predator is added to model (3.1) (resp. (5.1)). Thus in model (4.1) (resp. (6.1)) the prey population is modelled by (3.1) (resp. (5.1)). To model the predator-prey interaction, the standard generalized model of Gause (1934) for predator-prey interactions is employed. There is a vast literature on the generalized Gause model. Of particular importance to the investigations we are undertaking in this thesis are: the local stability criteria of Rosenzweig-MacArthur (1963) and Gause-Smaragdova-Witt (1936), the phase-plane analysis of Freedman (1976), and the global stability criteria of Hsu (1978) and Cheng-Hsu-Lin (1981). For model (4.1), there are two types of selection forces at work. On the one hand, there is the selection due to fertility / viability differences, and, on the other hand, there is the selection due to differential predation functional responses. The main theme here is to determine the interplay of these two selection forces in relation to the questions of persistence and non-persistence. It should be pointed out that the recent work of Freedman-So-Waltman (1984) shows that even in the absence of fertility / viability differences, it is possible for model (4.1) to possess periodic solutions. These periodic solutions are, of course, predator mediated. In model (6.1), we attempt to discover some similarities and differences between the one locus and the two loci theories in relation to the question of persistence and non-persistence.

The dissertation is organized as follows. In Chapter 2, a number of mathematical results used in the main body of this thesis will be described. Proofs are provided for those results that appear to be new. In the next four chapters, four continuous models in population genetics are discussed. Chapter 3 is concerned with a one-locus, two-allele model with nonlinear birth and death processes as well as fertility / viability differences. It is shown that the dynamics of this model is trivial (that is all solutions converge to some equilibrium). In Chapter 4, the model studied in Chapter 3 is extended to include a predator. We obtain conditions under which only one of the prey gamete types survives as well as conditions under which the system persists. Of particular interest and importance is the interplay between the fertility / viability and the predator functional responses of the prey genotypes. In Chapter 5, the model studied in Chapter 3 is extended to the two-locus, two-allele case but with no fertility / viability differences. Again the dynamics of this model is shown to be trivial and the analogue of the Hardy-Weinberg equilibrium relation for discrete models is obtained. In Chapter 6, the model studied in Chapter 5 is extended to include a predator. Same questions as in Chapter 4 are raised. It is shown that the predator functional response of the double heterozygote can change a non-persistent system (when considered as one-locus problems) to that of persistence. Finally, a concluding discussion is given in Chapter 7.

CHAPTER 2

MATHEMATICAL PRELIMINARIES

In this chapter, a number of concepts and results from the theory of autonomous differential equations and dynamical systems will be discussed. Some of the following sections also contain a number of simple but useful technical results which are new.

2.1. Standard Results.

The portion of the mathematical theory which is considered as standard or well-known will be listed below along with references where they can be found.

(i) Existence, uniqueness and continuous dependence on initial conditions and parameters theorem: Chapter 1 of Coddington - Levinson (1955).

(ii) Differential inequalities: Section I.6 of Hale (1969) and Section I.4 of Coppel (1965).

(iii) Flows, local flows and semi-flows: Chapter 2 of LaSalle (1976), Chapter II of Sell (1971), and, Chapter 1 of Bhatia-Szegö (1967).

(iv) Deriving a flow from an autonomous differential equation: Chapter 2 of LaSalle (1976) and Section 1.7 of Hale (1969).

(v) Poincaré - Bendixson theory and the theory of index for planar systems: Chapter 16 of Coddington - Levinson (1955) and Chapter VII of Hartman (1982).

(vi) Omega - limit sets, alpha - limit sets and their well-known properties: Section I.8 of Hale (1969) and Chapter 2 of LaSalle (1976).

(vii) Liapur and global stability for sets: Chapter 2 of LaSalle (1976) and Chapters 1 and 2 of Bhatia - Szegö (1967).

(viii) Flow equivalence and C^k - equivalence: Chapter 2 of Irwin (1980).

2.2. Conventions and Notations.

In this section, some conventions and notations that are used in the main body of the thesis will be discussed.

A. Conventions.

(i) In all our applications, the flows are defined by autonomous differential equations on subsets of R^n .

(ii) By boundedness of an orbit (or solution) is meant boundedness for all positive time.

B. Notations.

(i) R_+^n = the positive cone in R^n

(ii) $cl(R_+^n)$ = the closure of R_+^n in R^n

= the non-negative cone in R^n

(iii) $b(R_+^n)$ = the boundary of R_+^n in R^n

(iv) For $1 \leq i_1 < \cdots < i_k \leq n$, let $I = \{i_1, \cdots, i_k\}$ and $I' = \{1, \cdots, n\} \setminus I$.

$$H_{x_{i_1}, \cdots, x_{i_k}} = \{x \in cl(R_+^n) : x_i > 0 \text{ for } i \text{ in } I, \; x_i = 0 \text{ for } i \text{ in } I'\}$$

$$cl(H_{x_{i_1}, \cdots, x_{i_k}}) = \text{closure of } H_{x_{i_1}, \cdots, x_{i_k}} \text{ in } R^n$$

$$= \{x \in cl(R_+^n) : x_i = 0 \text{ for } i \text{ in } I'\} .$$

(v) For x in R^n and $1 \leq i \leq n$, x_i or $(x)_i$ denotes the i^{th} component of x.

(vi) d denotes the Euclidean metric on R^n or any given metric of a metric space.

(vii) Solutions of a differential equation are sometimes denoted by $x(t)$ with $x(0)$ denoted by x_0.

(viii) If a flow (X,ϕ) comes from a differential equation

$$\dot{x} = f(x) \qquad (x \in R^n)$$

and there is a need to emphasize f, then ϕ is also denoted by ϕ_f.

(ix) Lip denotes the class of locally Lipschitz continuous functions.

(x) $w(x)$ denotes the omega - limit set of x.

(xi) $O(x)$ (resp. $O^+(x)$) denotes the orbit through x (resp. the non-negative semi-orbit through x).

2.3. Positive Invariance.

Consider the differential equation

$$\dot{x} = f(x) \qquad (x \in R^n)$$

where $f \in$ Lip. If this system is to model interactions of populations, we should expect $cl(R^n_+)$ to be positively invariant. A necessary and sufficient condition for this is given by the following proposition.

Proposition 2.1: $cl(R^n_+)$ is positively invariant under the flow defined by f if and only if for all $1 \leq i \leq n$, we have,

$$f_i(x_1,\cdots,x_{i-1},0,x_{i+1},\cdots,x_n) \geq 0$$

for all $(x_1,\cdots,x_{i-1},0,x_{i+1},\cdots,x_n)$ in $cl(R^n_+)$.

Proof: First suppose there exists $1 \le i_0 \le n$ and $x^* = (x^*_1,\cdots,x^*_{i_0-1},0,x^*_{i_0+1},\cdots,x^*_n)$ in $cl(R^n_+)$ such that $f_{i_0}(x^*) < 0$. Let $x(t)$ be the solution such that $x(0) = x^*$. Then $x_{i_0}(t)$ is strictly decreasing for t small enough. Hence, $x_{i_0}(t) < 0$ for $t > 0$ small enough, contradicting the positive invariance of $cl(R^n_+)$.

Now consider the sequence of differential equations

$$\dot{x} = f(x) + \frac{1}{N} = f^N(x) \quad , \quad \text{for } N = 1,2,\cdots \; .$$

Since $f^N_i(x_1,\cdots,x_{i-1},0,x_{i+1},\cdots,x_n) > 0$ for all $(x_1,\cdots,x_{i-1},0,x_{i+1},\cdots,x_n)$ in $cl(R^n_+)$ and $1 \le i \le n$, by looking at the flow on $b(R^n_+)$ and using an argument similar to that above, we can show that $cl(R^n_+)$ is positively invariant under the flow ϕ_{f^N} defined by f^N for all $N = 1,2,\cdots$. Next, we suppose that $cl(R^n_+)$ is not positively invariant under the flow ϕ_f defined by f . Then there exists an $1 \le i_0 \le n$, a $t^* > 0$ and an $x^* = (x^*_1,\cdots,x^*_{i_0-1},0,x^*_{i_0+1},\cdots,x^*_n)$ in $cl(R^n_+)$ such that

$$d(\phi_f(x^*,t^*) \quad , \quad cl(R^n_+)) = d > 0 \; .$$

Now, by continuous dependence on parameters, (see Theorem 7.4 on p. 29 of Coddington-Levinson (1955)),

$$\phi_{f^N}(x^*,t^*) \text{ converges to } \phi_f(x^*,t^*) \text{ as } N \to +\infty \; .$$

But this leads to a contradiction because

$$d(\phi_{f^N}(x^*,t^*),cl(R^n_+)) = 0 \quad \text{for all} \quad N = 1,2,\cdots ,$$

completing the proof of the proposition.

q.e.d.

2.4. Boundedness.

Let (X,ϕ) be a semi-flow and let $A \subset X$.

Definition: (X,ϕ) is said to be A-dissipative if

(i) A is compact and positively invariant, and,

(ii) for all $x \in X$, $\phi(x,t) \to A$ as $t \to +\infty$.

Remark: (X,ϕ) is A-dissipative implies that all solutions are bounded.

The following is a situation which is applicable to all the models we study here and for which we can show the flow is A-dissipative.

Consider

$$\begin{aligned} \dot{x}_i &= f_i(x_1,\cdots,x_n,y) \qquad (i=1,\cdots,n) \\ \dot{y} &= g(x_1,\cdots,x_n,y) \end{aligned} \tag{2.1}$$

where f_i , $g \in$ Lip and $cl(R^{n+1}_+)$ is positively invariant. Let $x = x_1 + \cdots + x_n$ and suppose that

$$\dot{x} \le f(x)$$

$$k\dot{x} + \dot{y} \le kf(x) - sy \tag{2.2}$$

for some $k,s > 0$, where $f \in$ Lip satisfies: $f(0) = 0$, $f'(0) > 0$, there exists a unique $K > 0$ such that $f(K) = 0$, and, $f'(K) < 0$.

Proposition 2.2: *Let* $A = \{(x_1,\cdots,x_n,y) \in cl(R_+^{n+1}) : x \le K$ *and* $kx + y \le \frac{k}{s}(M + sK)\}$ *where* $M = \max\{f(x) : x \in [0,K]\}$. *Then system* (2.1) *when considered as a flow on* $cl(R_+^{n+1})$ *is A-dissipative.*

Proof: Consider the scalar differential equation $\dot{z} = f(z)$. By the properties of f, we have:

(i) if $z_0 \in (0,K]$, then $z(t) \nearrow K$ as $t \to +\infty$, and,

(ii) if $z_0 \in [K,+\infty)$, then $z(t) \searrow K$ as $t \to +\infty$.

Using a standard differential inequality argument (see Theorem 6.1 on p. 31 of Hale (1969)) and the fact that $cl(R_+^{n+1})$ is positively invariant, we can show that

(iii) if $x_0 \in [0,K]$, then $x(t) \in [0,K]$ for all $t \ge 0$, and,

(iv) if $x_0 \in cl(R_+^1)$, then $\overline{\lim}_{t\to+\infty} x(t) \le K$.

From (2.2), we have,

(v) $k\dot{x} + \dot{y} \le -s(kx + y) + k(f(x) + sx)$.

We first show that A is positively invariant. For if we let $(x_{1o},\cdots,x_{no},y_o) \in A$, then by (iii), $x(t) \leq K$ for all $t \geq 0$. On the other hand, by (v), we have,

$$kx(t) + y(t) \leq e^{-st}(kx_o + y_o) + ke^{-st}(M + sK)\int_0^t e^{s\tau}\,d\tau$$

$$= \frac{k}{s}(M + sK) - e^{-st}\left(\frac{k}{s}(M + sK) - (kx_o + y_o)\right).$$

Therefore, if $kx_o + y_o \leq \frac{k}{s}(M + sK)$, then

$$kx(t) + y(t) \leq \frac{k}{s}(M + sK) \quad \text{for all } t \geq 0 .$$

We now show that for all $(x_{1o},\cdots,x_{no},y_o) \in cl(R_+^{n+1})$,

$$(x_1(t),\cdots,x_n(t),y(t)) \to A \quad \text{as } t \to +\infty .$$

By (iv), it remains to prove that for all $\varepsilon > 0$, there exists $T > 0$ such that

$$kx(t) + y(t) \leq \frac{k}{s}(M + sK) + \varepsilon \quad \text{for all } t \geq T .$$

By (iv), there exists $T_1 > 0$ such that $x(t) \leq K + \frac{\varepsilon}{3k}$ for all $t \geq T_1$. Let $K' = \max\{x(t) : t \in [0,T_1]\}$. By (v), for all $t \geq T_1$ we have

$$kx(t) + y(t) \leq e^{-st}(kx_o + y_o) + ke^{-st}\int_0^{T_1}[f(x(\tau)) + sx(\tau)]\,e^{s\tau}\,d\tau$$

$$+ ke^{-st}\int_{T_1}^{t}[f(x(\tau)) + sx(\tau)]\,e^{s\tau}\,d\tau .$$

Since $f(x) \leq M$ for all $x \in cl(R^1_+)$, second term $\leq \frac{k}{s} e^{-s(t-T_1)}(M+sK')$, and third term $\leq \frac{k}{s}(M+sK) + \frac{\varepsilon}{3}$. We can choose $T \geq T_1$ so that for all $t \geq T$, the first and second terms are $< \frac{\varepsilon}{3}$. Then for all $t \geq T$,

$$kx(t) + y(t) \leq \frac{k}{s}(M+sK) + \varepsilon$$

as desired.

q.e.d.

Remark: The above proposition also shows that solutions can be continued for all positive time and hence system (2.1) defines a semi-flow on $cl(R^{n+1}_+)$.

2.5. Persistence.

Consider

$$\dot{x} = f(x) \qquad (x \in R^n) \tag{2.3}$$

where x_i $(i = 1,\cdots,n)$ can be thought of as the number / density / biomass of the organisms in the i^{th} population and that the interaction within and between the populations is described by system (2.3). Assume that $cl(R^n_+)$ is positively invariant and all solutions initiating from $cl(R^n_+)$ can be continued for all positive time.

Definition: (i) System (2.3) is said to be persistent if for all x in R_+^n, $\underline{\lim}_{t\to+\infty} x_i(t) > 0$ for all $i = 1,\cdots,n$.

(ii) System (2.3) is said to be non-persistent if it is not persistent. That is, there exists an $x_0 \in R_+^n$ and i_0 $(1 \le i_0 \le n)$ such that $\underline{\lim}_{t\to+\infty} x_{i_0}(t) = 0$. Equivalently, the omega-limit set of x_0 has non-empty intersection with the boundary $b(R_+^n)$.

Remarks: (i) It should be pointed out that there are many mathematical definitions of the concept of persistence. For example, in McGehee - Armstrong (1977) the authors defined persistence to mean the existence of an attractor in R_+^n. The one we choose to use here is the one used in Freedman-Waltman (1984).

(ii) According to the above definition of non-persistence, system (2.3) will be non-persistent if there exists an asymptotically stable rest point on $b(R_+^n)$.

2.6. Wazewski Sets.

In this section the basic properties of a Wazewski set will be discussed. More information can be found on pp. 24-25 of Conley (1978) and on Sections X.2 and X.3 of Hartman (1982).

Definition: Let (X,ϕ) be a continuous semi-flow and let $A \subset X$.

(i) The <u>eventual exit set</u>, A^o, of A is defined as

$$A^o = \{x \in A : \phi(x,t) \notin A \quad \text{for some} \quad t > 0\} \ .$$

(ii) The <u>immediate exit set</u>, A^-, of A is defined as

$$A^- = \{x \in A : \phi(x,[0,t)) \not\subset A \quad \text{for all} \quad t > 0\} \ .$$

(iii) A is called a <u>Wazewski set</u> if it satisfies:

(a) A is <u>flow closed</u>, i.e., if $x \in A$ and $\phi(x,[0,t)) \subset A$, then $\phi(x,[0,t]) \subset A$, and,

(b) A^- is closed relative to A^o.

(iv) The <u>time of exit map</u> $T : A^o \to [0,+\infty)$ is defined by

$$T(x) = \sup \{t \geq 0 : \phi(x,[0,t]) \subset A\} \ ,$$

for all $x \in A^o$.

<u>Theorem 2.3.</u> (Wazewski): <u>If A is a Wazewski set, then A^- is a strong deformation retract of A^o and A^o is open relative to A.</u>

<u>Proof:</u> The statement of the theorem as given on p. 24 of Conley (1977) is for flows but the proof remains valid without modification in the case of semi-flows.

q.e.d.

Another useful property of Wazweski sets is the following.

Corollary 2.4: If A is a Wazewski set, then the time of exit map is continuous.

Proof: This is contained in the proof of the theorem. In fact, conditions (a) and (b) are provided to ensure the time of exit map is upper semi-continuous and lower semi-continuous respectively.

q.e.d.

2.7 Chain Recurrence.

In this section the notion of chain recurrence, first used by C. Conley and R. Bowen will be introduced. (See pp. 36-38 of Conley (1978)). This concept turns out to be a very useful kind of recurrence from the application standpoint.

Let (X,ϕ) be a flow and let S be a compact (Hausdorff) invariant subset of X.

Definition: Let $\mathcal{U}$ be an open cover of S. Let $x,y \in S$ and $t > 0$. A $(\mathcal{U},t)$-chain from x to y means a sequence

$$x = x_1,\cdots,x_{n+1} = y \,;\, t_1,\cdots,t_n \qquad (t_i \geq t)$$

for all $i = 1,\cdots,n$ and such that for each pair $(\phi(x_i,t),x_{i+1})$ $(i = 1,\cdots,n)$ there is an element of the cover $\mathcal{U}$ containing both members of the pair.

Definition: The chain recurrent set $R(S)$ of S is defined to be the set of all $x \in S$ such that for any choice of cover $\mathcal{U}$ of S and any $t > 0$ there exists a $(\mathcal{U},t)$ - chain from x to x.

Definition: S is called chain recurrent if $R(S) = S$. It is called strong gradient like if $R(S)$ is totally disconnected (and consequently is equal to its rest point set).

Proposition 2.5: Given $x \in S$. Then $w(x)$, the omega-limit set of x, is chain recurrent.

Proof: (See p. 38 of Conley (1978).)

q.e.d.

2.8. Invariant Manifolds.

In this section the invariant manifold theory for rest points will be discussed. Some general references for this topic are: Chapter IX of Hartman (1982) and Section 9.2 of Chow-Hale (1982).

Definition: Let (X,ϕ) be a flow on a smooth manifold X with metric d. (Think of X as an open subset of R^n.) Given a rest point x^* of ϕ, the stable set, $W^s(x^*)$, of x^* is defined as the set

$$\{x \in X : d(\phi(x,t),x^*) \to 0 \quad \text{as} \quad t \to +\infty\}.$$

The unstable set, $W^u(x^*)$, of x^* is defined analogously by reversing time t.

If the rest point x^* is hyperbolic (i.e. all eigenvalues of the linearization (Jacobian matrix) have non-zero real parts), we have the following stable manifold theorem.

Theorem 2.6 (global stable manifold theorem): If the flow (X,ϕ) is C^k $(k \geq 1)$, and x^* is a hyperbolic rest point, then $W^s(x^*)$ (resp. $W^u(x^*)$) are C^k immersed submanifolds of X, tangent at x^* to the generalized eigenspace corresponding to those eigenvalues of the linearization which have negative real parts (resp. positive real parts).

Proof: (See Theorem 6.17 on p. 152 of Irwin (1980).)

q.e.d.

Remark: If x^* is hyperbolic, $W^s(x^*)$ (resp. $W^u(x^*)$) is also known as the stable manifold (resp. unstable manifold) of x^*.

When some of the eigenvalues of the linearization at x^* have zero real parts, there are a number of locally invariant manifolds through x^*.

Theorem 2.7 (strong stable manifold theorem): Consider

$$\dot{x} = Ax + u(x) \qquad (x \in R^n)$$

where $u \in C^1$, $u(0) = 0$ and $Du(0) = 0$. If the n by n matrix A possesses s $(s > 0)$ eigenvalues having negative real parts, then the set

$$\tilde{W}^{ss}(0) = \{x \in X : \overline{\lim_{t \to +\infty}} \frac{1}{t} \log d(\phi(x,t),0)) < +\infty\}$$

is a locally invariant C^1 manifold of dimension s .

Proof: (See Theorem 6.1 on p. 242 of Hartman (1982).)

q.e.d.

Definition: The set $W^{ss}(0)$ is called the strong stable manifold of $x = 0$. The strong unstable manifold, $W^{su}(0)$, can be defined in a similar manner.

Theorem 2.8 (center manifold theorem): Consider

$$\dot{x} = Ax + u(x,y) \qquad (x \in R^m)$$

$$\dot{y} = By + v(x,y) \qquad (y \in R^n)$$

near $(x,y) = (0,0)$, where all the eigenvalues of A have zero real parts and all the eigenvalues of B have non-zero real parts, $u,v \in C^k$ $(k \geq 1)$, $u(0,0) = 0$, $v(0,0) = 0$, $Du(0,0) = 0$, and, $Dv(0,0) = 0$. Then there exists a C^k function $h : (R^m,0) \to (R^n,0)$ such that

(i) the set

$$W^c(0) = \{(x,y) \in (R^{m+n},(0,0)) : y = h(x)\} ,$$

is a locally invariant C^k manifold in R^{m+n} , and,

(ii) $W^c(0)$ consists exactly of those solutions $(x(t),y(t))$ for which $|y(t)|$ $(t \in R)$ is small.

Proof: (See Theorem 2.1 on p. 313 of Chow-Hale (1982.)

q.e.d.

Definition: $W^c(0)$ is called the center manifold of $(x,y) = (0,0)$.

Theorem 2.9 (center stable manifold theorem): Consider

$$\dot{x} = Ax + u(x,y) \qquad (x \in R^m)$$

$$\dot{y} = By + v(x,y) \qquad (y \in R^n)$$

near $(x,y) = (0,0)$, where all the eigenvalues of A have non-positive real parts, all the eigenvalues of B have positive real parts, $u,v \in C^k$ $(k \geq 1)$, $u(0,0) = 0$, $v(0,0) = 0$, $Du(0,0) = 0$, and, $Dv(0,0) = 0$. Then there exists a C^k function $g : (R^m,0) \to (R^n,0)$ such that

(i) the set

$$W^{cs}(0) = \{(x,y) \in (R^{m+n},(0,0)) : y = g(x)\} ,$$

is a locally invariant C^k manifold, and,

(ii) $W^{cs}(0)$ consists of exactly those solutions $(x(t),y(t))$ for which $|y(t)|$ $(t \geq 0)$ is small.

Proof: (See Theorem 2.11 on p. 319 of Chow-Hale (1982).)

q.e.d.

Definition: $W^{cs}(0)$ is called the center stable manifold of $(x,y) = 0$. Similarly, one can define the center unstable manifold, $W^{cu}(0)$, of $(x,y) = (0,0)$.

Remark: It should be pointed out that these invariant manifolds are tangent to the respective generalized eigenspaces of the linearization.

2.9. Linearization Theorems.

Linearization theorems allow us to say something about the local structure of a flow near a point. To start with there is the so-called "straightening-out" theorem which states that near a regular point (i.e. not a rest point) of a C^2 flow, C^1 change of coordinates near the point can be made so that locally the flow becomes a parallel flow (see Theorem 21.6 on p. 56 of Abraham-Robbin (1967)). In the case of a hyperbolic rest point of a C^1 flow, we have the well-known theorem of Hartman and Grobman which says that locally (i.e. near the rest point), there is a flow equivalence between the original system and the linear system that arises from linearizing the original system at the rest point (see Theorem 7.1 on p. 244 of Hartman (1982) or Theorem 7.2 on p. 110 of Chow-Hale (1982)). In the general case, we have the following theorem due to Palis and Takens:

Theorem 2.10 (Palis-Takens): Consider

$$\begin{aligned} \dot{x} &= Ax + u(x,y) \qquad (x \in R^m) \\ \dot{y} &= By + v(x,y) \qquad (y \in R^n) \end{aligned} \tag{2.4}$$

near $(x,y) = (0,0)$, where $u,v \in C^k$ $(k \geq 1)$, $u(0,0) = 0$, $v(0,0) = 0$, $Du(0,0) = 0$, and, $Dv(0,0) = 0$. Assume that all eigenvalues of A have zero real parts and all eigenvalues of B have non-zero real parts. Then system (2.4) is locally C^0 - equivalent to the decoupled system

$$\begin{aligned} \dot{w} &= Aw + u(w,h(w)) \qquad (w \in R^m) \\ \dot{z} &= Bz \qquad (z \in R^n) \end{aligned} \tag{2.5}$$

near $(w,z) = (0,0)$, where h defines the center manifold of $(0,0)$.

Proof: See the second theorem on p. 341 of Palis-Takens (1977). This fact is also mentioned in Remark 2.16 on pp. 322-323 of Chow-Hale (1982).

q.e.d.

Using Hartman-Grobman's theorem, we can prove the following proposition which tells us when the stable manifold of a boundary hyperbolic rest point will have empty intersection with the positive cone, R_+^n.

Proposition 2.11: Consider

$$\dot{x} = f(x) \qquad (x \in R^n)$$

and assume that $cl(R_+^n)$ is positively invariant. Let $x_0 \in b(R_+^n)$ be a hyperbolic rest point. If $W^u(x_0) \cap (R^n \setminus cl(R_+^n)) \neq \emptyset$, then $W^s(x_0) \cap R_+^n = \emptyset$.

Proof: Suppose not, that is suppose $W^s(x_0) \cap R^n_+ \neq \emptyset$. If we can show that for fixed $x_1 \in W^s(x_0)$, $x_2 \in W^u(x_0)$ where $x_1, x_2 \neq x_0$, there is a point x which is arbitrarily close to x_1 and a time $t > 0$ so that $\phi(x,t)$ is arbitrarily close to x_2 , then this will contradict the positive invariance of $cl(R^n_+)$. Since this can essentially be reduced to a local problem, it suffices to establish the following.

Consider

$$\dot{x} = Ax \qquad (x \in R^n)$$

$$\dot{y} = By \qquad (y \in R^m)$$

where all the eigenvalues of A have negative real parts and all the eigenvalues of B have positive real parts. Fix $(x^*,0)$ and $(0,y^*) \in R^{m+n}$ with $x^* \neq 0$, $y^* \neq 0$. Then there exists $(x_N,y_N) \in R^{m+n}$ and $t_N > 0$ such that $(x_N,y_N) \to (x^*,0)$ and $\phi((x_N,y_N),t_N) \to (0,y^*)$ as $N \to +\infty$. For a proof, let $t_N = N$, $x_N = x^*$, and, $y_N = e^{-t_N B} y^*$. Then clearly $x_N \to x^*$ and $y_N \to 0$, since all eigenvalues of B have positive real parts. Furthermore we have,

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

as $N \to +\infty$ as desired.

q.e.d.

2.10. Saddle Nodes.

In this section a sufficient condition for the existence of saddle nodes and some related calculations will be discussed. (See pp. 323-329 of Chow-Hale (1982).)

Consider the system

$$\begin{aligned} \dot{y}_1 &= P(Y) \\ \dot{\bar{y}} &= A\bar{y} + Q(Y) \end{aligned} \tag{2.6}$$

where $\bar{y} = (y_2, \cdots, y_n) \in R^{n-1}$, $Y = (y_1, \bar{y}) \in R^n$, P and Q are of order two or higher in Y and all the eigenvalues of the $(n-1)$ by $(n-1)$ matrix A have negative real parts. Clearly $Y = 0$ is a rest point of system (2.6) and the variational matrix of (2.6) at $Y = 0$ has 0 as a simple eigenvalue and the remaining $(n-1)$ eigenvalues have negative real parts.

Theorem 2.12 (saddle-node): Let $\bar{y} = \psi_1(y_1)$ with $\psi_1(0) = 0$ be the solution of

$$A\bar{y} + Q(y_1, \bar{y}) = 0 \tag{2.7}$$

near $(y_1, \bar{y}) = (0,0)$ and let

$$\psi_2(y_1) = P(y_1, \psi_1(y_1)) \quad . \tag{2.8}$$

If

$$\psi_2(y_1) = \eta y_1^2 + O(|y_1|^3)$$

and $\eta \neq 0$ then $Y = 0$ is a saddle node: the strong stable manifold of $Y = 0$ is $(n-1)$-dimensional and is tangent to the hyperplane $y_1 = 0$, the 1-dimensional center manifold of $Y = 0$ is tangent to the y_1-axis, and, $Y = 0$ is stable on one side of its strong stable manifold and unstable on the other side.

Proof: Refer to Theorem 65 on pp. 340-346 of Andronov-Leontovich-Gordon-Maier (1975) for the case when $n = 2$ and pp. 326-327 of Chow-Hale (1982) for the general case.

q.e.d.

Remarks: (i) It turns out that

$$\eta = \frac{1}{2} \frac{\partial^2 P}{\partial y_1^2}(0) \qquad (2.9)$$

(ii) If $\eta > 0$, then the domain of stability of $Y = 0$ is on the side of the strong stable manifold for which $y_1 < 0$; if $\eta < 0$, it is just the reverse.

The above theorem is stated in "canonical" form. In applications, it is often necessary to transform the problem into this form. Some of that calculation will be carried out in the following.

Consider the system

$$\dot{Z} = G(Z) \qquad (2.10)$$

where $Z \in R^n$, $\acute{G}(0) = 0$, and the variational matrix of system (2.10) at $Z = 0$ has 0 as a simple eigenvalue and the remaining $(n-1)$ eigenvalues have negative real parts. Let v_1 be an eigenvector corresponding to the eigenvalue 0 and let $v_2,\cdots,v_n$ be a basis of the generalized eigenspace corresponding to the remaining $(n-1)$ eigenvalues. Let $N = [v_1,\cdots,v_n]$ be the n by n matrix whose i^{th} column is v_i and let $Y = N^{-1}Z$. Under this transformation, (2.10) takes the form (2.6). The $y_1 = 0$ hyperplane is transformed back to the hyperplane, in the Z - coordinates, spanned by the vectors $v_2,\cdots,v_n$ (denoted by $\langle v_2,\cdots,v_n \rangle$), the y_1 - axis is transformed back to the line spanned by the vector v_1 (denoted by $\langle v_1 \rangle$), and the positive y_1 axis is transformed back to the half line

$$\{\lambda v_1 \in R^n : \lambda > 0\} \quad .$$

Let $N = [n_{ij}]_{1 \leq i,j \leq n}$, $N^{-1} = [\overline{n_{ij}}]_{1 \leq i,j \leq n}$,

$G(Z) = (G_1(Z),\cdots,G_n(Z))$, and

$$\acute{G}_i(Z) = \sum_{1 \leq i_1 + \cdots + i_n \leq 2} g_i^{(i_1,\cdots,i_n)} z_1^{i_1} \cdots z_n^{i_n} + O(|Z|^3)$$

$(i = 1,\cdots,n)$. Also let $I_h = (0,\cdots,0,2,0,\cdots,0)$ with a "2" in the h^{th} column and the rest are all 0's , and, $I_{h,k} = (0,\cdots,0,1,0,\cdots,0,1,0,\cdots,0)$ with 1's in the h^{th} and k^{th} columns and the rest are all 0's . Then

$$n = \sum_{i=1}^{n} \overline{n_{1i}} \left(\sum_{h=1}^{n} g_i^{I_h} n_{h1}^2 + \sum_{1 \leq h < k \leq n} g_i^{I_{h,k}} n_{h1} n_{k1} \right) .$$

Hence, if $\eta \neq 0$, $Z = 0$ will be a saddle node. The strong stable manifold $W^{ss}(0)$ of $Z = 0$ is tangent to $\langle v_2, \cdots, v_n \rangle$ and the center manifold $W^c(0)$ is tangent to $\langle v_1 \rangle$.

2.11. Omega-Limit Sets.

In this section a number of simple but useful technical results relating to omega-limit sets will be presented. These results will be used repeatedly in the main body of the thesis.

Proposition 2.13: Consider

$$\dot{x} = f(x) \qquad (x \in R^n) \tag{2.11}$$

where $f \in$ Lip . Assume that $cl(R_+^n)$ is positively invariant, let x^* be a point on $b(R_+^n)$ with $x_i^* = 0$ and such that $f_i(x^*) > 0$. Then $x^* \notin w(x)$ for any $x \in cl(R_+^n)$.

Proof: Since x^* is a regular point, if f is C^2 we can use the "straightening-out theorem" to construct a C^1 change of coordinates near x^* so that locally the flow becomes a parallel flow. From this and the positive invariance of $cl(R_+^n)$, we can easily see that $x^* \notin w(x)$ for any $x \in cl(R_+^n)$. In the general case when $f \in$ Lip , $f_i(x^*) > 0$ implies that $x_i(t)$ is strictly increasing near $t = 0$, where $x(t)$ denotes the solution of system (2.11) such that $x(0) = x^*$. Since $x_i^* = 0$, for sufficiently small $t < 0$, $x(t) \notin cl(R_+^n)$. On the other hand, if $x^* \in w(x)$ for some $x \in cl(R_+^n)$ then $x(t) \in w(x)$ also. By choosing $t < 0$ sufficiently small, this implies $w(x) \not\subset cl(R_+^n)$, contradicting the positive invariance of $cl(R_+^n)$.

q.e.d.

Lemma 2.14 (Butler-McGehee): Consider

$$\dot{x} = f(x) \qquad (x \in R^n)$$

where $f \in C^1$. Let $x^* \in R^n$ be a hyperbolic rest point. If $x^* \in w(x)$ for some $x \in R^n$, then either $w(x) = \{x^*\}$ or both $w(x) \cap W^s(x^*)$ and $w(x) \cap W^u(x^*)$ contain points other than x^*.

Proof: (Refer to Appendix 1 in Freedman-Waltman (1984).)

q.e.d.

Remark: This lemma together with Proposition 2.11 provide us with a useful tool for proving persistence.

The following proposition shows that under certain conditions 0 is not in the omega-limit set of any orbit. The point here is that the flow is only continuous and we may not be able to use the Butler-McGehee lemma as stated.

Proposition 2.15: Consider

$$\dot{x}_i = f_i(x_1,\cdots,x_n,y) \qquad (i = 1,\cdots,n)$$

$$\dot{y} = g(x_1,\cdots,x_n,y)$$

where $f_i, g \in \text{Lip}$, $cl(R_+^{n+1})$ is positively invariant, and 0 is a rest point. Let $x = x_1 + \cdots + x_n$ and suppose that there is a neighbourhood U of 0 in $cl(R_+^{n+1})$ such that:

$$\dot{x} \geq k_1 x \quad \text{and} \quad \dot{y} \leq -k_2 y \tag{2.12}$$

in U, for some $k_1, k_2 > 0$. Moreover, assume that the non-negative y axis is invariant and 0 is globally stable over it. Then $0 \notin w(x_1,\cdots,x_n,y)$ for all $(x_1,\cdots,x_n,y) \in R_+^n$ for which $O^+(x_1,\cdots,x_n,y)$ is bounded.

f: Let $\varepsilon > 0$ be such that (2.12) is valid on

$$V = \{(x_1,\cdots,x_n,y) \in cl(R_+^{n+1}) : x \leq \varepsilon , y \leq \varepsilon\} .$$

Since $x(t) \geq x(0)\, e^{k_1 t}$ and $y(t) \leq y(0)\, e^{-k_2 t}$, the eventual exit set V^0 and the immediate exit set V^- are given by:

$$V^0 = \{(x_1,\cdots,x_n,y) \in V : x > 0\}$$

$$V^- = \{(x_1,\cdots,x_n,y) \in V : x = \varepsilon\} .$$

refore, V is a Wazewski set and hence the time of exit map is continuous. Based on this, we can complete the proof using an argument similar to the proof of the Butler-McGehee lemma.

q.e.d.

The following is an extension of the Butler-McGehee lemma to general (not necessarily hyperbolic) rest points.

Proposition 2.16: Consider

$$\dot{x} = f(x) \qquad (x \in R^n)$$

where $f \in C^2$. Let x^* be a rest point. If $x^* \in w(x)$ for some $x \in R^n$ and $x \notin W^{cs}(x^*)$, then $w(x) \cap W^{cs}(x^*)$ contains a point other than x^* .

Proof: Use Palis-Takens linearization theorem to construct a closed neighbourhood U of x^* such that $V = U \setminus W^{cs}(x^*)$ is a Wazewski set with $V^0 = V$. We can then repeat the argument as in the proof of the Butler-McGehee lemma to complete the proof.

q.e.d.

CHAPTER 3

A ONE-LOCUS, TWO-ALLELE MODEL WITH FERTILITY / VIABILITY DIFFERENCES

In this chapter, the global convergence to rest points of a continuous, one-locus, two-allele genetic model that incorporates non-linear birth and death rates as well as unequal genotypic fertilities / viabilities will be analyzed. This model will be derived in Appendix 1.

3.1. Introduction and the Model.

This chapter is concerned with a dynamical system of the form

$$\begin{aligned} \dot{x}_1 &= \frac{u^2}{(u+v)^2} B(x) - \frac{x_1}{x} D(x) \\ \dot{x}_2 &= \frac{2uv}{(u+v)^2} B(x) - \frac{x_2}{x} D(x) \\ \dot{x}_3 &= \frac{v^2}{(u+v)^2} B(x) - \frac{x_3}{x} D(x) \end{aligned} \tag{3.1}$$

where

$$\begin{aligned} u &= f_1 x_1 + \frac{1}{2} f_2 x_2 \\ v &= f_3 x_3 + \frac{1}{2} f_2 x_2 \end{aligned} \tag{3.2}$$

$$x = x_1 + x_2 + x_3 \tag{3.3}$$

$$f_1 , f_2 , f_3 > 0 \tag{3.4}$$

and

$$\cdot = \frac{d}{dt} = \text{derivative with respect to time } t.$$

Here x_1 , x_2 , and x_3 denote the number of organisms of genotype AA , Aa , and aa respectively of a one-locus, two-allele problem where A and a stand for the two allele types. System (3.1) is a generalization of the model (without predator) studied in Freedman-Waltman (1978, 1982). In these two papers, the f_i's are taken to be unity. In order to preserve some consistency, the same notations as in these two papers will be adopted. Models similar to system (3.1) have been used by K. Beck in her study of the population genetics of cystic fibrosis, Beck (1982). (See also Beck-Keener-Ricciardi (1982, 1984) for related models.) In Section 3.1 of Waltman (1984), there is a nice discussion on the derivation of these types of models. The effect of the introduction of a predator population to the persistence of the system for which the prey population (in the absence of the predator) is modelled by system (3.1) will be studied in Chapter 4. Other related works of interest, besides the ones mentioned above are: Akin (1979, 1983), Aronson-Weinberger (1975, 1978), Beck (1984), Butler-Freedman-Waltman (1982), Christiansen-Fenchel (1977), Conley-Fife (1982), Hadeler-Glas (1983), Hadeler-Liberman (1975), Losert-Akin (1983), Nagylaki (1977), Nagylaki-Crow (1974), and, Shahshahani (1979).

In system (3.1), $B(x)/x$ and $D(x)/x$ are the natural, intrinsic birth and death rates respectively of the entire population x. The f_i's can be thought of as corresponding to fertility or viability of the genotypes x_i's. (Refer to Appendix 1 for the derivation of the coefficients of $B(x)$.) We will make the following assumptions on the functions B and D:

(H1) $B, D : cl(R^1_+) \to cl(R^1_+)$ are C^2,

(H2) $B(0) = D(0) = 0$,

(H3) $B'(0) > D'(0)$,

(H4) $B'(x), D'(x) > 0$ for $x \in cl(R^1_+)$,

(H5) there exists a unique $K > 0$ ("carrying capacity") such that $B(K) = D(K)$, and,

(H6) $B'(K) < D'(K)$

where $' = \frac{d}{dx}$ = derivative with respect to x.

Assumption (H1) is sufficient to ensure existence and uniqueness of initial value problems for all $t \geq 0$ and for the invariant manifold and saddle node calculations to follow. Assumption (H2) implies that there can be no birth nor death when there is zero population. (H4) states that the birth and death functions are increasing functions of the entire population. (H3) implies that for small populations, the birth rate increases more rapidly than the natural death rate. (H5) states that there is a carrying capacity of the environment, at which point, birth rate equals natural death rate. (H6) says that at the carrying capacity the birth rate increases less rapidly than the natural death rate.

In Section 3.2, we will show that system (3.1) defines a continuous semi-flow ϕ on $cl(R_+^3)$ and ϕ is a smooth (C^2) local flow on R_+^3. Moreover, all solutions $\phi(x_0,t)$ with initial conditions

$$X_0 = (x_{10},x_{20},x_{30}) \in cl(R_+^3) \setminus \{(0,0,0)\}$$

approach the closed, positively invariant simplex

$$cl(U) = \{X \in cl(R_+^3) : x = K\} \tag{3.5}$$

where $U = \{X \in R_+^3 : x = K\}$. In Section 3.3, we discuss the rest points of the flow ϕ. A complete global picture of the flow ϕ on $cl(U)$ is described in Section 3.4 by means of the "projective" flow $\tilde{\phi}$ of ϕ on

$$cl(S) = \{(x_1,x_3) \in cl(R_+^2) : x_1 + x_3 \leq K\} \tag{3.6}$$

where

$$S = \{(x_1,x_3) \in R_+^2 : x_1 + x_3 < K\} .$$

Using these results, we show in Section 3.5 the main result of the chapter: for all $X \in cl(R_+^3)$, $\phi(X,t)$ converges to some rest point of ϕ, as t tends to $+\infty$. It turns out that which rest point $\phi(X,t)$ converges to is predictable and these results are directly analogous to the discrete case (see Chapter 3 of Roughgarden (1979)). Finally, Section 3.6 is a short discussion of the results.

3.2. The Associated Flow.

Let us define the right hand side of system (3.1) to be (0,0,0) when $X = (x_1,x_2,x_3) = (0,0,0)$. That is, define

$$F = (F_1,F_2,F_3) : cl(R^3_+) \to R^3$$

by

$$F(X) = (F_1(x_1,x_2,x_3),F_2(x_1,x_2,x_3),F_3(x_1,x_2,x_3)) ,$$

where

$$F_1(X) = \begin{cases} \dfrac{u^2}{(u+v)^2} B(x) - \dfrac{x_1}{x} D(x) & \text{if } X \in cl(R^3_+) \setminus \{(0,0,0)\} \\ 0 & \text{if } X = (0,0,0) \end{cases}$$

$$F_2(X) = \begin{cases} \dfrac{2uv}{(u+v)^2} B(x) - \dfrac{x_2}{x} D(x) & \text{if } X \in cl(R^3_+) \setminus \{(0,0,0)\} \\ 0 & \text{if } X = (0,0,0) \end{cases} \tag{3.7}$$

$$F_3(X) = \begin{cases} \dfrac{v^2}{(u+v)^2} B(x) - \dfrac{x_3}{x} D(x) & \text{if } X \in cl(R^3_+) \setminus \{(0,0,0)\} \\ 0 & \text{if } X = (0,0,0) \end{cases}$$

where u,v and x are given by (3.2) and (3.3). The system (3.1) becomes

$$\dot{X} = F(X) \tag{3.8}$$

Clearly, F is locally Lipschitz. For example, if $X \in cl(R_+^3)$ with $0 < |X| \leq r$,

$$|F(X) - F(0)| \leq 3[B(x) + D(x)] \leq C\ |x| \leq C'\ |X| \quad ,$$

for some constants $C, C' > 0$ depending on r only. Also, $F(0) = 0$.

We will summarize some of the properties of system (3.8) in the following proposition.

Proposition 3.1: System (3.8) defines a continuous positive semi-flow ϕ on $cl(R_+^3)$ which becomes a smooth local flow when restricted to R_+^3 . The simplex $cl(U)$ defined in (3.5) is closed, positively invariant under ϕ and is globally stable on $cl(R_+^3) \setminus \{(0,0,0)\}$. Furthermore, the vector field F points into R_+^3 on $b(R_+^3) \setminus cl(H_{x_1} \cup H_{x_3})$, H_{x_1} and H_{x_3} are positively invariant and $(0,0,0)$ is a repelling rest point of ϕ .

Proof: The definition of the flow ϕ by (3.8) and its smoothness properties are clear. It is also easy to see that F points into R_+^3 on $b(R_+^3) \setminus cl(H_{x_1} \cup H_{x_3})$. For example for $X \in H_{x_2}$, we have, $x_1 = x_3 = 0$, so that $F_1(X) = F_3(X) = \frac{1}{4} B(X) > 0$. Consequently $F(X)$ points into R_+^3 . From this and from the fact that H_{x_1} and H_{x_3} are invariant, it follows from Proposition 2.1 that $cl(R_+^3)$ is positively invariant.

On the other hand, since

$$\dot{x} = B(x) - D(x) \qquad (3.9)$$

the assumptions (H1) - (H6) in Section 3.1 imply that $x = K$ is a sink for system (3.9) and for all $x(0) = x_0 \in R_+^1$, we have, $0 < x(t) \to K$, as $t \to +\infty$. This shows that $cl(U)$ is globally stable over $cl(R_+^3) \setminus \{(0,0,0)\}$.

q.e.d.

<u>Remark</u>: Let $V : cl(R_+^3) \setminus \{(0,0,0)\} \to R_+^1$ be defined by $V(X) = x$. Then for all $K' \in R_+^1$, $V^{-1}(K')$ is a closed simplex and for all $K' \neq K$, the vector field F on $V^{-1}(K')$ points towards $V^{-1}(K) = cl(U)$.

3.3. The Rest Point Set.

By Proposition 3.1, all rest points on ϕ other than $(0,0,0)$ must lie on $cl(U)$. Hence $(K,0,0)$ and $(0,0,K)$ are the only rest points in $b(R_+^3)$ besides $(0,0,0)$.

<u>Proposition 3.2</u>: <u>Define the curve</u> $H : R_+^1 \to U$ <u>by</u>

$$H(c) = \left(\frac{c^2K}{(1+c)^2}, \frac{2cK}{(1+c)^2}, \frac{K}{(1+c)^2}\right) \qquad (3.10)$$

<u>for all</u> $c \in R_+^1$. <u>Then all rest points of</u> ϕ <u>in</u> R_+^3 <u>must lie on</u> $H(R_+^1)$.

Proof: Let $X^* = (x_1^*, x_2^*, x_3^*) \in R_+^3$ be a rest point for ϕ and let $c = \frac{x_2^*}{2\, x_3^*}$. Then $c > 0$ and $x^* = x_1^* + x_2^* + x_3^* = K$. Let

$$u^* = f_1 x_1^* + \frac{1}{2} f_2 x_2^*$$
$$v^* = f_3 x_3^* + \frac{1}{2} f_2 x_2^* \tag{3.11}$$

According to (3.1), we have,

$$\frac{u^{*2}}{(u^*+v^*)^2} B(K) - \frac{x_1^*}{K} D(K) = 0$$

$$\frac{2u^* v^*}{(u^*+v^*)^2} B(K) - \frac{x_2^*}{K} D(K) = 0$$

$$\frac{v^{*2}}{(u^*+v^*)^2} B(K) - \frac{x_3^*}{K} D(K) = 0 \quad ,$$

so that,

$$u^{*2} K = x_1^* (u^* + v^*)^2 \tag{3.12}$$

$$2u^* v^* K = x_2^* (u^* + v^*)^2 \tag{3.13}$$

$$v^{*2} K = x_3^* (u^* + v^*)^2 \tag{3.14}$$

since $B(K) = D(K)$. Therefore

$$\frac{(3.13)}{(3.12)} \cdot \frac{(3.13)}{(3.14)}$$

gives

$$4 = \frac{x_2^{*2}}{x_1^* \, x_3^*} \quad \text{or} \quad x_1^* = c^2 \, x_3^* \; .$$

Now, $x^* = K$ implies $(c^2 + 2c + 1)x_3^* = K$ and hence

$$X^* = \left(\frac{c^2 K}{(1+c)^2} , \frac{2cK}{(1+c)^2} , \frac{K}{(1+c)^2} \right)$$

as desired.

q.e.d.

Remarks: (i) $cl(H(R_+^1)) = H(R_+^1) \cup \{(K,0,0),(0,0,K)\}$ (3.15)

It will be referred to as the Hardy-Weinberg manifold. It is a closed segment of a parabolic curve in $cl(U)$.

(ii) $\lim_{c \to 0} H(c) = (0,0,K)$ and $\lim_{c \to +\infty} H(c) = (K,0,0)$. Let

$$a_1 = f_1 - f_2 \quad \text{and} \quad a_3 = f_3 - f_2 \tag{3.16}$$

Proposition 3.3:

(i) *If* $(a_1,a_3) = (0,0)$, *then* $H(R_+^1)$ *is the set of rest points of* ϕ *in* R_+^3 .

(ii) *If* $a_1 , a_3 > 0$ *or if* $a_1 , a_3 < 0$, *then* ϕ *has exactly one rest point in* R_+^3 , *namely,* $H(c)$ *with* $c = a_3 / a_1$.

(iii) *If* $a_1 \geq 0$, $a_3 \leq 0$ *and* $(a_1,a_3) \neq (0,0)$ *or if* $a_1 \leq 0$,

$a_3 \geq 0$ <u>and</u> $(a_1, a_3) \neq (0,0)$, <u>then</u> ϕ <u>has no rest points in</u> R_+^3 .

<u>Proof</u>: By the previous proposition, all rest points $X^\star$ of ϕ in R_+^3 are of the form $H(c)$ given by (3.10) for some $c \in R_+^1$. According to (3.11),

$$u^\star = \frac{cK}{(1+c)^2}(cf_1 + f_2)$$

$$v^\star = \frac{K}{(1+c)^2}(cf_2 + f_3) \quad . \tag{3.17}$$

Substituting this into (3.12) gives, after some simplifications,

$$(1+c)^2(cf_1+f_2)^2 = (c^2f_1+2cf_2+f_3)^2$$

or

$$cf_1 + f_2 = cf_2 + f_3 \tag{3.18}$$

or

$$c = a_3 \,/\, a_1 \tag{3.19}$$

provided $a_1 \neq 0$.

Thus, (3.12) imposes no restrictions on c in case (i), it requires c to be a_3 / a_1 in case (ii), and in case (iii) no $c \in R_+^1$ will satisfy (3.12). To complete the proof, all we need is to verify that any $c \in R_+^1$ satisfying (3.12) also satisfies (3.13) and (3.14). But this follows from a straightforward calculation. For example, (3.13) simplifies to (3.12) using (3.18).

q.e.d.

Remark: In case (i) we have a 1-dimensional manifold of rest points. In general, a manifold of rest points (critical points) is referred to as a critical manifold (see Conley-Fife (1982)).

3.4. Projective Flow.

In order to study the dynamics of ϕ on $cl(R^3_+)$, we will first study the global dynamics of ϕ on the globally stable positively invariant simplex $cl(U)$. This is equivalent to investigate the phase portrait of the "projective" semi-flow $\tilde{\phi}$ of ϕ on $cl(S)$ (defined in (3.6)). Here $\tilde{\phi}$ is defined by (3.1) with x_2 being replaced by $K - x_1 - x_3$ throughout. That is, we have,

$$\begin{aligned} \dot{x}_1 &= \frac{u^2}{(u+v)^2} L - \frac{x_1}{K} L \\ \dot{x}_3 &= \frac{v^2}{(u+v)^2} L - \frac{x_3}{K} L \end{aligned} \tag{3.20}$$

where, by (3.2),

$$\begin{aligned} u &= fK + (a_1 + f)x_1 - fx_3 \\ v &= fK - fx_1 + (a_3 + f)x_3 \end{aligned} \tag{3.21}$$

and

$$L = B(K) = D(K) \tag{3.22}$$

$$f = f_2 / f \tag{3.23}$$

By lifting the flow $\tilde{\phi}$ back to $cl(U)$ (that is, if $(x_1(t), x_3(t))$ is a solution of (3.20) in $cl(S)$, then $(x_1(t), x_2(t), x_3(t))$ with $x_2(t) = K - x_1(t) - x_3(t)$ will be a solution of (3.1) in $cl(U)$), we obtain the flow ϕ on $cl(U)$. Clearly, by Proposition 3.1 or by a direct verification, the vector field defined by system (3.20) points into S on $b(S) \setminus \{(K,0),(0,K)\}$ where $b(S)$ denotes the boundary of S in the x_1-x_3 plane and that $(K,0)$ and $(0,K)$ are the only rest points of $\tilde{\phi}$ in $b(S)$. Hence S is positively invariant under $\tilde{\phi}$. According to Proposition 3.3,

$$(x_1^*, x_3^*) = \left(\frac{c^2 K}{(1+c)^2}, \frac{K}{(1+c)^2}\right) \quad \text{with } c = a_3 / a_1 \tag{3.24}$$

is the only rest point of $\tilde{\phi}$ in S, provided $a_1, a_3 > 0$ or $a_1, a_3 < 0$; and when $a_1 \geq 0$, $a_3 \leq 0$, $(a_1, a_3) \neq (0,0)$ or when $a_1 \leq 0$, $a_3 \geq 0$, $(a_1, a_3) \neq (0,0)$, $\tilde{\phi}$ has no rest points in S.

For the remainder of this section, we will restrict our attention to the case when $(a_1, a_3) \neq (0,0)$. The case when $(a_1, a_3) = (0,0)$ for the "full" system (3.1) will be discussed in Section 3.5.

The variational matrix $M(x_1, x_3)$ of (3.20) at an arbitrary point (x_1, x_3) in $cl(S)$ is given by:

$$M(x_1, x_3) = L \begin{bmatrix} \dfrac{2u(fu+a_1v+fv)}{(u+v)^3} - \dfrac{1}{K} & -\dfrac{2u(a_3u+fu+fv)}{(u+v)^3} \\[2ex] -\dfrac{2v(fu+a_1v+fv)}{(u+v)^3} & \dfrac{2v(a_3u+fu+fv)}{(u+v)^3} - \dfrac{1}{K} \end{bmatrix} \tag{3.25}$$

in particular,

$$M(K,0) = \frac{L}{K}\begin{bmatrix} -\frac{a_1}{f_1} & -\frac{2(a_3+f)}{f_1} \\ 0 & -1 \end{bmatrix} \tag{3.26}$$

$$M(0,K) = \frac{L}{K}\begin{bmatrix} -1 & 0 \\ -\frac{2(a_1+f)}{f_3} & -\frac{a_3}{f_3} \end{bmatrix} \tag{3.27}$$

and, if (x_1^*,x_3^*) exists,

$$M(x_1^*,x_3^*) = \frac{L}{K}\begin{bmatrix} \frac{2a_3e_1}{RW} - 1 & -\frac{a_3e_3}{RW} \\ -\frac{a_1e_1}{RW} & \frac{2a_1e_3}{RW} - 1 \end{bmatrix} \tag{3.28}$$

where

$$R = a_1 + a_3 \ , \quad W = f_1f_3 - f_2^2 \ , \tag{3.29}$$

$$e_1 = a_1^2 + fR \ , \quad e_3 = a_3^2 + fR \ . \tag{3.30}$$

Note that under these notations,

$$x_1^* = \frac{a_3^2\,K}{R^2} \ , \quad x_3^* = \frac{a_1^2\,K}{R^2}$$

$$u^* = \frac{a_3KW}{R^2} \ , \quad v^* = \frac{a_1KW}{R^2} \ , \text{ and, } \quad u^* + v^* = \frac{KW}{R} \ .$$

Proposition 3.4: The linearized stability properties of the rest points of $\tilde{\phi}$ in cl(S) are given by the following diagram:

Parameter Region		Rest Points		
a_1	a_3	(K,0)	(0,K)	(x_1^*, x_3^*)
+	+	-,-	-,-	-,+
-	-	-,+	-,+	-,-
+	-	-,-	-,+	*
-	+	-,+	-,-	*
+	0	-,-	-,0	*
-	0	-,+	-,0	*
0	+	-,0	-,-	*
0	-	-,0	-,+	*

where a_i $(i = 1,3)$ is + (resp. -,0) means that a_i is positive (resp. negative, zero), "-,-" under a rest point means that both eigenvalues of the variational matrix M at that rest point are negative, "-,+" means that one eigenvalue is negative and the other is positive, "-,0" means that one eigenvalue is negative and the other is zero, and, "*" indicates that the rest point does not exist in that parameter region.

Proof: The eigenvalues of M(K,0) are: $-\frac{a_1 L}{f_1 K}$ and $-\frac{L}{K}$, those of M(0,K) are: $-\frac{a_3 L}{f_3 K}$ and $-\frac{L}{K}$ and those of $M(x_1^*, x_3^*)$, if (x_1^*, x_3^*) exists, are: $\frac{a_1 a_3 L}{WK}$ and $-\frac{L}{K}$. To complete the proof, all we need is to note that if $a_1, a_3 > 0$, then $W > 0$ and if $a_1, a_3 < 0$, then $W < 0$.

q.e.d.

Next, we will investigate the phase portrait of $\tilde{\phi}$ in a neighbourhood of each rest point.

Proposition 3.5: We have the following cases, depending on the parameter regions:

(i) $a_1 > 0$, $a_3 > 0$:

(K,0) and (0,K) are sinks, (x_1^*, x_3^*) is a saddle;

(ii) $a_1 < 0$, $a_3 < 0$:

(K,0) and (0,K) are saddles whose stable manifolds have trivial intersections with cl(S) , namely at (K,0) and (0,K) respectively, and whose unstable manifolds intersect cl(S) at a whole separatrix (out of four for a saddle), (x_1^*, x_3^*) is a sink;

(iii) $a_1 > 0$, $a_3 < 0$:

(K,0) is a sink, (0,K) is a saddle whose local phase portrait is similar to that of case (ii);

(iv) $a_1 < 0$, $a_3 > 0$:

(0,K) is a sink, (K,0) is a saddle whose local phase portrait is similar to that of case (ii);

(v) $a_1 > 0$, $a_3 = 0$:

(K,0) is a sink, (0,K) is a saddle node: it has a neighbourhood in R^2 which is the union of one parabolic sector, two hyperbolic sectors and three separatrices, $(0,K)$ is stable within the parabolic sector, the union of the two hyperbolic sectors covers a neighbourhood of $(0,K)$ in $cl(S)$ with the separtrix dividing the hyperbolic sectors lying wholly inside $cl(S)$;

(vi) $a_1 < 0$, $a_3 = 0$:

$(K,0)$ is a saddle whose local phase portrait is similar to that of case (ii), $(0,K)$ is a saddle node: it is stable within the parabolic sector which covers a neighbourhood of $(0,K)$ in $cl(S)$;

(vii) $a_1 = 0$, $a_3 > 0$:

$(0,K)$ is a sink, $(K,0)$ is a saddle node whose local phase portrait is similar to that of $(0,K)$ in case (v);

(viii) $a_1 = 0$, $a_3 < 0$:

$(0,K)$ is a saddle whose local phase portrait is similar to that of case (ii), $(K,0)$ is a saddle node whose local phase portrait is similar to that of $(0,K)$ in case (vi).

Proof: When $a_1 < 0$ (consequently $(K,0)$ is a saddle), $\left(\frac{2f_3-f_2}{f_2}, 1\right)$ is an eigenvector corresponding to the negative eigenvalue $-\frac{L}{K}$ of $M(K,0)$. Thus the corresponding 1-dimensional eigenspace has slope $\frac{f_2}{2f_3-f_2}$. (It is vertical if $2f_3 - f_2 = 0$). Now since the line $x_1 + x_3 = K$ has slope -1 and $\frac{f_2}{2f_3-f_2} \notin [-1,0]$, therefore the 1-dimensional stable manifold $W^s(K,0)$ of $(K,0)$ has trivial intersection with $cl(S)$, namely at $(K,0)$ itself (because of the stable manifold theorem, Theorem 2.6). On the other hand $(1,0)$ is an eigenvector corresponding to the positive eigenvalue $-\frac{a_1 L}{f_1 K}$ of $M(K,0)$. Therefore the unstable manifold $W^u(K,0)$ of $(K,0)$ has slope 0 and has non-trival intersection with $cl(S)$, namely in a whole separatrix (out of four for a saddle point), due to the positive invariance of $cl(S)$ and the Hartman-Grobman theorem (see Section 2.9). Similar arguments apply to the case when $a_3 < 0$. This discussion and Proposition 3.4 settle the cases (i) - (iv).

Next consider the case when $a_1 = 0$. We will use the procedure described in Section 2.10 to show that $(K,0)$ is a saddle node. Let

$$z_1 = x_1 - K$$

$$z_2 = x_3$$

$$N = \begin{bmatrix} 1 & \frac{2f_3 - f_2}{f_2} \\ 0 & 1 \end{bmatrix},$$

and $Y = N^{-1} Z$. Then (3.20) takes the form (2.6). Moreover, by a straightforward calculation, the η in (2.9) is equal to $\frac{a_3 L}{2 f_1 K^2}$. Since, as noted above, $\frac{f_2}{2f_3 - f_2} \notin [-1,0]$, the assertions made under the cases (vii) and (viii) are easily verified. The case when $a_3 = 0$ is similar.

q.e.d.

Knowing the local behavior of $\tilde{\phi}$ near each rest point, we can now describe the global dynamics of $\tilde{\phi}$ on $cl(S)$.

Theorem 3.6: For all $X \in cl(S)$, $\tilde{\phi}(X,t)$ converges to a rest point of $\tilde{\phi}$ in $cl(S)$. More precisely, we have the following cases depending on the parameter regions:

(i) $a_1 > 0$, $a_3 > 0$:

$cl(S)$ is the disjoint union of the three stable manifolds: $W^s(K,0)$, $W^s(0,K)$, and $W^s(x_1^*,x_3^*)$. $W^s(K,0)$ and $W^s(0,K)$ are 2-dimensional, and $W^s(x_1^*,x_3^*)$ is 1-dimensional which acts as a separatrix dividing the two regions of stability: $W^s(K,0)$ and $W^s(0,K)$ of the rest points $(K,0)$ and $(0,K)$;

(ii) $a_1 < 0$, $a_3 < 0$:

(x_1^*,x_3^*) is globally stable on $cl(S) \setminus \{(K,0),(0,K)\}$;

(iii) $a_1 > 0$, $a_3 < 0$:

$(K,0)$ is globally stable on $cl(S) \setminus \{(0,K)\}$;

(iv) $a_1 < 0$, $a_3 > 0$:

$(0,K)$ is globally stable on $cl(S) \setminus \{(K,0)\}$;

(v) $a_1 > 0$, $a_3 = 0$:

$(K,0)$ is globally stable on $cl(S) \setminus \{(0,K)\}$;

(vi) $a_1 < 0$, $a_3 = 0$:

$(0,K)$ <u>is globally stable on</u> $cl(S) \setminus \{(K,0)\}$;

(vii) $a_1 = 0$, $a_3 > 0$;

$(0,K)$ <u>is globally stable on</u> $cl(S) \setminus \{(K,0)\}$;

(viii) $a_1 = 0$, $a_3 < 0$;

$(K,0)$ <u>is globally stable on</u> $cl(S) \setminus \{(0,K)\}$.

<u>Proof</u>: In order to show that for all $X \in cl(S)$, $\tilde{\phi}(X,t)$ converges to a rest point of $\tilde{\phi}$ as t tends to $+\infty$, it suffices, according to the Poincare-Bendixson Theorem, to show that there is no periodic orbit nor rest points connecting orbit forming a loop in $cl(S)$. Using Proposition 3.5 and simple geometric arguments, one could easily show that there are no rest points connecting orbits in $cl(S)$.

On the other hand, since every periodic orbit must enclose a rest point, there can be no periodic orbit in cases (iii) - (viii). (Otherwise, the periodic orbit will have to enclose $(K,0)$ or $(0,K)$ contradicting the positive invariance of S .)

To show that there can be no periodic orbit enclosing the rest point (x_1^*,x_3^*) , one could use an index argument in case (ii) (since $x_1^*,x_3^*)$ is a saddle in the case). As for case (i), let L_1 be the open line segment joining $(K,0)$ and (x_1^*,x_3^*) (that is, end points are excluded) and let L_2 be the open line segment joining $(0,K)$ and (x_1^*,x_3^*) . Also let T denote the open triangle with vertices $(K,0)$, (x_1^*,x_3^*) , and $(K,0)$. Then a straightforward calculation shows that the vector field defined by system (3.20) points into $S \setminus cl(T)$ on

$L_1 \cup L_2$. For example, if $(x_1,x_3) \in L_1$, the dot product between the vector field at (x_1,x_3) and the outward normal $(1,1+2c)$ of L_1 is given by:

$$\left(\frac{u^2}{(u+v)^2} - \frac{x_1}{K}\right) L + \left(\frac{v^2}{(u+v)^2} - \frac{x_3}{K}\right) L(1+2c) = \frac{2v(cv-u)L}{(u+v)^2}$$

which is negative. Thus, there can be no periodic orbit enclosing (x_1^*,x_3^*). Hence, there is no periodic orbit in $cl(S)$.

The rest of the assertions follow directly from the above and Proposition 3.5.

q.e.d.

3.5. Global Dynamics.

We will first describe the linearized stability properties and the local stability properties of the rest points of ϕ.

Proposition 3.7: The linearized stability properties of the rest points of ϕ are given by the following diagram:

Parameter Region		Rest Point		
a_1	a_3	(K,0,0)	(0,0,K)	(x_1^*,x_2^*,x_3^*)
+	+	-,-,-	-,-,-	-,-,+
-	-	-,-,+	-,-,+	-,-,-
+	-	-,-,-	-,-,+	*
-	+	-,-,+	-,-,-	*
+	0	-,-,-	-,-,0	*
-	0	-,-,+	-,-,0	*
0	+	-,-,0	-,-,-	*
0	-	-,-,0	-,-,+	*

where "-,-,-" means that all three eigenvalues of the variational matrix at that rest point are negative, etc., as in Proposition 3.4.

Proof: This follows from Proposition 3.4 and the assumption (H6) in Section 3.1.

q.e.d.

Proposition 3.8: We have the following cases, depending on the parameter regions:

(i) $a_1 > 0$, $a_3 > 0$:

(K,0,0) and (0,0,K) are sinks (i.e. they are point attractors) (x_1^*,x_2^*,x_3^*) is a saddle with a 2-dimensional stable manifold and a 1-dimensional unstable manifold;

(ii) $a_1 < 0$, $a_3 < 0$:

(x_1^*, x_2^*, x_3^*) is a sink, $(K,0,0)$ is a saddle: its 2-dimensional stable manifold $W^s(K,0,0)$ has trivial intersection with $cl(R_+^3)$, namely at H_{x_1} , and its 1-dimensional unstable manifold $W^u(K,0,0)$ intersects $cl(R_+^3)$ in a whole branch (out of two for the 1-dimensional unstable manifold), $(0,0,K)$ is also a saddle whose local phase portrait is similar to that of $(K,0,0)$;

(iii) $a_1 > 0$, $a_3 < 0$:

$(K,0,0)$ is a sink, $(0,0,K)$ is a saddle whose local phase portrait is similar to that in case (ii);

(iv) $a_1 < 0$, $a_3 > 0$:

$(0,0,K)$ is a sink, $(K,0,0)$ is a saddle whose local phase portrait is similar to that in case (ii);

(v) $a_1 > 0$, $a_3 = 0$:

$(K,0,0)$ is a sink, $(0,0,K)$ is a saddle node: its strong stable manifold $W^{ss}(0,0,K)$, has trivial intersection with $cl(R_+^3)$, namely at H_{x_3} , $cl(R_+^3)$ is on the side of the strong stable manifold for which $(0,0,K)$ is unstable;

(vi) $a_1 < 0$, $a_3 = 0$:

$(K,0,0)$ is a saddle whose local phase portrait is similar to that in case (ii), (0,0,K) is a saddle node: its strong stable manifold has trivial intersection with $cl(R^3_+)$, namely at H_{x_3}, $cl(R^3_+)$ is on the side of the strong stable manifold for which (0,0,K) is stable;

(vii) $a_1 = 0$, $a_3 > 0$:

(0,0,K) is a sink, (K,0,0) is a saddle node whose local phase portrait is similar to that of (0,0,K) in case (v);

(viii) $a_1 = 0$, $a_3 < 0$:

(0,0,K) is a saddle whose local phase portrait is similar to that in case (ii), (K,0,0) is a saddle node whose local phase portrait is similar to that of (0,0,K) in case (vi).

Proof: The variational matrix of (3.1) at $X \in cl(R^3_+) \setminus \{(0,0,0)\}$ is given by

$$M(x_1,x_2,x_3) = \begin{bmatrix} M_{11} & M_{12} & M_{13} \\ M_{21} & M_{22} & M_{23} \\ M_{31} & M_{32} & M_{33} \end{bmatrix} \qquad (3.31)$$

where

$$M_{11} = \frac{2f_1uv}{(u+v)^3} B(x) + \frac{u^2}{(u+v)^2} B'(x) - \frac{x_2+x_3}{x^2} D(x) - \frac{x_1}{x} D'(x) \quad ,$$

$$M_{12} = \frac{f_2u(v-u)}{(u+v)^3} B(X) + \frac{u^2}{(u+v)^2} B'(x) + \frac{x_1}{x^2} D(x) - \frac{x_1}{x} D'(x) \quad ;$$

$$M_{13} = -\frac{2f_3u^2}{(u+v)^3} B(x) + \frac{u^2}{(u+v)^2} B'(x) + \frac{x_1}{x^2} D(x) - \frac{x_1}{x} D'(x)$$

$$M_{21} = \frac{2f_1v(v-u)}{(u+v)^3} B(x) + \frac{2uv}{(u+v)^2} B'(x) + \frac{x_2}{x^2} D(x) - \frac{x_2}{x} D'(x)$$

$$M_{22} = \frac{f_2(u-v)^2}{(u+v)^3} B(x) + \frac{2uv}{(u+v)^2} B'(x) - \frac{x_1+x_3}{x^2} D(x) - \frac{x_2}{x} D'(x)$$

$$M_{23} = \frac{2f_3u(u-v)}{(u+v)^3} B(x) + \frac{2uv}{(u+v)^2} B'(x) + \frac{x_2}{x^2} D(x) - \frac{x_2}{x} D'(x)$$

$$M_{31} = -\frac{2f_1v^2}{(u+v)^3} B(x) + \frac{v^2}{(u+v)^2} B'(x) + \frac{x_3}{x^2} D(x) - \frac{x_3}{x} D'(x)$$

$$M_{32} = \frac{f_2v(u-v)}{(u+v)^3} B(x) + \frac{v^2}{(u+v)^2} B'(x) + \frac{x_3}{x^2} D(x) - \frac{x_3}{x} D'(x)$$

$$M_{33} = \frac{2f_3uv}{(u+v)^3} B(x) + \frac{v^2}{(u+v)^2} B'(x) - \frac{x_1+x_2}{x^2} D(x) - \frac{x_3}{x} D'(x) \quad .$$

Thus,

$$M(K,0,0)\hat{} = \begin{bmatrix} -e & -e + \frac{a_1L}{f_1K} & -e + \frac{(f_1-2f_3)L}{f_1K} \\ 0 & -\frac{a_1L}{f_1K} & \frac{2f_3L}{f_1K} \\ 0 & 0 & -\frac{L}{K} \end{bmatrix} \qquad (3.32)$$

where

$$e = D'(K) - B'(K) > 0 \qquad (3.33)$$

by (H6) of Section 3.1. Hence the eigenvalues of $M(K,0,0)$ are: $-e$, $-\frac{a_1 L}{f_1 K}$, and, $-\frac{L}{K}$. When $a_1 > 0$ (consequently, $(K,0,0)$ is a saddle), the 2-dimensional eigenspace corresponding to the two negative eigenvalues: $-e$ and $-\frac{L}{K}$ is spanned by the vectors $(1,0,0)$ and $(0, -\frac{2f_3}{f_2}, 1)$. Since $-\frac{2f_3}{f_2} < 0$, the positive invariance of $cl(R^3_+)$ and the stable manifold theorem (Theorem 2.6) imply that the 2-dimensional stable manifold of $(K,0,0)$ intersects $cl(R^3_+)$ at H_{x_1} only. Similarly, one can show that when $a_3 < 0$, the 2-dimensional stable manifold of $(0,0,K)$ intersects $cl(R^3_+)$ at H_{x_3} only. This and Proposition 3.7 settle the cases (i) - (iv).

Next, consider the case when $a_1 = 0$. We will use the procedure described in Section 2.10 to show that $(K,0,0)$ is a saddle node.

Let

$$z_1 = x_1 - K$$

$$z_2 = x_2$$

$$z_3 = x_3$$

$$N = \begin{bmatrix} -1 & 1 & 0 \\ 1 & 0 & -\frac{2f_3}{f_1} \\ 0 & 0 & 1 \end{bmatrix} ,$$

and

$Y = N^{-1}Z$. Then (3.1) takes the form (2.6). Moreover, a straightforward calculation shows that the η in (2.9) is equal to $\frac{a_3 L}{2f_1 K^2}$. This settles the cases (vii) and (viii). The case when $a_3 = 0$ is similar.

q.e.d.

We can now describe the global dynamics of the flow ϕ on $cl(R^3_+)$.

Theorem 3.9: For all $X \in cl(R^3_+)$, $\phi(X,t)$ converges to a rest point of ϕ as t tends to $+\infty$. More precisely, we have the following cases depending on the parameters regions:

(i) $a_1 = 0$; $a_3 = 0$:

$cl(H(R^1_+))$ is the set of rest points of ϕ in $cl(R^3_+) \setminus \{(0,0,0)\}$. $cl(R^3_+) \setminus \{(0,0,0)\}$ is foliated by the strong stable manifolds, $W^{ss}(H(c))$ $(c \in [0,+\infty])$, of these rest points, where

$$W^{ss}(H(c)) \cap cl(R^3_+) = \{(x_1,x_2,x_3) \in cl(R^3_+) \setminus \{(0,0,0)\} : x_1 + \frac{1-c}{2} x_2 - cx_3 = 0\} \tag{3.34}$$

is 2-dimensional for all $c \in (0,+\infty)$,

$$W^{ss}(H(0)) \cap cl(R^3_+) = W^{ss}(0,0,K) \cap cl(R^3_+) = H_{x_3} \text{ , and,}$$

$$W^{ss}(H(+\infty)) \cap cl(R^3_+) = W^{ss}(K,0,0) \cap cl(R^3_+) = H_{x_1} \text{ are}$$

1-dimensional.

(ii) $a_1 > 0$, $a_3 > 0$:

$cl(R^3_+) \setminus \{(0,0,0)\}$ is the disjoint union of $W^s(K,0,0)$, $W^s(0,0,K)$ and $W^s(x_1^*,x_2^*,x_3^*)$. $W^s(K,0,0)$ and $W^s(0,0,K)$ are 3-dimensional, $W^s(x_1,x_2,x_3)$ is a 2-dimensional immersed submanifold of $cl(R^3_+) \setminus \{(0,0,0)\}$ forming a separatrix surface which divides $cl(R^3_+) \setminus \{(0,0,0)\}$ into the two regions of stabiliy: $W^s(K,0,0)$ and $W^s(0,0,K)$ of the rest points $(K,0,0)$ and $(0,0,K)$;

(iii) $a_1 < 0$, $a_3 < 0$:

(x_1^*,x_2^*,x_3^*) is globally stable on $cl(R^3_+) \setminus cl(H_{x_1} \cup H_{x_3})$, $(K,0,0)$ is globally stable on H_{x_1} and $(0,0,K)$ is globally stable on H_{x_3} ;

(iv) $a_1 > 0$, $a_3 < 0$:

$(K,0,0)$ is globally stable on $cl(R^3_+) \setminus cl(H_{x_3})$ and $(0,0,K)$ is globally stable on H_{x_3} ;

(v) $a_1 < 0$, $a_3 > 0$:

$(0,0,K)$ is globally stable on $cl(R^3_+) \setminus cl(H_{x_1})$ and $(K,0,0)$ is globally stable on H_{x_1} ;

(vi) $a_1 > 0$, $a_3 = 0$:

$(K,0,0)$ is globally stable on $cl(R^3_+) \setminus cl(H_{x_3})$ and $(0,0,K)$ is globally stable on H_{x_3} ;

(vii) $a_1 < 0$, $a_3 = 0$:

$(0,0,K)$ <u>is globally stable on</u> $cl(R^3_+) \setminus cl(H_{x_1})$ <u>and</u> $(K,0,0)$ <u>is globally stable on</u> H_{x_1} ;

(viii) $a_1 = 0$, $a_3 > 0$:

$(0,0,K)$ <u>is globally stable on</u> $cl(R^3_+) \setminus cl(H_{x_1})$ <u>and</u> $(K,0,0)$ <u>is globally stable on</u> H_{x_1} ;

(ix) $a_1 = 0$, $a_3 < 0$:

$(K,0,0)$ <u>is globally stable on</u> $cl(R^3_+) \setminus cl(H_{x_3})$ <u>and</u> $(0,0,K)$ <u>is globally stable on</u> H_{x_3} .

<u>Proof</u>: Case (i) is discussed in Freedman-Waltman (1978). It was shown there that if we let $u_0 = u(0)$, $v_0 = v(0)$ and $c = u_0 / v_0$ then $u(t) = cv(t)$ for all $t \in R^1$. Furthermore, $x_1(t) - c^2 x_3(t) \to 0$, and $x_2(t) - 2cx_3(t) \to 0$ as $t \to +\infty$. Hence,

$$(x_1(t),x_2(t),x_3(t)) \to \left(\frac{c^2K}{(1+c)^2}, \frac{2cK}{(1+c)^2}, \frac{K}{(1+c)^2}\right)$$

as $t \to +\infty$. (Note that the assumption "death is certain": $\int_0^{+\infty} \frac{D(x)}{x}\,dx = +\infty$ made in Freedman-Waltman (1978) is automatically satisfied under the hypotheses (H1) - (H6) in Section 3.1 because $\lim_{x \to +\infty} \frac{D(x)}{x} = \frac{L}{K} > 0$.) The assertions made under case (i) are just a rephrase of these results in geometric language.

We will now restrict ourselves to the case when $(a_1,a_3) \neq (0,0)$. Recall the following properties of the omega-limit set, $w(X)$, of a precompact non-negative orbit, $O^+(X)$, of a flow ϕ :

(a) $w(X)$ is compact, connected, invariant and chain recurrent (Proposition 2.5) and

(b) $\phi(X,t)$ approaches $w(X)$ as $t \to +\infty$.

For all $X \in cl(R^3_+) \setminus \{(0,0,0)\}$, $w(X) \subset cl(U)$ by the Proposition 3.1. According to the Theorem 3.6, the only compact, connected, invariant, chain recurrent subsets of $cl(U)$ are the singleton rest point sets. Thus $\phi(X,t)$ converges to a rest point in $cl(U)$.

The assertions made under the cases (ii) - (ix) follow from the above observation and Proposition 3.8.

q.e.d.

Remarks: (i) It is clear that one could weaken the assumption (H3) in Section 3.1 of strictly increasing B and D somewhat without changing the statement of the Theorem 3.9 nor its proof.

(ii) One could also add in an equation for the carrying capacity K of the form: $\dot{K} = G(K)$, as in Beck (1982). If we impose enough conditions on G so that $K_0 > 0$ is globally stable over the positive K axis then the asymptotic behavior described in Theorem 3.9 remains valid with K replaced by K_0.

3.6 Discussion.

The biological interpretation of the parameter regions in Theorem 3.9 are as follows:

(i) $a_1 = 0$, $a_3 = 0$: selection values are all equal,

(ii) $a_1 > 0$, $a_3 > 0$: heterozygote inferiority,

(iii) $a_1 < 0$, $a_3 < 0$: heterozygote superiority,

(iv) $a_1 > 0$, $a_3 < 0$: incomplete dominance,

(v) $a_1 < 0$, $a_3 > 0$: incomplete dominance,

(vi) $a_1 > 0$, $a_3 = 0$: selection against the dominant allele a ,

(vii) $a_1 < 0$, $a_3 = 0$: selection against the recessive allele A ,

(viii) $a_1 = 0$, $a_3 > 0$: selection against the dominant allele A , and,

(ix) $a_1 = 0$, $a_3 < 0$: selection against the recessive allele a .

Thus the results stated in Theorem 3.9 are directly analogous to the discrete case (see Chapter 3 of Roughgarden (1979)). The idea of convergence to rest points for a one-locus, n-allele genetic model is not new. One could refer to Butler-Freedman-Waltman (1982) and Hadeler-Glas (1983) for models along similar lines, and to Losert-Akin (1984) for the Fisher-Wright-Haldane model.

The usefulness of using a continuous model like system (3.1) lies in the possibility of adding other populations into the system in the form of differential equations. In the next chapter, the genotypic effects of predator-prey interactions will be studied using these ideas.

CHAPTER 4

A PREDATOR-PREY MODEL CONSISTING OF THREE PREY GENOTYPES WITH FERTILITY/VIABILITY DIFFERENCES

In this chapter a model of a predator-prey interaction, where the prey population consists of three genotypes and is modelled by system (3.1), is proposed. Sufficiency conditions leading to the evolution of pure strains are given. This extends results of Freedman-Waltman (1978, 1982). As well, conditions are derived which guarantee the persistence of all components of the system.

4.1 Introduction and the Model.

In this chapter, the model of the previous chapter is extended to include a predator. More specifically, the model is given by:

$$\begin{aligned}
\dot{x}_1 &= \frac{u^2}{(u+v)^2} B(x) - \frac{x_1}{x} [D(x) + yP_1(x)] \\
\dot{x}_2 &= \frac{2uv}{(u+v)^2} B(x) - \frac{x_2}{x} [D(x) + yP_2(x)] \\
\dot{x}_3 &= \frac{v^2}{(u+v)^2} B(x) - \frac{x_3}{x} [D(x) + yP_3(x)] \\
\dot{y} &= y[-s + k \sum_{i=1}^{3} \frac{x_i}{x} P_i(x)]
\end{aligned} \tag{4.1}$$

where x, given by (3.3), is the total prey population and y is the predator population, u and $\dot{v}$ are given by (3.2) and s and k are assumed to be positive.

The genetic component of this model arises by considering a one-locus, two-allele problem as given by system (3.1). The ecological component arises by imbedding an intermediate predator-prey model with continuous natural birth and death processes in a model which accounts for different predator functional responses (given by $P_i(x)$ $(i=1,2,3)$) by the predator on the different prey genotypes x_i $(i=1,2,3)$. For a discussion of intermediate predator-prey models, see Chapter 4 of Freedman (1980) and the literature cited there.

Besides the assumptions (H1) - (H6) made in Section 3.1 on the birth and death rates, we make the following assumptions on the predator functional responses:

(H7) $P_i : cl(R^1_+) \to cl(R^1_+)$ are C^2 $(i=1,2,3)$,

(H8) $P_i(0) = 0$ $(i=1,2,3)$

(H9) $P_i'(x) > 0$ $(i=1,2,3)$ for all $x \in cl(R^1_+)$.

Assumption (H7) is sufficient to ensure existence and uniqueness of initial value problems for $t \geq 0$. (H8) implies that there is no predation in the absence of the prey population. (H9) states that the predator functional responses are strictly increasing as functions of the number of prey.

The remainder of this chapter is organized as follows: In Section 4.2, we construct the flow on $cl(R^4_+)$ defined by system (4.1) and list some of its properties. The boundary rest points of this flow and their stability are considered in Section 4.3. In Section 4.4, conditions leading to the evolution of pure strains and the existence of a globally stable boundary rest point are given. The classification of the parameter values into persistence and non-persistence cases is discussed in Section 4.5. We finish with a short discussion of the results in Section 4.6.

4.2 The Associated Flow.

In this section we will show that system (4.1) defines a continuous semi-flow on $cl(R^4_+)$ which becomes a smooth (C^1) local flow when restricted to R^4_+. We will also show that it is A-dissipative and discuss its boundary invariant sets.

As in system (3.1), system (4.1) is not defined when $x = 0$. Let us redefine system (4.1) as follows. We define system (4.2) to be

$$\dot{x}_1 = \frac{u^2}{(u+v)^2} B(x) - \frac{x_1}{x} [D(x) + yP_1(x)]$$

$$\dot{x}_2 = \frac{2uv}{(u+v)^2} B(x) - \frac{x_2}{x} [D(x) + yP_2(x)] \quad , \quad x > 0$$

$$\dot{x}_3 = \frac{v^2}{(u+v)^2} B(x) - \frac{x_3}{x} [D(x) + yP_3(x)]$$

$$\dot{y} = y[-s + k \sum_{i=1}^{3} \frac{x_i}{x} P_i(x)] \qquad (4.2)$$

$$\dot{x}_i = 0 \quad (i = 1,2,3) \quad , \quad x = 0$$

$$\dot{y} = -sy$$

or

$$\dot{x}_i = F_i(x_1,x_2,x_3,y) \qquad (i = 1,2,3)$$

$$\dot{y} = F_4(x_1,x_2,x_3,y) = G(x_1,x_2,x_3,y) \quad .$$

Let

$$F = (F_1,F_2,F_3,F_4) \quad . \tag{4.3}$$

Clearly, $F_i \in \text{Lip}$ $(i=1,\cdots,4)$ on $\text{cl}(R^4_+)$. For example, consider the two points (x_1,x_2,x_3,y) and $(0,0,0,\overline{y})$ where $x = x_1 + x_2 + x_3 > 0$. Then

$$|G(x_1,x_2,x_3,y) - G(0,0,0,\overline{y})| \leq s\,|y-\overline{y}| + ky \sum_{i=1}^{3} P_i(x)$$

$$\leq s\,|y-\overline{y}| + ky \sum_{i=1}^{3} P_i'(z_i)x$$

for some $0 \leq z_i \leq x$ $(i = 1,2,3)$ and hence $G \in \text{Lip}$.

Proposition 4.1: System (4.2) defines a continuous semi-flow on $\text{cl}(R^4_+)$ which becomes a C^1 local flow when restricted to R^4_+ . It is A-dissipative where

$$A = \{(x_1,x_2,x_3,y) \in \text{cl}(R^4_+) : x \leq K \quad \text{and} \quad kx + y \leq \frac{k}{s}(M+sK)\} \tag{4.4}$$

and $M = \max\{B(x) - D(x) : x \in [0,K]\}$. The edges and faces H_{x_1} , H_{x_3} , H_y ,

$H_{x_1,y}$, $H_{x_3,y}$, H_{x_1,x_2,x_3} <u>are invariant under the flow and the vector field</u> F, <u>defined in (4.3), points into</u> R^4_+ <u>on</u> $b(R^4_+) \setminus cl(H_{x_1,y} \cup H_{x_2,y} \cup H_{x_1,x_2,x_3})$.

<u>Proof</u>: Using Proposition (2.1) it is easily seen that $cl(R^4_+)$ is positively invariant. System (4.2) is A-dissipative follows from

$$\dot{x} = B(x) - D(x) - y \sum_{i=1}^{3} \frac{x_i}{x} P_i(x) \leq B(x) - D(x)$$

$$k\dot{x} + \dot{y} = k[B(x) - D(x)] - sy$$

and Proposition 2.2. The rest of the assertions can be easily verified, similar to the proof of Proposition 3.1.

q.e.d.

<u>Remarks</u>: (i) The invariance of H_{x_1} can be interpreted as: if there were no "a" gamete nor predator to start with, then there would not be any "a" gamete nor predator for any other time. The invariance of the other boundary invariant sets can be interpreted similarly.

(ii) The global dynamics of system (4.1) on the invariant set $cl(H_{x_1,x_2,x_3})$ is given by Theorem 3.9. Its dynamics on $cl(H_{x_i,y})$ $(i = 1,3)$ is given by the intermediate predator-prey model:

$$\begin{aligned} \dot{x}_i &= B(x_i) - D(x_i) - yP_i(x_i) \\ \dot{y} &= y[-s + kP_i(x_i)] \end{aligned} \qquad (4.5)$$

4.3 Boundary Rest Points and Their Stability.

In this section those rest points of system (4.1) lying on $b(R_+^4)$ and their stability properties will be considered. Clearly, $E_0(0,0,0,0)$ is an unstable rest point (because $\dot{y}\big|_{\substack{x=0\\y>0}} < 0$ and $\dot{x}\big|_{\substack{0<x<<1\\y=0}} > 0$). In fact, we have the following proposition.

Proposition 4.2: $E_0 \notin w(x_1,x_2,x_3,y)$ for any $(x_1,x_2,x_3,y) \in R_+^4$.

Proof: Since in a neighbourhood of E_0 in $cl(R_+^4)$, we have,

$$\dot{x} \geq B(x) - D(x) - yP(x) \geq k_1 x$$

$$\dot{y} \leq y[-s+kP(x)] \leq -k_2 y \qquad \text{for some } k_1, k_2 > 0 \quad ,$$

and the flow on $cl(H_y)$ is given by $\dot{y} = -sy$, where $P(x) = \max\{P_i(x) : 1 \leq i \leq 3\}$, the result follows immediately from Proposition 2.15.

q.e.d.

Corollary 4.3: Let $(0,0,0,y) \in cl(H_y)$. Then $(0,0,0,y) \notin w(x_1,x_2,x_3,y)$ for any $(x_1,x_2,x_3,y) \in R_+^4$.

Proof: Suppose not, since $w(x_1,x_2,x_3,y)$ is compact, connected and invariant, the global stability of E_0 on $cl(H_y)$ implies that $E_0 \in w(x_1,x_2,x_3,y)$ contradicting Proposition 4.2.

q.e.d.

Clearly, $E_1(K,0,0,0)$ (resp. $E_2(0,0,K,0)$) is the only rest point in H_{x_1} (resp. H_{x_3}).

Let

$$b_i = -s + kP_i(K) \qquad (i = 1,2,3) \quad . \tag{4.6}$$

A necessary and sufficient condition for $H_{x_1,y}$ (resp. $H_{x_3,y}$) to contain a rest point is b_1 (resp. b_3) > 0 . Moreover, (H9) in Section 4.1 implies that these rest points, if they exist, are unique. Let us denote them by $E_3(\bar{x}_1,0,0,\bar{y}_1)$ and $E_4(0,0,\bar{x}_3,\bar{y}_3)$.

Rest points lying in H_{x_1,x_2,x_3} are of the form $E_5(x_1^*,x_2^*,x_3^*,0) = (H(c),0)$ where $H(c)$ is given by (3.10). According to Proposition 3.3, in the case when $a_1 = a_3 = 0$, $(H(c),0)$ is a rest point for all $c \in (0,+\infty)$. Hence there is a curve of rest points. In the other cases, E_5 exists if and only if $a_1 a_3 > 0$; and if it exists, then it is unique and is given by $(H(c),0)$ with $c = a_3 / a_1$.

The linearized stability of E_h $(h = 1,\cdots,5)$ is governed by the sign of the real parts of the eigenvalues of the variational matrix $M = [M_{ij}]_{1 \le i,j \le 4}$ of system (4.1) evaluated at E_h , where

$M_{ij} = \dfrac{\partial F_i}{\partial z_j}$, $z_i = x_i$ $(i = 1,2,3)$, and, $z_4 = y$.

Recall the definition of a_i $(i = 1,3)$, L , and, e from (3.16), (3.22), and, (3.33) in Chapter 3.

Clearly,

$$M(E_1) = \begin{bmatrix} -e & -e + \frac{a_1 L}{f_1 K} & -e + \frac{(f_1 - 2f_3)L}{f_1 K} & -P_1(K) \\ 0 & -\frac{a_1 L}{f_1 K} & \frac{2f_3 L}{f_1 K} & 0 \\ 0 & 0 & -\frac{L}{K} & 0 \\ 0 & 0 & 0 & b_1 \end{bmatrix} \tag{4.7}$$

$M(E_1)$ has eigenvalues: $-e$, $-\frac{a_1 L}{f_1 K}$, $-\frac{L}{K}$, and, b_1. Since two of these, $-e$ and $-\frac{L}{K}$ are negative, E_1 has a stable manifold of at least two dimensions. The actual dimensions of $W^s(E_1)$ and $W^u(E_1)$ depend on the signs of a_1 and b_1. Analogous statements can be made for E_2.

$M(E_3)$ is given by

$$M_{11} = B'(\bar{x}_1) - D'(\bar{x}_1) - \bar{y}_1 P_1(\bar{x}_1) \quad ,$$

$$M_{12} = B'(\bar{x}_1) - D'(\bar{x}_1) - \frac{f_2 B(\bar{x}_1)}{f_1 \bar{x}_1} + \frac{D(\bar{x}_1)}{\bar{x}_1} - \bar{y}_1 P_1'(\bar{x}_1) + \frac{\bar{y}_1 P_1(\bar{x}_1)}{\bar{x}_1} \quad ,$$

$$M_{13} = B'(\bar{x}_1) - D'(\bar{x}_1) - \frac{2f_3 B(\bar{x}_1)}{f_1 \bar{x}_1} + \frac{D(\bar{x}_1)}{\bar{x}_1} - \bar{y}_1 P_1'(\bar{x}_1) + \frac{\bar{y}_1 P_1(\bar{x}_1)}{\bar{x}_1} \, ,$$

$$M_{14} = -P_1(\bar{x}_1) \; , \; M_{21} = 0 \; , \; M_{22} = \frac{f_2 B(\bar{x}_1)}{f_1 \bar{x}_1} - \frac{D(\bar{x}_1)}{\bar{x}_1} - \frac{\bar{y}_1 P_2(\bar{x}_1)}{\bar{x}_1} \quad ,$$

$$M_{23} = \frac{2f_3 B(\bar{x}_1)}{f_1 \bar{x}_1} \; , \; M_{24} = 0 \; , \; M_{31} = 0 \; , \; M_{32} = 0 \; ,$$

$$M_{33} = -\frac{D(\bar{x}_1) + \bar{y}_1 P_3(\bar{x}_1)}{\bar{x}_1} \quad , \quad M_{34} = 0 \ , \ M_{41} = k\bar{y}_1 P_1'(\bar{x}_1) \quad ,$$

$$M_{42} = k\bar{y}_1 \left[P_1'(\bar{x}_1) - \frac{P_1(\bar{x}_1)}{\bar{x}_1} + \frac{P_2(\bar{x}_1)}{\bar{x}_1} \right] \quad ,$$

$$M_{43} = k\bar{y}_1 \left[P_1'(\bar{x}_1) - \frac{P_1(\bar{x}_1)}{\bar{x}_1} + \frac{P_3(\bar{x}_1)}{\bar{x}_1} \right] \quad , \quad M_{44} = 0 \quad . \tag{4.8}$$

After interchaning the second and fourth row and columns respectively of $M(E_3)$ and calling the resulting matrix $\bar{M}$, we see that $\bar{M}_{31} = \bar{M}_{32} = \bar{M}_{41} = \bar{M}_{42} = \bar{M}_{43} = 0$. Analysis of this matrix shows that the eigenvalues corresponding to vectors lying in $H_{x_1,y}$ are such that the sign of their real parts is the same as the sign of M_{11}. The other two eigenvalues of $M(E_3)$ are given by M_{22} and M_{33}. Clearly $M_{33} < 0$ but M_{22} has undetermined sign. Analogous statements can be made regarding E_4. For future reference, we denote $M_{22}(E_3)$ and $M_{22}(E_4)$ by d_1 and d_3 respectively. That is, we define

$$d_i = \frac{1}{\bar{x}_i} \left[\frac{f_2 B(\bar{x}_i)}{f_i} - D(\bar{x}_i) - \bar{y}_i P_2(\bar{x}_i) \right] \qquad (i = 1,3) \quad . \tag{4.9}$$

The stability of $E_5(x_1^*, x_2^*, x_3^*, 0)$ on H_{x_1,x_2,x_3} is given by Proposition 3.7. To compute the stability of E_5 in the y-direction we note that

$$d = -s + \frac{k}{K} \sum_{i=1}^{3} x_i^* P_i(K) \tag{4.10}$$

is an eigenvalue of $M(E_5)$ corresponding to eigenvectors in y-direction, and hence E_5 is asymptotically stable or unstable in the y-direction as d is negative or positive. The case when $f_1 = f_2 = f_3$ is of special interest. For each $E_5 = (H(c),0)$ $(c \in (0,+\infty))$, $M(E_5)$ has one zero and two negative eigenvalues corresponding to eigenvectors on H_{x_1,x_2,x_3}. As for the y-direction, we have the following proposition.

<u>Proposition 4.4</u>: <u>Let</u> $f_1 = f_2 = f_3$ <u>and</u> $b_1, b_3 > 0$. <u>If</u>

$$P_2(K) > \frac{s}{k} - \sqrt{(P_1(K) - \frac{s}{k})(P_3(K) - \frac{s}{k})} \tag{4.11}$$

<u>then for all</u> $(x_{1o}, x_{2o}, y_{3o}, y_o) \in R_+^4$, $\lim_{t\to+\infty} y(t) > 0$.

<u>Proof</u>: Let $h_i = P_i(K) - \frac{s}{k}$ $(i = 1,2,3)$. $b_i > 0$ $(i = 1,3)$ implies that $h_i > 0$ $(i = 1,3)$. Moreover, $h_2 > -\sqrt{h_1 h_3}$ by (4.11). According to Lemma 4.5 (see below), we have,

$$d = -s + \frac{k}{(1+c)^2}[c^2 P_1(K) + 2cP_2(K) + P_3(K)]$$

$$= \frac{1}{(1+c)^2}[c^2 h_1 + 2ch_2 + h_3] > 0$$

for all $c \in [0,+\infty]$, where d is defined in (4.10). Hence the Hardy-Weinberg manifold, $cl(H(R_+^1))$ is normally hyperbolic. Suppose that $\lim_{t\to+\infty} y(t) = 0$. Using an argument similar to the Butler-McGehee lemma

(Lemma 2.14) and its extension (Proposition 2.16), one shows that $w = w(x_{10}, x_{20}, x_{30}, y_0)$ must intersect $cl(H_{x_1,x_2,x_3})$ at a point other than $cl(H(R_+^1))$. The global dynamics of system (4.1) on $cl(H_{x_1,x_2,x_3})$ as given in case (i) of Theorem 3.9 implies that $E_0 \in w$ or w is unbounded. In either case we have a contradiction.

q.e.d.

Remark: For $b_1, b_3 > 0$, (4.11) is satisfied if $b_2 > 0$.

Lemma 4.5: Let $h_1, h_2, h_3 \in R$. Then

$$I(c) = \frac{1}{(1+c)^2} [c^2 h_1 + 2ch_2 + h_3] > 0 \quad \text{for all } c \in [0,+\infty]$$

if and only if $h_1, h_3 > 0$ and $h_2 > -\sqrt{h_1 h_3}$.

Proof: Since $I(0) = h_3$ and $I(+\infty) = h_1$, the conditions $h_1 > 0$ and $h_3 > 0$ are clearly necessary. Now for $c \in (0,+\infty)$, $I(c) > 0$ if and only if $c^2 h_1 + 2ch_2 + h_3 > 0$, and,

$$c^2 h_1 + 2ch_2 + h_3 = (c\sqrt{h_1} - \sqrt{h_3})^2 + 2c(h_2 + \sqrt{h_1 h_3}).$$

This completes the proof of the lemma.

q.e.d.

4.4 Evolution to Pure Strains.

In this section, criteria will be given which guarantee the disappearance of one of the gamete types. As well, sufficiency conditions ensuring E_3 or E_4 to be globally stable over R^4_+ will be considered.

From the definition of u and v in (3.2),

$$\dot{u} = u\left[\frac{f_1 u + f_2 v}{(u+v)^2} B(x) - \frac{1}{x} D(x)\right] - \frac{y}{x}\left[f_1 x_1 P_1(x) + \frac{1}{2} f_2 x_2 P_2(x)\right]$$

$$\dot{v} = v\left[\frac{f_3 v + f_2 u}{(u+v)^2} B(x) - \frac{1}{x} D(x)\right] - \frac{y}{x}\left[f_3 x_3 P_3(x) + \frac{1}{2} f_2 x_2 P_2(x)\right] \quad . \tag{4.12}$$

Therefore,

$$\frac{\dot{v}}{v} - \frac{\dot{u}}{u} = -\frac{a_1 u - a_3 v}{(u+v)^2} B(x) - \frac{y}{xuv}\left[\frac{1}{2} f_1 f_2 (P_2(x) - P_1(x)) x_1 x_2 + f_1 f_3 (P_3(x) - P_1(x)) x_1 x_3 + \frac{1}{2} f_2 f_3 (P_3(x) - P_2(x)) x_2 x_3\right] \quad . \tag{4.13}$$

<u>Theorem 4.6</u>: <u>Assume that</u>

(i) $f_1 = f_2 = f_3$,

(ii) $P_1(x) \leq P_2(x) \leq P_3(x)$ <u>for all</u> $x \in [0,K]$,

(iii) $-s + kP_1(K) > 0$, <u>and,</u>

(iv) <u>there exist</u> $k_1, k_3 \geq 0$ <u>not both zero such that</u> $P_2(x) - P_1(x) \geq k_1 x$ <u>and</u> $P_3(x) - P_2(x) \geq k_3 x$ <u>for all</u> $x \in [0,K]$.

Then for all $(x_{10},x_{20},x_{30},y_0) \in R_+^4$, $x_2(t)$, $x_3(t) \to 0$ as $t \to +\infty$.

Proof: The proof proceeds in four steps.

Step 1. $\lim_{t\to+\infty} y(t) > 0$. (ii) and (iii) implies $b_i > 0$ $(i=1,2,3)$. Hence this follows from Proposition 4.4.

Step 2. One can assume that $x(t) \le K$ for all $t \ge 0$. This is because system (4.1) is A-dissipative, where A is given in (4.4), and that there are no invariant sets in $\{(x_1,x_2,x_3,y) \in cl(R_+^4) : x = K\}$ other than those that lie in $cl(H_{x_1,x_2,x_3})$.

Step 3. Points of the form $(\hat{x}_1,\hat{x}_2,\hat{x}_3,\hat{y})$ where $\hat{x}_2 > 0$, and, $\hat{x}_1 = 0$ or $\hat{x}_3 = 0$ are not in $w(x_{10},x_{20},x_{30},x_{40})$. Consider the case when $\hat{x}_1 = 0$ and $\hat{x}_2 > 0$. Then $F_1(\hat{x}_1,\hat{x}_1,\hat{x}_2,\hat{y}_3) > 0$ and we can apply Proposition 2.13. Similarly we can deal with the case when $\hat{x}_3 = 0$ and $\hat{x}_2 > 0$.

Step 4. Since $a_1 = a_3 = 0$, according to (4.13), we have,

$$\frac{\dot{v}}{v} - \frac{\dot{u}}{u} \le -\frac{y}{uv}[\frac{1}{2} k_1x_1x_2 + (k_1+k_3)x_1x_3 + \frac{1}{2} k_3x_2x_3]$$

$$\le -[\frac{k_1}{v} x_1y + \frac{k_3}{u} x_3y] \le -\frac{1}{K} [k_1x_1y + k_3x_3y] \quad ,$$

since $0 \le u,v \le K$.

Case 1: $k_1 > 0$. Then, by integrating,

$$v(t) \leq \frac{v_0}{u_0} u(t) \exp\left[- \frac{k_1}{K} \int_0^t x_1(\tau)y(\tau)\, d\tau\right] . \tag{4.14}$$

If the last integral diverges, then $\lim_{t\to+\infty} v(t) = 0$. Otherwise, $(x_1 y)(t)$ is in $L^1[0,+\infty)$. Since $\frac{d}{dt}[x_1 y(t)]$ is bounded, $(x_1 y)(t)$ is uniformly continuous. As uniformly continuous $L^1[0,+\infty)$ functions have limit zero when $t \to +\infty$, this shows that $\lim_{t\to+\infty} (x_1 y)(t) = 0$. $\underline{\lim}_{t\to+\infty}\, y(t) > 0$ implies $\lim_{t\to+\infty} x_1(t) = 0$ and hence $\lim_{t\to+\infty} x_2(t) = 0$, by Step 3. Thus $\lim_{t\to+\infty} u(t) = 0$ and consequently $\lim_{t\to+\infty} v(t) = 0$, by (4.14). But this contradicts Corollary 4.3.

Case 2: $k_3 > 0$. This is similar to Case 1.

q.e.d.

Remark: The case when $P_2 = P_3$ and $k_1 > 0$ was studied in Freedman-Waltman (1978) and the case when $P_1 = P_2$ and $k_3 > 0$ was studied in Freedman-Waltman (1982).

Corollary 4.7: If, in addition, we assume that E_3 exists and is globally stable (resp. globally exponentially stable) on $H_{x_1,y}$, then it is globally attracting (resp. globally stable) on R_+^4 .

Proof: The global attractivity of E_3 follows from Theorem 4.6, $\underline{\lim}_{t\to+\infty}\, y(t) > 0$ and a chain recurrence argument. In the case when E_3

is exponentially stable on $H_{x_1,y}$ (i.e. the two eigenvalues of $M(E_3)$ corresponding to eigenvectors on $H_{x_1,y}$ have negative real parts), the dimension of $W^{ss}(E_3)$ is at least three. Therefore $W^c(E_3)$ must be at most 1-dimensional and, according the Theorem 4.6, E_3 is stable on $W^c(E_3) \cap R_+^4$. The stability of E_3 on R_+^4 then follows from the Palis-Takens linearization theorem (Theorem 2.10).

q.e.d.

Remark: Conditions for E_3 to be globally stable on $H_{x_1,y}$ can be found in Hsu (1978) and Cheng-Hsu-Lin (1981).

Theorem 4.8: Assume that

(i) $f_1 \geq f_2 \geq f_3$ and they are not all equal, and,

(ii) $P_1(x) \leq P_2(x) \leq P_3(x)$ for all $x \in [0,K']$, for some $K' > K$.

Then for all $(x_{10},x_{20},x_{30},y_0) \in R_+^4$, $x_2(t),x_3(t) \to 0$ as $t \to +\infty$.

Proof: Again, since system (4.1) is A-dissipative, we can assume that $x(t) \leq K'$ for all $t \geq 0$. Since $a_1 \geq 0$ and $a_3 \leq 0$, from (4.13), we have

$$\frac{\dot{v}}{v} - \frac{\dot{u}}{u} \leq - \frac{a_1 u - a_3 v}{(u+v)^2} B(x) \quad . \tag{4.15}$$

If $a_1 > 0$ (and $a_3 \leq 0$), then from (4.15),

$$\frac{\dot{v}}{v} - \frac{\dot{u}}{u} \leq - \frac{a_1 u}{(u+v)^2} B(x) \quad .$$

Integration yields:

$$v(t) \leq \frac{v_0}{u_0} u(t) \exp\left[-\int_0^t \frac{a_1 u(\tau)}{(u(\tau)+v(\tau))^2} B(x(\tau))\, d\tau\right] .$$

If $\lim_{t\to+\infty} u(t) = 0$, then $\lim_{t\to+\infty} v(t) = 0$ which in turn implies $\lim_{t\to+\infty} x(t) = 0$ contradicting Corollary 4.3. Therefore $\lim_{t\to+\infty} u(t) = \hat{u} > 0$. This implies the integral

$$\int_0^{+\infty} \frac{a_1 u(\tau)}{(u(\tau)+v(\tau))^2} B(x(\tau))\, d\tau = +\infty \quad \text{and hence} \quad \lim_{t\to+\infty} v(t) = 0 .$$

Suppose now that $a_1 = 0$ and hence $a_3 < 0$. Then from (4.15)

$$\frac{\dot{v}}{v} - \frac{\dot{u}}{u} \leq \frac{a_3 v}{(u+v)^2} B(x)$$

and

$$v(t) \leq \frac{v_0}{u_0} u(t) \exp\left[\int_0^t \frac{a_3 v(\tau)}{(u(\tau)+v(\tau))^2} B(x(\tau))\, d\tau\right] .$$

If this last integral diverges, then again $\lim_{t\to+\infty} v(t) = 0$. Suppose not, i.e. suppose $z(t) = \frac{v(t)}{(u(t)+v(t))^2} B(x(t))$ is in $L^1[0,+\infty)$. By Corollary 4.3, $x(t)$ is bounded away from zero. Therefore, $\frac{d}{dt} z(t)$ is bounded and so $z(t)$ is uniformly continuous. Thus $\lim_{t\to+\infty} z(t) = 0$. Since $\lim_{t\to+\infty} B(x(t)) > 0$, we have, $\lim_{t\to+\infty} v(t) = 0$.

q.e.d.

Corollary 4.9: If, in addition, we assume E_3 exists and is globally stable (resp. globally exponentially stable) on $H_{x_1,y}$, then it is globally attracting (resp. globally stable) on R_+^4.

Proof: Let $(x_{1o},x_{2o},x_{3o},y_o) \in R_+$. Then $w = w(x_{1o},x_{2o},x_{3o},y) \subset cl(H_{x_1,y})$, by Theorem 4.8. We first show that $E_1 \not\in w$. Suppose not, i.e. suppose $E_1 \in w$, then by Proposition 2.16, $w \cap W^{cs}(E_1)$ contains a point other than E_1. Since $W^{cs}(E_1) \cap cl(R_+^4) \subset cl(H_{x_1,x_2,x_3})$, this means that w contains a point in $cl(H_{x_1})$ other than E_1, which is a contradiction. Therefore $E_1 \not\in w$. The global dynamics on $cl(H_{x_1,y})$ and the chain recurrence of w imply that $w = \{E_3\}$. Hence E_3 is globally attracting on R_+^4.

The proof of the stability of E_3 on R_+^4 when it is exponentially stable on $H_{x_1,y}$ is similar to that given in the proof of Corollary 4.7.

q.e.d.

Remark: In Theorems 4.6 and 4.8, one could interchange the roles of the gamete types A and a and obtain conditions for which $x_1(t),x_2(t) \to 0$ as $t \to +\infty$. The same observation applies to Corollaries 4.7 and 4.9.

4.5 Persistence and Non-Persistence Results.

In this section, conditions leading to the persistence and non-persistence of system (4.1) will be considered.

In the case when all selective values are equal, we have the following theorem for persistence.

Theorem 4.10: Let $f_1 = f_2 = f_3$. Assume that both E_3 and E_4 exist and are globally stable on $H_{x_1,y}$ and $H_{x_3,y}$ respectively. If $d_1 , d_3 > 0$ and (4.11) holds, then system (4.1) is persistent.

Proof: Let $(x_{10},x_{20},x_{30},y) \in R_+^4$ and $w = w(x_{10},x_{20},x_{30},y)$. The existence of E_3 and E_4 implies $b_1 , b_3 > 0$. Proposition 4.5 shows that $w \cap cl(H_{x_1,x_2,x_3}) = \phi$. Next we show that $E_3 \notin w$. Since $d_1 > 0$, $\dim W^u(E_1) = 1$ and $W^{cs}(E_3) \cap cl(R_+^4) \subset cl(H_{x_1,y})$. By proposition 2.16, $w \cap W^{cs}(E_3)$ contains a point other than E_3 and hence w contains a point in $cl(H_{x_1,y})$ other than E_3 . But this is impossible because of the global dynamics of system (4.1) on $cl(H_{x_1,y})$ and that $E_0 , E_1 \notin w$. Similarly, we can show that $E_4 \notin w$. Knowing these facts, it is then easy to show that $w \cap b(R_+^4) = \phi$.

q.e.d.

Remark: Since $B(\bar{x}_i) - D(\bar{x}_i) - \bar{y}_i P_i(\bar{x}_i) = 0$, in the case when $f_1 = f_2 = f_3$, the condition $d_i > 0$ $(i=1,3)$ simplifies to $P_2(\bar{x}_i) > P_i(\bar{x}_i)$ $(i=1,3)$.

In the case when the selective values are different, we have the following theorem.

Theorem 4.11. Assume that E_3 (resp. E_4) is globally exponentially stable on $H_{x_1,y}$ (resp. on $H_{x_3,y}$) if it exists. We have the following table for persistence and non-persistence of system (4.1):

	a_1	a_3	b_1	b_3	d_1	d_3	d	P / NP
1a	-	-	-	-			-	NP
1b	-	-	-	-			+	P
2a	-	-	-	+	-			NP
2b	-	-	-	+			-	NP
2c	-	-	-	+	+		+	P
3a	-	-	+	-		-		NP
3b	-	-	+	-			-	NP
3c	-	-	+	-		+	+	P
4a	-	-	+	+	-			NP
4b	-	-	+	+		-		NP
4c	-	-	+	+			-	NP
4d	-	-	+	+	+	+	+	P
5	-	+	-	-				NP
6a	-	+	-	+		-		NP
6b	-	+	-	+		+		P
7	-	+	+	-				NP
8a	-	+	+	+	-			NP

8b	-	+	+	+		-		NP
8c	-	+	+	+	+	+		P
9	+	-	-	-				NP
10	+	-	-	+				NP
11a	+	-	+	-	-			NP
11b	+	-	+	-	+			P
12a	+	-	+	+	-			NP
12b	+	-	+	+		-		NP
12c	+	-	+	+	+	+		P
13	+	+	-	-				NP
14	+	+	-	+				NP
15	+	+	+	-				NP
16a	+	+	+	+	-			NP
16b	+	+	+	+		-		NP
16c	+	+	+	+	+	+		P

where a "+" (resp. a "-") means that the corresponding parameter is positive (resp. negative), a blank means that the corresponding parameter value is irrelevant, and, P (resp. NP) stands for persistence (resp. non-persistence) of system (4.1).

Proof: We will illustrate the proof by proving the non-persistence case (1a) and the persistence case (1b). Under case (1), E_3 and E_4 do not exist, E_1 (resp. E_2) is globally stable on $H_{x_1,y}$ (resp. $H_{x_3,y}$), E_5

is unique and is globally stable on H_{x_1,x_2,x_3} (case (iii) of Theorem 3.9). In case (1a), $d < 0$. Therefore E_5 is asymptotically stable on R_+^4 and hence system (4.1) is non-persistent. In case (1b), it is easily seen that $E_0, E_1, E_2, E_5 \notin w(x_{1o}, x_{2o}, x_{3o}, y_o)$ for all $(x_{1o}, x_{2o}, x_{3o}, y_o) \in R_+^4$. (This type of argument has been used in the proof of Corollary 4.9 and will not be reproduced here.) Therefore the global dynamics on $b(R_+^4)$ implies that $w \cap b(R_+^4) = \phi$ as desired.

q.e.d.

4.6 Discussion.

In this chapter we have considered a predator-prey model where the prey population consists of three genotypes with fertility / viability differences, and with different predator functional responses. We have given conditions for persistence and non-persistence of the prey genotypes.

The results in Section 4 can be interpreted as: if a prey gamete type has selective disadvantages as well as predation disadvantages, then it will die out eventually. As the results in Section 5 show, the ordering of the selective values and of the predation functional responses are necessary for the results in Section 4 to hold.

As part of the conditions for persistence in Theorem 4.11, we have shown that in some cases where the subsystem modelling the prey population growth exhibits non-persistence, the total system exhibits persistence. This may be viewed as predator regulated survival among prey genotypes, which otherwise, due to fertility / viability differences, would become extinct.

In Freedman-Waltman (1978, 1980), conditions were given under the assumption of no fertility / viability differences, for two of the genotypes to become extinct. Here we have generalized these conditions to include the case of fertility differences. We have also given conditions changing the outcome to one of persistence, this time due to fertility / viability differences.

CHAPTER 5

A TWO-LOCUS, TWO-ALLELE MODEL

In this chapter, the model considered in Chapter 3 for one locus, two allele will be extended to two loci. The fertility / viability of the genotypes will be taken to be equal. It is shown that solutions converge to rest points on the Hardy-Weinberg manifold.

5.1 Introduction and the Model.

Consider a two-locus, two-allele problem where A , a denote the two allele types at the first locus and B , b denote the two allele types at the second locus. There are four gamete types and ten genotypes. If the number of gametes of type AB , Ab , aB and ab are denoted by u_1 , u_2 , u_3 and u_4 respectively, then it is natural to denote the number of organisms of genotype AB/AB , AB/Ab , AB/aB , AB/ab , Ab/Ab , Ab/aB , Ab/ab , aB/aB , aB/ab and ab/ab by x_{11} , x_{12} , x_{13} , x_{14} , x_{22} , x_{23} , x_{24} , x_{33} , x_{34} , x_{44} respectively. In the two-locus, two-allele model proposed here, the genotypes AB/ab and Ab/aB will not be distinguished. We use x_{11} to denote the number of organisms of the genotype AB/AB (another notation: AABB) and use x_{12} , x_{13} , x_{21} , x_{22} , x_{23} , x_{31} , x_{32} and x_{33} respectively for that of the genotypes AABb , AAbb , AaBB , AaBb (AB/a b and Ab/aB) , Aabb , aaBB , aaBb and aabb .

The model we wish to consider in this chapter is of the form:

$$\dot{x}_{11} = \frac{u_1^2}{x^2} B(x) - \frac{x_{11}}{x} D(x)$$

$$\dot{x}_{12} = \frac{2u_1u_2}{x^2} B(x) - \frac{x_{12}}{x} D(x)$$

$$\dot{x}_{13} = \frac{u_2^2}{x^2} B(x) - \frac{x_{13}}{x} D(x)$$

$$\dot{x}_{21} = \frac{2u_1u_3}{x^2} B(x) - \frac{x_{21}}{x} D(x)$$

$$\dot{x}_{22} = \frac{2(u_1u_4 + u_2u_3)}{x^2} B(x) - \frac{x_{22}}{x} D(x) \qquad (5.1)$$

$$\dot{x}_{23} = \frac{2u_2u_4}{x^2} B(x) - \frac{x_{23}}{x} D(x)$$

$$\dot{x}_{31} = \frac{u_3^2}{x^2} B(x) - \frac{x_{31}}{x} D(x)$$

$$\dot{x}_{32} = \frac{2u_3u_4}{x^2} B(x) - \frac{x_{32}}{x} D(x)$$

$$\dot{x}_{33} = \frac{u_4^2}{x^2} B(x) - \frac{x_{33}}{x} D(x)$$

where

$$u_1 = x_{11} + \frac{1}{2} x_{12} + \frac{1}{2} x_{21} + \frac{1}{4} x_{22}$$

$$u_2 = x_{13} + \frac{1}{2} x_{12} + \frac{1}{2} x_{23} + \frac{1}{4} x_{22} \qquad (5.2)$$

$$u_3 = x_{31} + \frac{1}{2} x_{21} + \frac{1}{2} x_{32} + \frac{1}{4} x_{22}$$

$$u_4 = x_{33} + \frac{1}{2} x_{23} + \frac{1}{2} x_{32} + \frac{1}{4} x_{22}$$

and

$$x = x_{11} + \cdots + x_{33} \quad . \tag{5.3}$$

For a derivation of system (5.1), see Appendix 2. The birth and death functions (B and D) are assumed to satisfy the same hypotheses as those for system (3.1), namely, (H1) - (H6) of Section 3.1. System (5.1) is a no fertility / viability difference generalization of system (3.1) to two loci. It can also be considered as a continuous version of the well-known model of two loci for non-overlapping generations (see Chapter 8 of Roughgarden (1979)). For the discrete model of two loci (with random mating, no selection, linked or unlinked loci), it is known that the Hardy-Weinberg equilibrium relation is attained gradually over a number of generations (see, for example, Section 2.6 of Crow-Kimura (1970)). An analogous result is true for system (5.1). In contrast to this, the recent work of Akin, Akin (1979, 1982, 1983), shows that in the Kimura model for two loci with selection and recombination (see p. 197 of Crow-Kimura, 1970), it is possible for stable periodic solutions to exist. Other related work of interest are: Nagylaki-Crow (1974), Karlin (1975), Karlin-Carmelli (1975a, 1975b), and Nagylaki (1977).

The rest of this chapter is organized as follows. In Section 5.2, the semi flow on $cl(R^9_+)$ defined by system (5.1) is described and some of its elementary invariance properties are considered. The rest points for system (5.1) are described in Section 5.3. It is shown that the rest point set (excluding the origin), forms a 2-dimensional surface (with boundary) and has a global parametrization. In Section 5.4, we prove the main result of this chapter: every solution of system (5.1) converges to a rest point as t tends to $+\infty$. It turns out that which rest point a solution converge to is predictable and is dependent only on the initial condition. Finally, Section 5.5 is a short discussion of the results.

5.2 The Associated Flow.

As with system (3.1), system (5.1) is not defined when $X = (x_{11},\cdots,x_{33}) = (0,\cdots,0)$. Let $F = (F_{11},\cdots,F_{33})$ denote the vector field defined by system (5.1) (i.e. the right hand side of (5.1)). Define $F = (0,\cdots,0)$ when $X = (0,\cdots,0)$. Then system (5.1) becomes

$$\dot{X} = F(X) \quad . \tag{5.4}$$

Clearly $F : cl(R_+^9) \to R^9$ is locally Lipschitz. As in (3.5), we define the simplex

$$U = \{X \in R_+^9 : x = K\}$$

and let

$$cl(U) = \{X \in cl(R_+^9) : x = K\} \tag{5.5}$$

be the closure of U in R^9. We will summarize some of the properties of system (5.4) in the following proposition.

Proposition 5.1: System (5.4) defines a continuous semi-flow on $cl(R_+^9)$ which becomes a smooth (C^1) local flow when restricted to R_+^9. The

<u>closed simplex</u> cl(U) <u>defined in</u> (5.5) <u>is positively invariant and is globally stable on</u> $cl(R^9_+) \setminus \{(0,\cdots,0)\}$. $(0,\cdots,0)$ <u>is a repelling rest point</u>. $H_{x_{11}}$, $H_{x_{13}}$, $H_{x_{31}}$, $H_{x_{33}}$, $H_{x_{11},x_{12},x_{13}}$, $H_{x_{11},x_{21},x_{31}}$, $H_{x_{13},x_{23},x_{33}}$, <u>and</u>, $H_{x_{31},x_{32},x_{33}}$ <u>are invariant</u>. <u>The vector field</u> F <u>points into</u> R^9_+ on $b(R^9_+) \setminus cl(H_{x_{11},x_{12},x_{13}} \cup H_{x_{11},x_{21},x_{31}} \cup H_{x_{13},x_{23},x_{33}} \cup H_{x_{31},x_{32},x_{33}})$.

<u>Proof</u>: The positive invariance of $cl(R^9_+)$ can be easily shown using Proposition 2.1. As with system (3.1),

$$\dot{x} = B(x) - D(x) \quad . \tag{5.6}$$

Hence, for all $x(0) > 0$,

$$x(t) \to K \tag{5.7}$$

as $t \to +\infty$. The positive invariance and global stability properties of cl(U) follow from (H5), (H6) of Section 3.1 and (5.7). The rest of the assertions can be proved as in Proposition 3.1.

q.e.d.

5.3 The Rest Point Set.

In this section the set of rest points for system (5.1) will be described. By Proposition 5.1, all rest points of (5.1) other than $(0,\cdots,0)$ must lie in $cl(U)$. First, we consider the interior rest points.

Proposition 5.2: Define $H : R_+^2 \to U$ by

$$H(c_1,c_2) = (H_{11}(c_1,c_2),\cdots,H_{33}(c_1,c_2)) \quad \text{for} \quad (c_1,c_2) \in R_+^2$$

where

$$H_{11}(c_1,c_2) = c_1^2c_2^2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{12}(c_1,c_2) = 2c_1^2c_2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{13}(c_1,c_2) = c_1^2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{21}(c_1,c_2) = 2c_1c_2^2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{22}(c_1,c_2) = 4c_1c_2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{23}(c_1,c_2) = 2c_1 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{31}(c_1,c_2) = c_2^2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{32}(c_1,c_2) = 2c_2 \frac{K}{(1+c_1)^2(1+c_2)^2}$$

$$H_{33}(c_1,c_2) = \frac{K}{(1+c_1)^2(1+c_2)^2} \quad . \tag{5.8}$$

<u>Then</u> $H(R_+^2)$ <u>is the set of all rest points of system</u> (5.1) <u>in</u> R_+^9 .

<u>Proof</u>: First we show that all points of the form $H(c_1,c_2)$ where $(c_1,c_2) \in R_+^2$ are rest points of system (5.1). Let $H(c_1,c_2) = X^* = (x_{11}^*,\cdots,x_{33}^*)$. Clearly $X^* \in R_+^9$. Define

$$\begin{aligned} u_1^* &= x_{11}^* + \frac{1}{2} x_{12}^* + \frac{1}{2} x_{21}^* + \frac{1}{4} x_{22}^* \\ u_2^* &= x_{13}^* + \frac{1}{2} x_{12}^* + \frac{1}{2} x_{23}^* + \frac{1}{4} x_{22}^* \\ u_3^* &= x_{31}^* + \frac{1}{2} x_{21}^* + \frac{1}{2} x_{32}^* + \frac{1}{4} x_{22}^* \\ u_4^* &= x_{33}^* + \frac{1}{2} x_{23}^* + \frac{1}{2} x_{32}^* + \frac{1}{4} x_{22}^* \end{aligned} \tag{5.9}$$

and

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

Then

$$u_1^* = \frac{c_1 c_2 K}{(1+c_1)(1+c_2)} \qquad u_2^* = \frac{c_1 K}{(1+c_1)(1+c_2)}$$

$$u_3^* = \frac{c_2 K}{(1+c_1)(1+c_2)} \qquad u_4^* = \frac{K}{(1+c_1)(1+c_2)}$$

and $x^* = K$. Therefore

$$F_{11}(X^*) = \frac{u_1^{*2}}{x^{*2}} B(x^*) - \frac{x_{11}^*}{x^*} D(x^*) = (u_1^{*2} - x_{11}^* K) \frac{B(K)}{K^2} = 0 \quad .$$

Similarly, one shows that

$$F_{12}(X^*) = \cdots = F_{33}(X^*) = 0$$

and hence X^* is a rest point.

Next, we show that every interior rest point of system (5.1) is of the form $H(c_1,c_2)$ for some $(c_1,c_2) \in R_+^2$. Let $X^* = (x_{11},\cdots, x_{33}^*)$ be a rest point of system (5.1) with $x_{ij}^* > 0$ $(i,j = 1,2,3)$. Define $u_1^*, u_2^*, u_3^*, u_4^*$, and x^* as in (5.9). Clearly $x^* = K$. Also define

$$d_{ij} = \frac{x_{ij}^*}{x_{33}^*} \qquad (i,j = 1,2,3) \tag{5.10}$$

and

$$r_i = \frac{u_i^*}{x_{33}^*} \qquad (i = 1,\cdots,4) \quad . \tag{5.11}$$

Then

$$r_1^2 \, x_{33}^* = d_{11} \, K \qquad \text{(i)}$$

$$2r_1 r_2 \, x_{33}^* = d_{12} \, K \qquad \text{(ii)}$$

$$r_2^2 \, x_{33}^* = d_{13} K \qquad \text{(iii)}$$

$$2r_1 r_3 \, x_{33}^* = d_{21} K \qquad \text{(iv)}$$

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

$$2r_2r_4\, x_{33}^* = d_{23}K \qquad \text{(vi)}$$

$$r_3^2\, x_{33}^* = d_{31}K \qquad \text{(vii)}$$

$$2r_3r_4\, x_{33}^* = d_{32}K \qquad \text{(viii)}$$

$$r_4^2\, x_{33}^* = d_{33}K = K \qquad \text{(ix)} \;.$$

Define $c_1, c_2 > 0$ by

$$c_1 = \frac{x_{23}^*}{2x_{33}^*} \quad \text{and} \quad c_2 = \frac{x_{32}^*}{2x_{33}^*} \;.$$

Then $2c_1 = d_{23}$ and $2c_2 = d_{32}$.

$\frac{(ii)}{(i)} : \frac{2r_2}{r_1} = \frac{d_{12}}{d_{11}}$ and $\frac{(ii)}{(iii)} : \frac{2r_1}{r_2} = \frac{d_{12}}{d_{13}}$ give $\frac{(ii)}{(i)} \cdot \frac{(ii)}{(iii)}$: $d_{12}^2 = 4d_{11}d_{13}$. $\frac{(viii)}{(vii)} : \frac{2r_4}{r_3} = \frac{d_{32}}{d_{31}}$ and $\frac{(viii)}{(ix)} : \frac{2r_3}{r_4} = \frac{d_{32}}{d_{33}} = d_{32}$ give $\frac{(viii)}{(vii)} \cdot \frac{(viii)}{(ix)} : d_{31} = c_2^2$. $\frac{(iv)}{(i)} : \frac{2r_3}{r_1} = \frac{d_{21}}{d_{11}}$ and $\frac{(iv)}{(vii)}$: $\frac{2r_1}{r_3} = \frac{d_{21}}{d_{31}}$ give $\frac{(iv)}{(i)} \cdot \frac{(iv)}{(vii)} : \; d_{21} = 2c_2\sqrt{d_{11}}$. $\frac{(vi)}{(iii)} : \frac{2r_4}{r_2} = \frac{d_{23}}{d_{13}}$ and $\frac{(vi)}{(ix)} : \frac{2r_2}{r_4} = \frac{d_{23}}{d_{33}} = d_{23}$ give $\frac{(vi)}{(iii)} \cdot \frac{(vi)}{(ix)} : \; d_{13} = c_1^2$. Thus,

$$d_{12} = 2c_1\sqrt{d_{11}} \;.$$

Since

$$\frac{r_2}{r_1} = \frac{c_1}{\sqrt{d_{11}}} \;, \quad \frac{r_3}{r_1} = \frac{c_2}{\sqrt{d_{11}}} \;, \quad \frac{r_4}{r_1} = \frac{1}{\sqrt{d_{11}}} \;, \text{ and,}$$

$\frac{(v)}{(i)}$: $\frac{2r_4}{r_1} + \frac{2r_2r_3}{r_1^2} = \frac{d_{22}}{d_{11}}$, therefore

$$d_{22} = 2c_1c_2 + 2\sqrt{d_{11}} .$$

Substituting all of the above into the equation $x^* = K$, we have,

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

which in turn implies that

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

Substituting this into (i) and by noting $r_1 = d_{11} + \frac{1}{2} d_{12} + \frac{1}{2} d_{21} + \frac{1}{4} d_{22}$, we have, $d_{11} = c_1^2c_2^2$. From this, one can easily show that $X^* = H(c_1,c_2)$.

q.e.d.

Next, we observe that the boundary rest points of system (5.1) must lie on $cl(H_{x_{11},x_{12},x_{13}})$, $cl(H_{x_{11},x_{21},x_{31}})$, $cl(H_{x_{31},x_{32},x_{33}})$ or $cl(H_{x_{13},x_{23},x_{33}})$. From this we have the following proposition.

<u>Proposition 5.3</u>: $cl(H(R_+^2))$ <u>is the set of rest points of system</u> (5.1) <u>in</u> $cl(R_+^9) \setminus \{(0,\cdots,0)\}$.

<u>Proof</u>: This follows from Proposition 5.2, the above observation and case (i) of Proposition 3.3. Note that, for example, $cl(H(R_+^2)) \cap cl(H_{x_{11},x_{21},x_{31}})$ is the Hardy-Weinberg parabolic segment given in

Proposition 3.3.

q.e.d.

Remark: As in Section 3.3, $cl(H(R_+^2)) = H([0,+\infty]\times[0,+\infty])$ is called the Hardy-Weinberg manifold. In this case it is a 2-dimensional manifold (surface) with boundary.

5.4 Global Convergence to the Hardy-Weinberg Manifold.

In this section we will show that every solution $X(t)$ of system (5.1) with $X(0) \in cl(R_+^9) \setminus \{(0,\cdots,0)\}$ converges to a rest point in $cl(H(R_+^2))$ as $t \to +\infty$.

First we define some auxiliary quantities. Define

$$\begin{cases} x_{AA} = x_{11} + x_{12} + x_{13} \\ x_{Aa} = x_{21} + x_{22} + x_{23} \\ x_{aa} = x_{31} + x_{32} + x_{33} \end{cases} , \tag{5.12}$$

$$\begin{cases} x_{BB} = x_{11} + x_{21} + x_{31} \\ x_{Bb} = x_{12} + x_{22} + x_{32} \\ x_{bb} = x_{13} + x_{23} + x_{33} \end{cases} , \tag{5.13}$$

$$u_A = x_{AA} + \frac{1}{2} x_{Aa} \qquad u_a = x_{aa} + \frac{1}{2} x_{Aa} , \tag{5.14}$$

and,

$$u_B = x_{BB} + \frac{1}{2} x_{Bb} \qquad u_b = x_{bb} + \frac{1}{2} x_{Bb} \tag{5.15}$$

Clearly

$$\begin{aligned} u_A + u_a &= x_{AA} + x_{Aa} + x_{aa} = x \\ u_B + u_b &= x_{BB} + x_{Bb} + x_{bb} = x \end{aligned} \tag{5.16}$$

and

$$\begin{aligned} u_A &= u_1 + u_2 \qquad u_a = u_3 + u_4 \\ u_B &= u_1 + u_3 \qquad u_b = u_2 + u_4 \end{aligned} \tag{5.17}$$

<u>Proposition 5.4</u>: <u>Let</u> $c_1 = \frac{u_A(0)}{u_a(0)}$ <u>and</u> $c_2 = \frac{u_B(0)}{u_b(0)}$. <u>Then</u>

(i) $u_A(t) = c_1 u_a(t) \quad , \quad u_B(t) = c_2 u_b(t)$ (5.18)

<u>for all</u> $t \geq 0$,

(ii) $(u_A(t), u_a(t)) \to \left(\frac{c_1 K}{1+c_1}, \frac{K}{1+c_1}\right)$ (5.19)

<u>and</u>

$(u_B(t), u_b(t)) \to \left(\frac{c_2 K}{1+c_2}, \frac{K}{1+c_2}\right)$ (5.20)

<u>as</u> $t \to +\infty$, <u>and</u>,

(iii) $(x_{AA}(t), x_{Aa}(t), x_{aa}(t)) \to \left(\frac{c_1^2 K}{(1+c_1)^2}, \frac{2c_1 K}{(1+c_1)^2}, \frac{K}{(1+c_1)^2}\right)$ (5.21)

$(x_{BB}(t), x_{Bb}(t), x_{bb}(t)) \to \left(\frac{c_2^2 K}{(1+c_2)^2}, \frac{2c_2 K}{(1+c_2)^2}, \frac{K}{(1+c_2)^2}\right)$ (5.22)

<u>as</u> $t \to +\infty$.

<u>Proof</u>: Clearly

$$\dot{x}_{AA} = \frac{u_A^2}{x^2} B(x) - \frac{x_{AA}}{x} D(x)$$

$$\dot{x}_{Aa} = \frac{2u_A u_a}{x^2} B(x) - \frac{x_{Aa}}{x} D(x) \tag{5.23}$$

$$\dot{x}_{aa} = \frac{u_a^2}{x^2} B(x) - \frac{x_{aa}}{x} D(x) \quad ,$$

and

$$\dot{x}_{BB} = \frac{u_B^2}{x^2} B(x) - \frac{x_{BB}}{x} D(x)$$

$$\dot{x}_{Bb} = \frac{2u_B u_b}{x^2} B(x) - \frac{x_{Bb}}{x} D(x) \tag{5.24}$$

$$\dot{x}_{bb} = \frac{u_b^2}{x^2} B(x) - \frac{x_{bb}}{x} D(x) \quad .$$

Using a result in Freedman-Waltman (1978) (mentioned in the proof of case (i) of Theorem 3.9), we know that (i) holds and that

$$\begin{aligned} &x_{AA}(t) - c_1^2 x_{aa}(t) \to 0 \quad , \quad x_{Aa}(t) - 2c_1 x_{aa}(t) \to 0 \\ &x_{BB}(t) - c_2^2 x_{bb}(t) \to 0 \quad , \quad x_{Bb}(t) - 2c_2 x_{bb}(t) \to 0 \quad , \end{aligned} \tag{5.25}$$

as $t \to +\infty$. (ii) and (iii) follow from (5.7), (5.16) and (5.25).

q.e.d.

Remark: Proposition 5.4 and (5.17) show that

$$u_1(t) = c_2u_b(t) - u_a(t) + u_4(t) = c_1u_a(t) - u_b(t) + u_4(t)$$

$$u_2(t) = u_b(t) - u_4(t) \tag{5.26}$$

$$u_3(t) = u_a(t) - u_4(t)$$

for all $t \geq 0$, where

$$c_1 = \frac{u_A(0)}{u_a(0)} \quad \text{and} \quad c_2 = \frac{u_B(0)}{u_b(0)} .$$

Proposition 5.5. Let $c_1 = \frac{u_A(0)}{u_a(0)}$ and $c_2 = \frac{u_B(0)}{u_b(0)}$. Then

$$(u_1(t),u_2(t),u_3(t),u_4(t)) \to$$

$$\left(\frac{c_1c_2K}{(1+c_1)(1+c_2)}, \frac{c_1K}{(1+c_1)(1+c_2)}, \frac{c_2K}{(1+c_1)(1+c_2)}, \frac{K}{(1+c_1)(1+c_2)}\right) \tag{5.27}$$

as $t \to +\infty$.

Proof: The proof is divided into three steps.

Step 1: u_1, u_2, u_3, u_4 satisfy the following system of differential equations.

$$\dot{u}_1 = (u_1^2 + u_1u_2 + u_1u_3 + \frac{1}{2}u_1u_4 + \frac{1}{2}u_2u_3)\frac{B(x)}{x^2} - u_1\frac{D(x)}{x}$$

$$\dot{u}_2 = (u_2^2 + u_1u_2 + u_2u_4 + \frac{1}{2}u_1u_4 + \frac{1}{2}u_2u_3)\frac{B(x)}{x^2} - u_2\frac{D(x)}{x}$$

$$\dot{u}_3 = (u_3^2 + u_1u_3 + u_3u_4 + \frac{1}{2}\,u_1u_4 + \frac{1}{2}\,u_2u_3)\,\frac{B(x)}{x^2} - u_3\,\frac{D(x)}{x}$$

$$\dot{u}_4 = (u_4^2 + u_2u_4 + u_3u_4 + \frac{1}{2}\,u_1u_4 + \frac{1}{2}\,u_2u_3)\,\frac{B(x)}{x^2} - u_4\,\frac{D(x)}{x}\,, \qquad (5.28)$$

where $x = u_1 + u_2 + u_3 + u_4$. This follows directly from (5.1), (5.2), and (5.3).

Step 2:

$$u_1(t)-c_2u_2(t) = (u_{1o}-c_1u_{2o})\,\exp\left[\int_0^t \left(\frac{(1+c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)}\right)d\tau\right]$$

$$u_3(t)-c_2u_4(t) = (u_{3o}-c_2u_{4o})\,\exp\left[\int_0^t \left(\frac{(1+c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)}\right)d\tau\right]$$

$$u_1(t)-c_1u_3(t) = (u_{1o}-c_1u_{3o})\,\exp\left[\int_0^t \left(\frac{(1+c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)}\right)d\tau\right]$$

$$u_2(t)-c_1u_4(t) = (u_{2o}-c_1u_{4o})\,\exp\left[\int_0^t \left(\frac{(1+c_1)u_a(\tau)B(x(\tau))}{2x^2(\tau)} - \frac{D(x(\tau))}{x(\tau)}\right)d\tau\right]$$

(5.29)

This can be proved by writing down the linear differential equation that each of these functions satisfies. For example, by (5.26) and (5.28),

$$\dot{u}_2-c_1\dot{u}_4 = (u_2-c_1u_4)\left[\frac{(1+c_2)u_bB(x)}{2x^2} - \frac{D(x)}{x}\right]$$

$$= (u_2-c_1u_4)\left[\frac{(1+c_1)u_aB(x)}{2x^2} - \frac{D(x)}{x}\right].$$

Step 3:

$$u_1(t) - c_2u_2(t) \to 0 \qquad u_3(t) - c_2u_4(t) \to 0$$

$$u_1(t) - c_1u_3(t) \to 0 \qquad u_2(t) - c_1u_4(t) \to 0 \quad , \tag{5.30}$$

as $t \to +\infty$. By (5.7), (5.19), and, (5.20),

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

as $t \to +\infty$. Therefore, the integral in (5.29) is divergent and consequently we have (5.30).

Using (5.30), it is then easy to see that (5.27) holds because

$$u_1 + u_2 + u_3 + u_4 = x \quad . \tag{5.31}$$

q.e.d.

<u>Theorem 5.6</u>: <u>Let</u> $c_1 = \dfrac{u_A(0)}{u_a(0)}$ <u>and</u> $c_2 = \dfrac{u_B(0)}{u_b(0)}$. <u>Then</u>

$$(x_{11}(t),\cdots,x_{33}(t)) \to H(c_1,c_2) \tag{5.32}$$

<u>as</u> $t \to +\infty$, <u>where</u> $H(c_1,c_2)$ <u>is defined in</u> (5.8).

<u>Proof</u>: To show (5.32), it suffices to show

$$x_{11}(t) - c_1^2c_2^2x_{33}(t) \ , \ x_{12}(t) - 2c_1^2c_2x_{33}(t) \ , \ x_{13}(t) - c_1^2x_{33}(t) \ ,$$

$$x_{21}(t) - 2c_1c_2^2x_{33}(t) \ , x_{22}(t) - 4c_1c_2x_{33}(t) \ , \ x_{23}(t) - 2c_1x_{33}(t) \ ,$$

$$x_{31}(t) - c_2^2x_{33}(t) \ , \ x_{32}(t) - 2c_2x_{33}(t) \to 0 \tag{5.33}$$

as $t \to +\infty$. We illustrate this by showing $z(t) \equiv x_{32}(t) - 2c_2x_{33}(t) \to 0$ as $t \to +\infty$. Clearly $z(t)$ satisfies the linear differential equation

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

where $Q_1(t) = \dfrac{D(x(t))}{x(t)}$, $Q_2(t) = 2u_4(t)[u_3(t) - c_2u_4(t)]\dfrac{B(x(t))}{x(t)}$.

Solving this equation yields

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

We will show that the first and second terms tend to 0 as t tends to $+\infty$.

Since $\lim\limits_{t\to+\infty} Q_1(t) = \dfrac{D(K)}{K}$, by (3.7), therefore

$$\int_0^{+\infty} Q_1(t)dt = +\infty \text{ , and hence, } \lim_{t\to+\infty} \exp[-\int_0^t Q_1(\tau)d\tau] = 0\ .$$

On the other hand, by (5.29),

$$\int_0^t \exp[-\int_s^t Q_1(\tau)d\tau]\, Q_2(s)ds = 2(u_3(0) - c_2u_4(0))\exp[-\int_0^t \frac{D(x(\tau))}{x(\tau)}d\tau]\ \cdot$$

$$\cdot \int_0^t u_4(s)\exp[\frac{1+c_2}{2}\int_0^s \frac{u_4(\tau)B(x(\tau))}{x^2(\tau)}d\tau]\,\frac{B(x(\tau))}{x^2(\tau)}\,ds\ . \qquad (5.34)$$

To show that the L.H.S. of (3.34) tends to 0 as t tends to $+\infty$, it suffices, by L'Hospital's rule, to show that

$$\lim_{t\to+\infty} \frac{u_4(t)\exp[\frac{1+c_2}{2}\int_0^t \frac{u_4(\tau)B(x(\tau))}{x(\tau)}\,d\tau]\,\frac{B(x(t))}{x^2(t)}}{\exp[\int_0^t \frac{D(x(\tau))}{x(\tau)}\,d\tau]\,\frac{D(x(t))}{x(t)}} = 0 \quad . \tag{5.35}$$

Since

$$\lim_{t\to+\infty} u_4(t) = \frac{K}{(1+c_1)(1+c_2)} > 0 \ ,$$

$$\lim_{t\to+\infty} \frac{B(x(t))}{x(t)} = \frac{B(K)}{K} > 0 \ , \text{ and, } \lim_{t\to+\infty} \frac{D(x(t))}{x(t)} = \frac{D(K)}{K} > 0 \ ,$$

therefore, it suffices to show,

$$\lim_{t\to+\infty} \int_0^t \left[\frac{D(x(\tau))}{x(\tau)} - \frac{(1+c_2)u_4(\tau)B(x(\tau))}{x^2(\tau)}\right] d\tau = +\infty .$$

But this follows from

$$\lim_{t\to+\infty} \left[\frac{D(x(t))}{x(t)} - \frac{(1+c_2)u_4(t)B(x(t))}{x^2(t)}\right] = \frac{D(K)}{K} - \frac{1+c_2}{2}\cdot\frac{K}{1+c_2}\cdot\frac{B(K)}{K^2} = \frac{B(K)}{2K} > 0 \ .$$

q.e.d.

Remark: Theorem 5.6 implies that $cl(R_+^9) \setminus \{(0,\cdots,0)\}$ is foliated by the strong stable manifolds $W^{ss}(H(c_1,c_2))$, $((c_1,c_2) \in [0,+\infty]\times[0,+\infty])$ of the rest points $H(c_1,c_2)$ on the Hardy-Weinberg manifold, $cl(H(R_+^2))$. For $0 < c_1 , c_2 < +\infty$,

$$W^{ss}(H(c_1,c_2)) \cap cl(R_+^9) = \{(x_{11},\cdots,x_{33}) \in cl(R_+^9) \setminus \{(0,\cdots,0)\} \ :$$

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

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

is 7-dimensional. For $c_1 = 0$, $0 < c_2 < +\infty$,

$$W^{ss}(H(0,c_2)) \cap cl(R^9_+) = \{(x_{11},\cdots,x_{33}) \in cl(H_{x_{31},x_{32},x_{33}}) \setminus \{(0,\cdots,0)\}:$$

$$x_{31} + \frac{1-c_2}{2}x_{32} - c_2x_{33} = 0\}$$

is 2-dimensional. For $0 < c_1 < +\infty$, $c_2 = 0$,

$$W^{ss}(H(c_1,0)) \cap cl(R^9_+) = \{(x_{11},\cdots,x_{33}) \in cl(H_{x_{13},x_{23},x_{33}}) \setminus \{(0,\cdots,0)\}:$$

$$x_{13} + \frac{1-c_1}{2}x_{23} - c_1x_{33} = 0\}$$

is 2-dimensional. For $c_1 = +\infty$, $0 < c_2 < +\infty$,

$$W^{ss}(H(+\infty,c_2)) \cap cl(R^9_+) = \{(x_{11},\cdots,x_{33}) \in cl(H_{x_{11},x_{12},x_{13}}) \setminus \{(0,\cdots,0)\}:$$

$$x_{11} + \frac{1-c_2}{2}x_{12} - c_2x_{13} = 0\}$$

is 2-dimensional. For $0 < c_1 < +\infty$, $c_2 = +\infty$,

$$W^{ss}(H(c_1,+\infty)) \cap cl(R^9_+) = \{(x_{11},\cdots,x_{33}) \in cl(H_{x_{11},x_{21},x_{31}}) \setminus \{(0,\cdots,0)\}:$$

$$x_{11} + \frac{1-c_1}{2}x_{21} - c_1x_{31} = 0\}$$

is 2-dimensional. Finally,

$$W^{ss}(H(0,0)) \cap cl(R^9_+) = H_{x_{33}}$$

$$W^{ss}(H(0,+\infty)) \cap cl(R^9_+) = H_{x_{31}}$$

$$W^{ss}(H(+\infty,0)) \cap cl(R^9_+) = H_{x_{13}}$$

$$W^{ss}(H(+\infty,+\infty)) \cap cl(R^9_+) = H_{x_{11}}$$

are 1-dimensional.

5.5 Discussion.

In this chapter we have shown that if $(x_{11}(t),\cdots,x_{33}(t))$ is a solution of system (5.1) other than $(0,\cdots,0)$, then

$$x_{11}(t):x_{12}(t):x_{13}(t):x_{21}(t):x_{22}(t):x_{23}(t):x_{31}(t):x_{32}(t):x_{33}(t)$$

$$\to c_1^2c_2^2 : 2c_1^2c_2 : c_1^2 : 2c_1c_2^2 : 4c_1c_2 : 2c_1 : c_2^2 : 2c_2 : 1$$

at $t \to +\infty$, where

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

and

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

This is directly analogous to the discrete case as discussed in Section 2.6 of Crow-Kimura (1970). It should be mentioned that model (5.1) is a first attempt to extend the one-locus, two-allele model (3.1) to two loci. And as such, many of the standard two loci features (for example, selection, recombination, etc.) are not incorporated. In the next chapter, the effect of predator mediated selection will be studied using a predator-prey model in which the prey population is modelled by system (5.1). The selection comes from choosing different predator functional responses for the various prey genotypes.

CHAPTER 6

A PREDATOR-PREY MODEL CONSISTING OF NINE PREY GENOTYPES

In this chapter a model of predator-prey interaction, for which the prey population consists of nine genotypes corresponding to a two-locus, two-allele problem and modelled by system (5.1), is proposed. Some sufficiency conditions leading to the evolution of pure strains as well as to the persistence of all components of the system are given. These conditions serve to illustrate the similarity as well as differences between the one-locus and the two-locus models.

6.1 Introduction and the Model.

In this chapter, the model of the previous chapter is extended to include a predator. More specifically, the model to be studied is given by:

$$\dot{x}_{11} = \frac{u_1^2}{x^2} B(x) - \frac{x_{11}}{x} [D(x) + yP_{11}(x)]$$

$$\dot{x}_{12} = \frac{2u_1u_2}{x^2} B(x) - \frac{x_{12}}{x} [D(x) + yP_{12}(x)]$$

$$\dot{x}_{13} = \frac{u_2^2}{x^2} B(x) - \frac{x_{13}}{x} [D(x) + yP_{13}(x)]$$

$$\dot{x}_{21} = \frac{2u_1u_3}{x^2} B(x) - \frac{x_{21}}{x} [D(x) + yP_{21}(x)]$$

$$\dot{x}_{22} = \frac{2(u_1u_4 + u_2u_3)}{x^2} B(x) - \frac{x_{22}}{x} [D(x) + yP_{22}(x)] \tag{6.1}$$

$$\dot{x}_{23} = \frac{2u_2u_4}{x^2} B(x) - \frac{x_{23}}{x} [D(x) + yP_{23}(x)]$$

$$\dot{x}_{31} = \frac{u_3^2}{x^2} B(x) - \frac{x_{31}}{x} [D(x) + yP_{31}(x)]$$

$$\dot{x}_{32} = \frac{2u_3u_4}{x^2} B(x) - \frac{x_{32}}{x} [D(x) + yP_{32}(x)]$$

$$\dot{x}_{33} = \frac{u_4^2}{x^2} B(x) - \frac{x_{33}}{x} [D(x) + yP_{33}(x)]$$

$$\dot{y} = y[-s + k \sum_{i,j=1}^{3} \frac{x_{ij}}{x} P_{ij}(x)]$$

where u_1, u_2, u_3, u_4 are given by (5.2), x is given by (5.3), and, $s,k > 0$. As in the case of systems (4.1) and (5.1), x_{ij} $(i,j=1,2,3)$ are the nine genotypes of the prey population and y denotes the predator population. The birth and death functions (B and D) are assumed to satisfy the assumptions (H1) - (H6) Section 3.1. The predator functional responses P_{ij} $(i,j = 1,2,3)$ are assumed to satisfy (H7) - (H9) of Section 4.1, namely,

(H7) $P_{ij} : cl(R_+^1) \to cl(R_+^1)$ $(i,j = 1,2,3)$ are C^1

(H8) $P_{ij}(0) = 0$ $(i,j = 1,2,3)$

(H9) $P'_{ij}(x) > 0$ $(i,j = 1,2,3)$ for $x \in cl(R_+^1)$.

In Section 6.2, we construct the flow defined by (6.1) and study its boundedness and invariance properties. Some of the boundary rest points of system (6.1) and their stability properties are considered in Section 6.3. In Section 6.4, some sufficiency conditions leading to the evolution of pure strains as well as the global stability of a boundary rest point will be given. In Section 6.5, some sufficiency conditions which guarantee the persistence of the system will be discussed. We finish with a short discussion of the results in Section 6.6.

6.2 The Associated Flow.

As in the case of system (4.1), system (6.1) is not defined when $x = 0$. When $x = 0$, we define system (6.1) to be

$$\dot{x}_{ij} = 0 \qquad \dot{y} = -sy \tag{6.2}$$

and write (6.1) and (6.2) as

$$\dot{x}_{ij} = F_{ij}(x_{11},\cdots,x_{33},y) \qquad \dot{y} = G(x_{11},\cdots,x_{33},y) \ . \tag{6.3}$$

We have the following analogue of Proposition 4.1:

<u>Proposition 6.1</u>: F_{ij} $(i,j=1,2,3)$, $G \in \mathrm{Lip}$ <u>on</u> $cl(R_+^{10})$ <u>and</u> F_{ij} $(i,j=1,2,3)$, $G \in C^1$ <u>on</u> R_+^{10} . <u>Thus system</u> (6.3) <u>defines a continuous semi-flow on</u> $cl(R_+^{10})$ <u>which becomes a smooth</u> (C^1) <u>local flow</u>

when restricted on R_+^{10}. It is A-dissipative with

$$A = \{(x_{11},\cdots,x_{33},y) \in cl(R_+^{10}) : x \leq K \text{ and }$$
$$kx + y \leq \frac{k}{s}(M + sK)\} \tag{6.4}$$

where $M = \max\{B(x) - D(x) : x \in [0,K]\}$. $H_{x_{11}}, H_{x_{13}}, H_{x_{31}}, H_{x_{33}}, H_y$, $H_{x_{11},y}, H_{x_{13},y}, H_{x_{31},y}, H_{x_{33},y}, H_{x_{11},x_{12},x_{13}}, H_{x_{11},x_{21},x_{31}}, H_{x_{13},x_{23},x_{33}}$, $H_{x_{31},x_{32},x_{33}}, H_{x_{11},x_{12},x_{13},y}, H_{x_{11},x_{21},x_{31},y}, H_{x_{13},x_{23},x_{33},y}$, $H_{x_{31},x_{32},x_{33},y}$, and $H_{x_{11},\cdots,x_{33}}$ are invariant. The vector field $(f_{11},\cdots,F_{33},G)$ points into R_+^{10} on $b(R_+^{10}) \setminus V$, where

$$V = cl(H_{x_{11},x_{12},x_{13},y} \cup H_{x_{11},x_{21},x_{31},y} \cup H_{x_{13},x_{23},x_{33},y}$$
$$\cup H_{x_{31},x_{32},x_{33},y} \cup H_{x_{11},\cdots,x_{33}}) . \tag{6.5}$$

Proof: To show that $F_{11} \in$ Lip on $cl(R_+^{10})$, it suffices to consider two points in $cl(R_+^{10})$ of the form $(x_{11},\cdots,x_{33},y)$ and $(0,\cdots,0,\bar{y})$ where $x = x_{11} + \cdots + x_{33} > 0$. Then

$$\left|F_{11}(x_{11},\cdots,x_{33},y) - F_{11}(0,\cdots,0,\bar{y})\right| \leq \frac{u_1^2}{x^2} B(x) + \frac{x_{11}}{x}[D(x) + yP_{11}(x)]$$
$$\leq B(x) + D(x) + yP_{11}(x)$$
$$\leq [B'(z_1) + D'(z_2) + yP'_{11}(z_3)]\ |x|$$

for some $0 \le z_1, z_2, z_3 \le x$. Therefore $F_{11} \in$ Lip on $cl(R_+^{10})$ and similarly we show that $F_{12}, \cdots, F_{33}, G \in$ Lip.

The positive invariance of $cl(R_+^{10})$ can be easily verified using Proposition 2.1. Hence system (6.3) defines a continuous local semi-flow on $cl(R_+^{10})$ which becomes a C^1 local flow when restricted to R_+^{10}.

To show that system (6.3) is A-dissipative for A defined in (6.4), it suffices to observe that

$$\dot{x} \le B(x) - D(x)$$

$$k\dot{x} + \dot{y} \le k[B(x) - D(x)] - sy$$

and use Proposition 2.2. This also shows that system (6.1) defines a continuous semi-flow on $cl(R_+^{10})$.

The invariance of the sets listed is clear. It is also easy to show that the vector field $(F_{11}, \cdots, F_{33}, G)$ points into R^{10} on $b(R_+^{10}) \setminus V$. For example, for $(X,y) = (x_{11}, \cdots, x_{33}, y) \in b(R_+^{10})$ with $x_{11} = 0$, $F_{11}(X,y) = \frac{u_1^2}{x^2} B(x) \ge 0$ and $F_{11}(X,y) = 0$ if and only if $u_1 = 0$ (i.e. $x_{11} = x_{12} = x_{21} = x_{22}$).

q.e.d.

6.3 Some Boundary Rest Points and Their Stability.

In this section some of the rest points of system (6.1) which lie on $b(R_+^{10})$ will be considered. According to Proposition 6.1, these rest points must lie on V. Clearly, $E_0(0,\cdots,0)$ is a rest point and by Proposition 5.3, $E = \{(H(c_1,c_2),0) : (c_1,c_2) \in [0,+\infty]\times[0,+\infty]\}$ is the set of rest points of system (6.1) in $cl(H_{x_{11},\cdots,x_{33}}) \setminus \{E_0\}$. Let

$$b_{ij} = -s + k\, P_{ij}(K) \qquad (i,j=1,3) \quad . \tag{6.6}$$

Then $H_{x_{ij},y}$ $(i,j = 1,3)$ contains a rest point if and only if $b_{ij} > 0$ $(i,j = 1,3)$. If they exist these rest points are unique. Let us denote these rest points by E_i $(i=1,2,3,4)$ if they exist. That is, let $E_1 = (\bar{x}_{11},0,\cdots,0,\bar{y}_{11})$, $E_2 = (0,0,\bar{x}_{13},0,\cdots,0,\bar{y}_{13})$, $E_3 = (0,\cdots,0,\bar{x}_{31},0,0,\bar{y}_{31})$, and $E_4 = (0,\cdots,0,\bar{x}_{33},\bar{y}_{33})$. The 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 rest points. Some conditions are known which guarantee the existence or non-existence of these rest points (see Freedman-So-Waltman (1984)). In this thesis we will not use these conditions.

The rest point E_0 is unstable. Indeed we have the following Proposition.

<u>Proposition 6.2</u>: $E_0 \notin w(x_{11},\cdots,x_{33},y)$ <u>for all</u> $(x_{11},\cdots,x_{33},y) \in R_+^{10}$.

<u>Proof</u>: This follows from Proposition 2.15 because in a small enough neighbourhood of E_0, we have,

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

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

where $P(x) = \max \{P_{ij}(x) : i,j = 1,2,3\}$, and the flow on $cl(H_y)$ is given by $\dot{y} = -sy$.

q.e.d.

<u>Corollary 6.3</u>: $(0,\cdots,0,y) \notin w(x_{11},\cdots,x_{33},y)$ <u>for all</u> $(x_{11},\cdots,x_{33},y) \in R_+^{10}$.

<u>Proof</u>: This follows from Proposition 6.2 and the global stability of E_0 on the invariant set $cl(H_y)$.

q.e.d.

The stability properties of each $(H(c_1,c_2),0)$ in $cl(X_{x_{11},\cdots,x_{33}}) \setminus \{E_0\}$ is determined by Theorem 5.6. To compute the stability of $(H(c_1,c_2),0)$ in the y-direction we note that

$$\begin{aligned} d(c_1,c_2) = -s + \frac{k}{(1+c_1)^2(1+c_2)^2} [& c_1^2c_2^2P_{11}(K) + 2c_1^2c_2P_{12}(K) \\ & + c_1^2P_{13}(K) + 2c_1c_2^2P_{21}(K) + 4c_1c_2P_{22}(K) + 2c_1P_{23}(K) \\ & + c_2^2P_{31}(K) + c_2P_{32}(K) + P_{33}(K)] \end{aligned} \tag{6.6}$$

is the eigenvalue of the variational matrix of system (6.1) at $(H(c_1,c_2),0)$ that corresponds to eigenvectors that have a non-zero y component. A condition for the persistence of y is given by the following proposition.

Proposition 6.4: If $d(c_1,c_2) > 0$ for all $c_1,c_2 \in [0,+\infty]$, then $\lim_{t\to+\infty} y(t) > 0$ for all $(x_{11o},\cdots,x_{33o},y_o) \in R_+^{10}$.

Proof: The proof is similar to that of Proposition 4.4. Again we know that E is repelling in the y-direction and therefore in order for $\lim_{t\to+\infty} y(t) = 0$, the omega-limit set $w(x_{11o},\cdots,x_{33o},y_o)$ of $(x_{11o},\cdots,x_{33o},y_0)$ must intersect the stable manifold, $W^s(E)$, of the invariant set E at a point other than E itself. Now $W^s(E) \cap cl(R_+^{10}) \subset cl(H_{x_{11},\cdots,x_{33}})$. The global dynamics on $cl(H_{x_{11},\cdots,x_{33}})$ as given by Theorem 5.6 implies that either w contains E_0 or w is unbounded. In either case, we have a contradiction.

q.e.d.

Remark. Unlike as in Lemma 4.5, we are unable to obtain a necessary and sufficient condition on $P_{ij}(K)$ so that $d(c_1,c_2) > 0$ for all $c_1, c_2 \in [0,+\infty]$. However, from the definition of $d(c_1,c_2)$ given in (4.7), it is clear that $d(c_1,c_2) \leq 0$ for all $c_1, c_2 \in [0,+\infty]$ if $P_{ij}(K) \geq \frac{s}{k}$ for all $i,j = 1,2,3$.

The linear 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 system (6.1) evaluated at E_i $(i=1,2,3,4)$. For illustration, we will present $M(E_1)$ below. To simplify notations, we use

$M_{ij,hk}$ to denote $\frac{\partial F_{ij}}{\partial x_{hk}}(E_1)$, $M_{y,ij}$ to denote $\frac{\partial G}{\partial x_{ij}}(E_1)$, etc. and we move y to the second row.

	x_{11}	y	x_{12}	x_{13}	x_{21}	x_{22}	x_{23}	x_{31}	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). Furthermore, the non-zero entries are given by:

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

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

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

$$M_{11,22} = -\frac{1}{2\bar{x}_{11}} B(\bar{x}_{11}) + B'(\bar{x}_{11}) - D'(\bar{x}_{11}) - \bar{y}_{11}P'_{11}(\bar{x}_{11}) .$$

$$M_{11,ij} = -\frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) + B'(\bar{x}_{11}) - D'(\bar{x}_{11}) - \bar{y}_{11}P'_{11}(\bar{x}_{11})$$

(for $(i,j) = (1,3), (2,3), (3,1), (3,2)$ or $(3,3)$)

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

$$M_{y,ij} = \frac{k\bar{y}_{11}}{\bar{x}_{11}} [\bar{x}_{11}P'_{11}(\bar{x}_{11}) + P_{ij}(\bar{x}_{11}) - P_{11}(\bar{x}_{11})] \quad , (i,j) \neq (1,1)$$

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

$$M_{12,13} = \frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{12,22} = \frac{1}{2\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{12,23} = \frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{13,13} = \frac{1}{\bar{x}_{11}} [D(\bar{x}_{11}) + \bar{y}_{11}P_{13}(\bar{x}_{11})] < 0$$

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

$$M_{21,22} = \frac{1}{2\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{21,31} = \frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{21,32} = \frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

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

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

$$M_{22,23} = \frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{22,32} = \frac{1}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{22,33} = \frac{2}{\bar{x}_{11}} B(\bar{x}_{11}) > 0$$

$$M_{23,23} = -\frac{1}{\bar{x}_{11}} [D(\bar{x}_{11}) + \bar{y}_{11}P_{23}(\bar{x}_{11})] < 0$$

$$M_{31,31} = -\frac{1}{\bar{x}_{11}} [D(\bar{x}_{11}) + \bar{y}_{11}P_{31}(\bar{x}_{11})] < 0$$

$$M_{32,32} = -\frac{1}{\bar{x}_{11}} [D(\bar{x}_{11}) + \bar{y}_{11}P_{32}(\bar{x}_{11})] < 0$$

$$M_{33,33} = -\frac{1}{\bar{x}_{11}} [D(\bar{x}_{11}) + \bar{y}_{11}P_{33}(\bar{x}_{11})] < 0 \quad .$$

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

6.4 Some Conditions Which Lead to Evolution of Pure Strains.

In this section, conditions leading to the global stability of boundary rest points will be considered. Due to the complexity of the problem, we are forced to focus on a small number of cases. In our analysis, we will need to know the global dynamics of system (6.1) on the boundary invariant set V. The assumptions are essentially those in Theorem 4.6 applied to each of the four 4-dimensional boundary invariant sets $H_{x_{11},x_{12},x_{13},y}$, $H_{x_{11},x_{21},x_{31},y}$, $H_{x_{13},x_{23},x_{33}}$, and $H_{x_{31},x_{32},x_{33}}$. The added assumptions for this section and the next are as follows.

($H\bar{1}$) The predator y persists. Mathematically speaking, this means that, according to Proposition 6.4, we require $d(c_1,c_2) > 0$ for all $c_1, c_2 \in [0,+\infty]$.

($H\bar{2}$) E_1 (resp. E_2,E_3,E_4) is globally exponentially stable on $H_{x_{11},y}$ (resp. $H_{x_{13},y}$, $H_{x_{31},y}$, $H_{x_{33},y}$),

($H\bar{3}$) The four sets of predator functional responses: $P_{11}/P_{12}/P_{13}$ $P_{11}/P_{21}/P_{31}$, $P_{13}/P_{23}/P_{33}$, and, $P_{31}/P_{32}/P_{33}$ are ordered with the heterozygote one between the two homozygotes ones. There are 16 possibilities. By interchanging the roles of the allele types A (resp. B) and a (resp. b), if necessary, we are left with 3 cases to consider:

(1) $P_{11} \le P_{12} \le P_{13}$, $P_{11} \le P_{21} \le P_{31}$, $P_{13} \le P_{23} \le P_{33}$, $P_{31} \le P_{32} \le P_{33}$.

(2) $P_{11} \leq P_{12} \leq P_{13}$, $P_{11} \leq P_{21} \leq P_{31}$, $P_{33} \leq P_{23} \leq P_{13}$, $P_{33} \leq P_{32} \leq P_{31}$, and

(3) $P_{11} \leq P_{12} \leq P_{13}$, $P_{11} \leq P_{21} \leq P_{31}$, $P_{13} \leq P_{23} \leq P_{33}$, $P_{33} \leq P_{32} \leq P_{31}$.

The case when $P_{11} \leq P_{12} \leq P_{13} \leq P_{23} \leq P_{33} \leq P_{23} \leq P_{31} \leq P_{21} \leq P_{11}$ is excluded because we require at least one of the inequalities to be strict.

In each of the above three cases (1) - (3), we require the differences of the appropriate P_{ij}'s be bounded below by a non-negative linear function of x on $[0,K]$. For example $P_{11} \leq P_{12} \leq P_{13}$ in case (1) should read: there exist $k_{11,12}, k_{12,13} \geq 0$, not both zero, such that $P_{12}(x) - P_{11}(x) \geq k_{11,12}x$ and $P_{13}(x) - P_{12}(x) \geq k_{12,13}x$ for $x \in [0,K]$.

The following is a theorem which provides conditions under which the rest point E_1 is globally stable.

Theorem 6.5: Suppose $(H\bar{1})$ and $(H\bar{2})$ hold. Furthermore assume that

(i) $P_{11} \leq P_{12} \leq P_{13} \leq P_{21} \leq P_{22} \leq P_{23} \leq P_{31} \leq P_{32} \leq P_{33}$,

(ii) there exist $e_{12}, e_{13}, e_{21}, e_{22}, e_{23}, e_{31}, e_{32}, e_{33} \geq 0$, such that

$P_{12}(x) - P_{11}(x) \geq e_{12}x$, $P_{13}(x) - P_{12}(x) \geq e_{13}x$;

$P_{21}(x) - P_{13}(x) \geq e_{21}x$, $P_{22}(x) - P_{21}(x) \geq e_{22}x$,

$P_{23}(x) - P_{22}(x) \geq e_{23}x$, $P_{31}(x) - P_{23}(x) \geq e_{31}x$,

$$P_{32}(x) - P_{31}(x) \geq e_{32}x \quad , \quad P_{33}(x) - P_{32}(x) \geq e_{33}x$$

<u>for all</u> $x \in [0,K]$, <u>and</u>,

(iii) $\bar{y}_{13}[\frac{s}{k} - P_{22}(\bar{x}_{13})] \neq \frac{1}{2} B(\bar{x}_{13})$,

$\bar{y}_{31}[\frac{s}{k} - P_{22}(\bar{x}_{31})] \neq \frac{1}{2} B(\bar{x}_{31})$, <u>and</u>

$\bar{y}_{33}[\frac{s}{k} - P_{22}(\bar{x}_{33})] \neq \frac{1}{2} B(\bar{x}_{33})$,

<u>then</u> E_1 <u>is globally stable on</u> R_+^{10} .

<u>Proof</u>: (H2) , (ii), and (iii) imply that the rest points E_i $(i = 1,2,3,4)$ are hyperbolic. In fact by studying the eigenvalues of the variational matrix at each of these rest points, as given in Section 6.3, we know, $\dim W^u(E_1) = 0$, $\dim W^u(E_2) \geq 1$, $\dim W^u(E_3) \geq 1$, $\dim W^u(E_4) \geq 2$. Therefore E_1 is asymptotically stable and $W^u(E_i)$ $(i = 2,3,4)$ must have non-empty intersection with $R^{10} \setminus cl(R_+^{10})$. By Proposition 2.11, $W^s(E_i) \cap cl(R_+^{10})$ must lie in $b(R_+^{10})$. Theorem 4.6 tells us that $W^s(E_4) \cap cl(R_+^{10}) \subset cl(H_{x_{33},y})$, $W^s(E_3) \cap cl(R_+^{10}) \subset cl(H_{x_{31},x_{32},x_{33},y})$, and $W^s(E_2) \cap cl(R_+^{10}) \subset cl(H_{x_{13},x_{23},x_{33},y})$. From this one can easily show that E_1 is the only point in $b(R_+^{10})$ that can lie in $w = w(x_{11},\cdots,x_{33},y)$ for any $(x_{11},\cdots,x_{33},y)$ in R_+^{10} . Moreover, if $E_1 \in w$, then the orbit converges to E_1 as $t \to +\infty$. Using REDUCE 2 (a programming language for algebraic manipulations), one shows that

$$\frac{\dot{u}_a}{u_a} - \frac{\dot{u}_A}{u_A} \leq - \frac{y}{u_A u_a} [e_{33}x_{12}x_{33} + \text{other non-negative terms}] .$$

Therefore, as in the proof of Theorem 4.6,

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

If the integral diverges, then $\lim\limits_{t\to+\infty} u_a(t) = 0$ so that $w \cap b(R_+^{10}) \neq \phi$ and hence the orbit converges to E_1. Now suppose $z(t) = (x_{12}x_{33}y)(t) \in L^1[0,+\infty)$, then $\lim\limits_{t\to+\infty} z(t) = 0$ and hence $\underline{\lim}_{t\to+\infty} x_{12}(t) = 0$ or $\underline{\lim}_{t\to+\infty} x_{33}(t) = 0$ (since $\underline{\lim}_{t\to+\infty} y(t) > 0$ by $(H\overline{1})$). This again implies $w \cap b(R_+^{10}) \neq \phi$ and so the orbit converges to E_1 as before. This shows that E_1 is globally attracting and it completes the proof of the theorem.

q.e.d.

Remark: The assumption (iii) in the above theorem is technical and is necessary in order for the rest points E_i $(i=1,2,3,4)$ to be hyperbolic. This assumption is "generically" satisfied.

6.5 Some Persistence Results.

In this section we will consider conditions which lead to the persistence of system (6.1). Besides the conditions $(H\overline{1}) - (H\overline{3})$ made in the previous section, we will also assume that the rest points E_i $(i=1,2,3,4)$ are hyperbolic. This amounts to requiring the $k_{ij,hl}$'s in $(H\overline{3})$ be positive and that $\overline{y}_{ij}[\frac{S}{K} - P_{22}(\overline{x}_{ij})] - \frac{1}{2} B(\overline{x}_{ij})$ $(i,j=1,3)$ be non-zero.

Theorem 6.6: Under the above assumptions, system (2.1) is persistent if

(i) $\overline{y}_{11}[\frac{S}{K} - P_{22}(\overline{x}_{11})] - \frac{1}{2} B(\overline{x}_{11}) > 0$ holds under cases (1) and

(3) in $(H\overline{3})$ of Section 6.4, and,

(ii) $\overline{y}_{11}[\frac{s}{k} - P_{22}(\overline{x}_{11})] - \frac{1}{2} B(\overline{x}_{11}) > 0$, and

$\overline{y}_{33}[\frac{s}{k} - P_{22}(\overline{x}_{33})] - \frac{1}{2} B(\overline{x}_{33}) > 0$

hold under case (2) of $(H\overline{3})$ in Section 6.4.

Proof: We will only discuss case (1) of $(H\overline{3})$ in Section 6.4. The other two cases are similar. Let $(x_{11},\cdots,x_{33},y) \in R_+^{10}$ and let $w = w(x_{11},\cdots,x_{33},y)$. Our aim is to show $w \cap b(R_+^{10}) = \phi$, or equivalently $w \cap V = \phi$, where V was given in (6.5). Recall that $\lim_{t\to+\infty} y(t) > 0$ by $(H\overline{1})$. First we will show that $E_4 \notin w$. Suppose not, that is, suppose $E_4 \in w$. Since $\dim W^u(E_4) \geq 2$, therefore $W^u(E_4) \cap (R_+^{10} \setminus cl(R_+^{10})) \neq \phi$, and hence, by Proposition 2.11, $W^s(E_4) \cap R_+^{10} = \phi$. It follows from the global dynamics on $cl(H_{x_{13},x_{23},x_{33},y})$ and $cl(H_{x_{31},x_{32},x_{33},y})$ as given in Theorem 6.1 that $W^s(E_4) \cap cl(R_+^{10}) \subset cl(H_{x_{33},y})$. The Butler-McGehee lemma then implies that w contains a point in $cl(H_{x_{33},y})$ other than E_4 which is a contradiction. Next we show that $E_3 \notin w$. As in the case of E_4 , $W^u(E_3) \geq 1$ implies $W^u(E_3) \cap (R_+^{10} \setminus cl(R_+^{10})) \neq \phi$ and therefore, by Proposition 2.11, $W^s(E_3) \cap R_+^{10} = \phi$. The global dynamics on $cl(H_{x_{11},x_{21},x_{31},y})$ and $cl(H_{x_{31},x_{32},x_{33},y})$ imply that $W^s(E_3) \cap cl(R_+^{10}) \subset cl(H_{x_{31},x_{32},x_{33},y})$. The Butler-McGehee lemma says that w must contain a point in $cl(H_{x_{31},x_{32},x_{33},y})$ other than E_3, which is a contradiction.

Hence $E_3 \notin w$. Similarly $E_2 \notin w$. One could repeat the above argument for E_1 because $M_{22}(E_1) > 0$ by assumption. Hence $E_i \notin w$ $(i = 1,2,3,4)$ and $w \cap V = \phi$ follows from the global dynamics on V .

6.6 Discussion.

Due to the complexity of (6.1), our analysis for this system is not as complete as the other models (3.1), (4.1) and (5.1), that we studied in the previous chapters. However, Theorem 6.6 points to a way of making the system persistent which otherwise would not be by adjusting the predator functional response of the double heterozygote (AaBb). This result indicates a situation for which a two-locus problem cannot be analyzed as the "sum" effect of two one-locus problems.

CHAPTER 7

CONCLUDING DISCUSSION & REMARKS

In this thesis we study four continuous models in population genetics / ecology both for the one-locus, two-allele problem and for the two-locus, two-allele problem.

In Chapter 3, a continuous model (system (3.1)) for a one-locus, two-allele problem with non-linear birth (B) and death (D) processes as well as fertility / viability differences is considered. The population x under consideration is divided into three subpopulations x_1, x_2, x_3 corresponding to the three different genotypes AA, Aa and aa with fertility / viabilities denoted by f_1, f_2 and f_3. The main result for this model is Theorem 3.9 which provides a complete picture of the global dynamics of system (3.1). This theorem can be summarized as follows.

(i) When $f_1 = f_2 = f_3$ (no selection), all solutions converge to some equilibrium. More precisely, if $(x_1(t), x_2(t), x_3(t))$ is a solution, then it converges to the equilibrium: $\frac{K}{(1+c)^2}(c^2, 2c, 1)$ where c is determined by initial conditions, namely $c = \dfrac{x_1(0) + \frac{1}{2}x_2(0)}{x_3(0) + \frac{1}{2}x_2(0)}$. Hence, all solutions converge to a polymorphism (positive interior equilibrium). Which equilibrium it converges to depends on initial conditions. Phrased in another way, this result also says that the proportion $x_1(x) : x_2(t) : x_3(t)$ tends to $c^2 : 2c : 1$ as t tends to positive infinity. This is the analogue of the Hardy-Weinberg equilibrium relation for discrete one-locus, two-allele models with random mating and no selection.

(ii) When $f_1, f_3 > f_2$ (homozygous advantage), the positive x_1-x_2-x_3 cone is divided into two regions by a separatrix (dividing) surface. Solutions initiating from one region will converge to the boundary equilibrium $(x_1,x_2,x_3) = (K,0,0)$ whereas solutions initiating from the other region will converge to the boundary equilibrium $(0,0,K)$. Solutions initiating on the separatrix surface converge to the unique unstable polymorphism: $\frac{K}{(1+c)^2}(c^2,2c,1)$. Unlike the case when there is no selection, c is independent of initial conditions in this case. Instead, it is determined by the fertilities f_1, f_2 and f_3, namely, $c = \frac{f_3 - f_2}{f_1 - f_2}$. Hence, under "most" initial conditions, one of the gamete types becomes extinct. Which one will actually become extinct depends on initial conditions.

(iii) When $f_2 > f_1, f_3$ (heterozygous advantage), all (positive) solutions converge to the unique stable polymorphism: $\frac{K}{(1+c)^2}(c^2,2c,1)$. Hence all three genotypes coexist. As in the case of homozygous advantage, c is independent of initial conditions and is dependent solely on fertility differences, namely, $c = \frac{f_2 - f_3}{f_2 - f_1}$.

(iv) When $f_1 > f_2 > f_3$ (selection for allele A which has incomplete dominance over allele a) or when $f_1 > f_2 = f_3$ (selection for the recessive allele A), or when $f_1 = f_2 > f_3$ (selection for the dominant allele A), all solutions converge to the boundary equilibrium $(K,0,0)$. Hence, the gamete type a becomes extinct.

(v) When $f_3 > f_2 > f_1$ (selection for allele a which has incomplete dominance over allele A), or when $f_3 > f_2 = f_1$ (selection for the recessive allele a), or when $f_3 = f_2 > f_1$ (selection for the dominant allele a), all solutions converge to the boundary equilibrium (0,0,K) . Hence, the gamete type A becomes extinct.

All of the above results have their analogue with discrete models.

In Chapter 4, the model in Chapter 3 is extended to include a predator y (system (4.1)). The prey population x is modelled by (3.1). For the prey population, there are two types of selection forces at work. First, there is the one studied in Chapter 3, namely, selection due to fertility / viability differences. The other type is selection due to differential predator functional responses. (Recall that the predator functional response of x_i $(i = 1,2,3)$ was denoted by P_i $(i = 1,2,3)$.) Of particular interest are the following two questions.

(1) Under what conditions will one of the prey gamete types become extinct?

(2) When will all the prey genotypes coexist with the predator?

The concept of coexistence is formulated in terms of the definition of persistence: if $x_i(0) > 0$ $(i=1,2,3)$ and $y(0) > 0$, then $\liminf_{t\to+\infty} x_i(t) > 0$ $(i = 1,2,3)$ and $\liminf_{t\to+\infty} y(t) > 0$. In the case of no selection due to fertility / viability differences, the answer to question (1) is provided by Theorem 4.6. This theorem (modulo a number of technicalities) can be summarized as follows.

If the predator functional responses of the prey genotypes are ordered: $P_1 < P_2 < P_3$ (hence x_1 can be thought of as the one which is the most difficult to catch) and the predator y can survive on x_1 alone (hence it will also be able to survive on the other two prey genotypes alone), then gamete type a becomes extinct.

This result can be interpretated as saying that the predator exhausted the two prey genotypes x_2 and x_3 which are easier to catch and lives on the prey genotype x_1 alone. In the case when there is selection due to fertility / viability differences, the answer to question (1) is provided by Theorem 4.8. In summary this theorem states the following.

If the fertilities are ordered: $f_1 \geq f_2 \geq f_3$ and not all equal (hence x_1 has fertility advantage) and the predator functional responses are also ordered: $P_1 \leq P_2 \leq P_3$ (hence x_1 has predation advantage), then gamete a becomes extinct.

Note that in this theorem, it is not required that the predator y must survive. In fact it can also go extinct along with x_2 and x_3. This result is intuitively clear in view of the previous results for no selection due to differential predator functional responses and for no selection due to fertility / viability differences.

The answer to question (2) in the case of no selection due to fertility / viability differences is provided by Theorem 4.10. In summary, this theorem states the following.

We assume that

(i) the subsystem with only x_1 and y has a globally stable positive interior equilibrium $E_3 = (\bar{x}_1, 0, 0, \bar{y}_1)$ (consequently $P_1(K) > \frac{s}{k}$) and the subsystem with only x_3 and y has a globally stable positive interior equilibrium $E_4 = (0, 0, \bar{x}_3, \bar{y}_3)$ (consequently $P_3(K) > \frac{s}{k}$),

(ii) $P_2(\bar{x}_1) < \frac{s}{k}$, $P_2(\bar{x}_3) < \frac{s}{k}$, and,

(iii) $P_2(K) > \frac{s}{k} - \sqrt{(P_1(K) - \frac{s}{k})(P_3(K) - \frac{s}{k})}$

then system (4.1) is persistent.

Recall that s is the death rate of the predator y in the absence of prey and k is the conversion factor from prey biomass to predator biomass. Condition (iii) is a condition to guarantee y survives. It says that $P_2(K)$ should be large enough so that y will not go extinct. Condition (ii) is a condition to guarantee neither E_3 nor E_4 are asymptotically stable. It says that $P_2(\bar{x}_1)$ (resp. $P_2(\bar{x}_3)$) should be small enough so that for solutions that start near E_3 (resp. E_4), the gamete type a (resp. A) will not become extinct. Note that conditions (ii) and (iii) are not mutually exclusive because $\bar{x}_i < K$ $(i = 1,3)$ and P_2 is strictly increasing.

In the case when the fertilities / viabilities are all different, the answer to question (2) is provided by Theorem 4.11. In order to explain the results of this theorem, let us recall the following assumptions and notations.

It is assumed that if the subsystem consisting of x_1 and y only contains a positive interior equilibrium $E_3 = (\bar{x}_1, 0, 0, \bar{y}_1)$, then it is globally stable. Similarly, if the subsystem consisting of x_3 and y only contains a positive interior equilibrium $E_4 = (0, 0, \bar{x}_3, \bar{y}_3)$, then it is globally stable.

$$a_i = f_i - f_2 \qquad (i = 1,3)$$

$$b_i = -s + kP_i(K) \qquad (i = 1,3)$$

$$d_i = \frac{1}{\bar{x}_i}\left[\frac{f_2 B(\bar{x}_i)}{f_i} - D(\bar{x}_i) - \bar{y}_i P_2(\bar{x}_i)\right] \qquad (i = 1,3)$$

$$d = -s + \frac{k}{(1+c)^2}[c^2 P_1(K) + 2cP_2(K) + P_3(K)]$$

where $c = \frac{a_3}{a_1}$. Note that d_1 (resp. d_3) is defined only when E_3 (resp. E_4) exists and d is defined only when a_1 and a_3 are of the same sign. Moreover, $b_i > 0$ $(i = 1,3)$ is the necessary and sufficient condition for the existence of E_i $(i = 1,3)$. By noting $B(\bar{x}_i) - D(\bar{x}_i) - \bar{y}_i P_i(\bar{x}_i) = 0$, the meaning of d_i will become a little bit more transparent if we rewrite it as $\frac{1}{\bar{x}_i}\left[\bar{y}_i\left(\frac{s}{k} - P_2(\bar{x}_i)\right) - \frac{a_i}{f_i} B(\bar{x}_i)\right]$.

Since there are thirty two persistence and non-persistence cases studied, we will only highlight the results of the theorem by discussing two of these cases here. (See Theorem 4.11 for the labelling of the cases.)

(I) Persistence due to predation.

In case (8c): $a_1 < 0$, $a_3 > 0$, $b_1 > 0$, $b_3 > 0$, $d_1 > 0$, $d_3 > 0$, system (4.1) is persistent. Since $a_1 < 0$ and $a_3 > 0$, we know that gamete A (consequently x_1 and x_2) will go extinct in the absence of the predator y . $b_1 , b_3 > 0$ says that y can survive on either x_1 or x_3 alone. $d_i > 0$ $(i = 1,3)$ reduces to

$P_2(\bar{x}_i) < \frac{s}{k} - \frac{a_i}{f_i \bar{y}_i} B(\bar{x}_i)$. Hence the persistence of the system is due to P_i $(i = 1,2,3)$.

(II) Persistence due to fertility / viability differences.

In case (1b): $a_1 < 0$, $a_3 < 0$, $b_1 < 0$, $b_3 < 0$, $d > 0$, system (4.1) is persistent. In the absence of fertility / viability differences (that is, assume $a_1 = a_3 = 0$), the system is non-persistent, because $b_i < 0$ $(i = 1,3)$. However, if the heterozygote x_2 has selection advantage due to fertilities / viabilities and the predator functional response P_2 of x_2 is large enough to make $d > 0$, then the system is persistent.

In Chapter 5 the model studied in Chapter 3 is extended to a two-locus, two-allele model. Only the no selection case is considered. The whole population is again denoted by x and the subpopulations of the nine genotypes: AABB , AABb , AAbb , AaBB , AaBb , Aabb , aaBB , aaBb , and, aabb are denoted by x_{11} , x_{12} , x_{13} , x_{21} , x_{22} , x_{23} , x_{31} , x_{32} , and, x_{33} respectively. The main result of this chapter is Theorem 5.6 which provides a complete picture of the global dynamics of system (5.1). It is an analogue of the Hardy-Weinberg equilibrium relation for a discrete two-locus, two-allele with random mating and no selection model. In summary, this theorem states the following.

All solutions of system (5.1) converge to some equilibrium. More precisely, if $(x_{11}(t), x_{12}(t), x_{13}(t), x_{21}(t), x_{22}(t), x_{23}(t), x_{31}(t), x_{32}(t), x_{33}(t))$ is a solution of system (5.1), then it converges to the equilibrium: $\frac{K}{(1+c_1)^2(1+c_2)^2}(c_1^2c_2^2, 2c_1^2c_2, c_1^2, 2c_1c_2^2, 4c_1c_2, 2c_1, c_2^2, 2c_2, 1)$ as t tends to positive infinity. As in the one-locus case, c_1, c_2 depend on initial conditions, namely

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

and

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

Hence, the dynamics of system (5.1) is trivial. Rephrased in terms of proportions, this theorem also says that $x_{11}(x) : x_{12}(t) : x_{13}(t) : x_{21}(t) : x_{22}(t) : x_{23}(t) : x_{31}(t) : x_{32}(t) : x_{33}(t)$ tends to $c_1^2c_2^2 : 2c_1^2c_2 : c_1^2 : 2c_1c_2^2 : 4c_1c_2 : 2c_1 : c_2^2 : 2c_2 : 1$ as t tends to positive infinity, which is the more usual form in population genetics literature.

In Chapter 6, the model in Chapter 5 is extended to include a predator y. The dynamics of the prey population is modelled by system (5.1). Again the two questions in Chapter 4 are raised. A partial answer to question (1) is provided by Theorem 6.5 which, modulo a number of technicalities, can be summarized as follows.

Assume that each of the four two-population subsystems constituting y and x_{ij} $(i,j=1,3)$ contains a globally stable positive interior equilibrium. If there is a complete ordering of the predator functional responses: $P_{11} < P_{12} < P_{13} < P_{21} < P_{22} < P_{23} < P_{31} < P_{32} < P_{33}$, and, if the predator y can survive on the most difficult to catch prey genotype x_{11}, then the gamete types Ab, aB, and, ab go extinct. Hence only x_{11} and y survive.

This result is intuitively clear in view of the similar result for the onè-locus case.

A partial answer to question (2) is provided by Theorem 6.6 which, modulo a number of technicalities, can be summarized as follows.

Assume that the predator y survives and that each of the four subsystems consisting of y and x_{11} (resp. x_{13}, x_{31}, x_{33}) contains a globally stable positive interior equilibrium
$E_1 = (\bar{x}_{11},0,\cdots,0,\bar{y}_{11})$ (resp. $E_2 = (0,0,\bar{x}_{13},0,\cdots,0,\bar{y}_{13})$,
$E_3 = (0,\cdots,0,\bar{x}_{31},0,0,\bar{y}_{31})$, $E_{33} = (0,\cdots,0,\bar{x}_{33},\bar{y}_{33})$). Under each of the following three cases,

(i) $P_{11} < P_{12} < P_{13} < P_{23} < P_{33}$, $P_{11} < P_{21} < P_{31} < P_{32} < P_{33}$ and $P_{22}(\bar{x}_{11}) < \frac{s}{k} - \frac{1}{2\bar{y}_{11}} B(\bar{x}_{11})$,

(ii) $P_{11} < P_{12} < P_{13}$, $P_{11} < P_{21} < P_{31}$, $P_{33} < P_{23} < P_{13}$, $P_{33} < P_{32} < P_{31}$, $P_{22}(\bar{x}_{11}) < \frac{s}{k} - \frac{1}{2\bar{y}_{11}} B(\bar{x}_{11})$ and

$$P_{22}(\bar{x}_{33}) < \frac{s}{k} - \frac{1}{2\bar{y}_{33}} B(\bar{x}_{33}) \quad \text{, and,}$$

(iii) $P_{11} < P_{12} \leq P_{13} < P_{23} < P_{33} < P_{32} \leq P_{31}$, $P_{11} < P_{21} < P_{31}$

and $P_{22}(\bar{x}_{11}) < \frac{s}{k} - \frac{1}{2\bar{y}_{11}} B(\bar{x}_{11})$,

system (6.1) is persistent.

One could interpret these results as saying that if we consider the system as a one-locus problem, then the system is non-persistent; but as a two-locus problem, the predator functional response P_{22} of the double heterozygote x_{22} can change (by making x_{22} more difficult to catch) a non-persistent system to one of persistence.

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APPENDIX 1

DERIVATION OF THE ONE-LOCUS TWO-ALLELE MODEL (3.1)

If we denote the two alleles at the locus by A and a, then there are three genotypes: AA, Aa, and, aa. The mating table looks like:

Mating Type	AA	Aa	aa
AA × AA	1	-	-
AA × Aa	1/2	1/2	-
AA × aa	-	1	-
Aa × Aa	1/4	1/2	1/4
Aa × aa	-	1/2	1/2
aa × aa	-	-	1

There are two ways of arriving at the coefficients of $B(x)$ in system (3.1).

(i) f_i's as fertilities:

f_i $(i = 1,2,3)$ is to be thought of as the number of gametes produced by each individual in the x_i population. For example, there will be $\frac{1}{2} f_2 x_2$ A gametes and $\frac{1}{2} f_2 x_2$ a gametes produced by the x_2 population. Thus, there are

$f_1x_1 + \frac{1}{2} f_2x_2 = u$ that many A gametes and

$f_3x_3 + \frac{1}{2} f_2x_2 = v$ that many a gametes in the gamete pool.

By random union of gametes, the proportion of AA genotype produced is: $(\frac{u}{u+v})(\frac{v}{u+v}) = \frac{u^2}{(u+v)^2}$. Similarly one can arrive at the other coefficients in system (3.1) this way.

(ii) f_i's as viabilities:

The fraction $\frac{f_ix_i}{f_1x_1 + f_2x_2 + f_3x_3}$ $(i = 1,2,3)$ is to be thought of as the proportion of x_i that involves in random mating. Since the AA genotype is obtained from the mating types: AA×AA, AA×Aa, Aa×AA, and, Aa×Aa with probabilities: 1, 1/2, 1/2, and, 1/4 respectively, we have

$$\left(\frac{f_1x_1}{f_1x_1 + f_2x_2 + f_3x_3}\right)\left(\frac{f_1x_1}{f_1x_1 + f_2x_2 + f_3x_3}\right)$$
$$+ \frac{1}{2}\left(\frac{f_1x_1}{f_1x_1 + f_2x_2 + f_3x_3}\right)\left(\frac{f_2x_2}{f_1x_1 + f_2x_2 + f_3x_3}\right)$$
$$+ \frac{1}{2}\left(\frac{f_2x_2}{f_1x_1 + f_2x_2 + f_3x_3}\right)\left(\frac{f_1x_1}{f_1x_1 + f_2x_2 + f_3x_3}\right)$$
$$+ \frac{1}{4}\left(\frac{f_2x_2}{f_1x_1 + f_2x_2 + f_3x_3}\right)\left(\frac{f_2x_2}{f_1x_1 + f_2x_2 + f_3x_3}\right) = \frac{u^2}{(u+v)^2}$$

as the proportion of AA genotypes produced. The other two coefficients of $B(x)$ in system (3.1) are arrived at in a similar way.

APPENDIX 2

DERIVATION OF THE TWO-LOCUS TWO-ALLELE MODEL (5.1)

The derivation is similar to the one-locus case in Appendix 1. We denote the two allele types at the first locus by A and a and the two allele types at the second locus by B and b. There are nine genotypes: AABB, AABb, AAbb, AaBB, AaBb, Aabb, aaBB, aaBb, and, aabb, the number of which we denote by $x_{11}, x_{12}, \cdots, x_{33}$ respectively. Therefore the number of AB (resp. Ab, aB, ab) gametes in gamete pool is given by fu_1 (resp. fu_2, fu_3, fu_4) where the u_i's were defined in (5.2) and f is the common fertility of the genotypes. The total number of gametes in the gamete pool is given by $fu_1 + fu_2 + fu_3 + fu_4 = fx$. By random union of gametes, the proportion of AABB genotype produced is: $(\frac{fu_1}{fx})(\frac{fu_1}{fx}) = \frac{u_1^2}{x^2}$. Similarly one can arrive at the other coefficients of B(x) in system (5.1) this way.

The alternative derivation given in Appendix 1 can also be carried out. Since it is lengthy but similar, we will not write it down here.