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Global attractors for a discrete selection model with periodic immigration

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A one-island selection-migration model is used to study the periodic immigration of a population of fixed allele frequency into a natural population. Density-dependent selection and immigration are the primary factors affecting the demographic and genetic change in the island population. With the assumptions of complete dominance (CD) or no dominance (ND) and homozygote superiority in fitness, the existence and location of global attractors are established. Analysis of this model provides rudimentary information about the migration of transgenes into a natural population.

Keywords: Natural selection; Periodic immigration; Complete dominance; No dominance; Global attractor

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1. Introduction

Natural selection and immigration are two forces that can profoundly affect the genetic composition of populations [6,17]. If immigrants come from a population of individuals with fitness characteristics different from those of individuals in the recipient population, for example, because of genetic transformation, genes affecting fitness in the former population may become established in the latter, e.g., see [2,3,16]. Understanding how such gene movement influences gene frequency in the recipient population is important because of the way it impacts genetic variability and mean population fitness. How the migration rate and migrating allele frequency affect the type and location of attractors in a natural population is currently unknown.

To study this process in the simplest setting we consider the one-island model discussed by Roberds and Selgrade, see Refs [11,15], for a diploid population with two alleles, A and a, at a single locus. In each generation a population of constant allele frequency migrates into the island from an external source and reproduces with the island population. This model is a discrete-time system of two nonlinear difference equations which track the A allele frequency p and island population density or size x over generations. For this study, we assume that density-dependent selection and immigration are the primary factors affecting the demographic and genetic

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evolution of the island population. Because of periodic environmental factors such as seasons, climate and food supply, we permit periodic variations in the immigration.

Such a model might represent the migration into a natural population of a population with a genetically engineered gene, a transgene. Other discrete models have been proposed to investigate the mixing of transgenic and natural populations. For instance, Li [8,9] studied three-dimensional models which track population numbers of the three genotypes for the interaction between transgenic mosquitoes resistant to malaria and the wild type nonresistant mosquitoes. Li [9] discovered tristable equilibrium behavior and chaotic behavior in genotype numbers. His models have neither an immigration term nor periodicity.

In this paper, Section 2 discusses model background and development. In Section 3, we introduce two classical types of fitness relationships (complete dominance (CD) and no dominance (ND)). Section 4 proves the existence of global attractors for models with these fitness restrictions and calculates attractor approach rates. If q denotes the constant A allele frequency in the immigrating population then the global attractor is contained within either the region where $p < q$ or the region where $p > q$, depending on which homozygote fitness dominates. Section 5 provides examples of cyclic attractors and chaotic attractors. Section 6 considers immigration of a transgene A by assuming that the island population is devoid of the A allele, i.e. the initial condition for p is zero, and by allowing immigration with a large A allele frequency q. Because a transgene may confer a fitness advantage, we assume CD of the AA-genotype. Then the results of Section 4 are used to estimate the rate of evolution of the system toward the attractor in the region where $p > q$. In fact, numerical simulations of an example where immigration is constant and the attractor is an equilibrium indicate that the evolution is much more rapid than the crude estimates of Section 4. Hence, for this model an immigrating transgene exhibiting CD will ultimately maintain itself in the natural population with at least the frequency that it enters the population.

2. Model background

For the one island model, the island population density or size x consists of individuals with one of three genotypes, AA, Aa or aa. Let p denote the frequency of the A allele in the island population, where $0 \leq p \leq 1$, and hence $1 - p$ is the frequency of the a allele. The effects of density-dependent natural selection determine an average per capita replacement rate or *fitness* $f_{ij}(x)$ for the ij-genotype, where $i, j = $ A, a, which measures fertility and viability of that genotype. Allele fitnesses f_A and f_a are linear combinations of genotype fitnesses weighted by allele frequency and are defined by $f_A \equiv pf_{AA} + (1 - p)f_{Aa}$ and $f_a \equiv pf_{Aa} + (1 - p)f_{aa}$. The population mean fitness f is given by $f \equiv pf_A + (1 - p)f_a$.

Following selection in each generation, assume gametes are contributed to the island population by immigration from a population with constant allele frequency q where $0 \leq q \leq 1$. Random mating occurs following migration so that the number of additional zygotes in the next generation produced as a consequence of immigration is denoted by y. The following system of difference equations describes changes in allele frequency and population size between generations n and $n + 1$, see Refs [11,15]:

$$p_{n+1} = \frac{p_n x_n f_A + qy}{x_n f + y}$$

$$x_{n+1} = x_n f + y. \tag{1}$$

When $y = 0$, this system is identical to the system previously studied for density-dependent selection, e.g. see Ref. [13].

Because periodic variations may affect ecosystem behavior, Costantino *et al.* [1], King and Schaffer [10], Henson [7], Selgrade and Roberds [14] and others have investigated the effects of periodic fluctuations in ecosystem parameters. Here we allow for periodic immigration. For a positive integer k and $0 \leq \alpha < 1$, to study immigration of period k, we multiply the constant immigration y by the factor $1 + \alpha g_k(n)$ where $-1 \leq g_k(n) \leq 1$ and $g_k(n + k) = g_k(n)$ for $n = 0, 1, 2, \ldots$. This provides immigration of period k varying between $y(1 + \alpha)$ and $y(1 - \alpha)$. Hence αy is the maximum variation in migration from the amount y. If $\sum_{n=0}^{k-1} g_k(n) = 0$, e.g. when $g_k(n) = \sin(2\pi n/k)$, then the average immigration over the time period k is y. For $g_2(n) = (-1)^n$, the immigration has period 2. The system of difference equations corresponding to equation (1) that represents immigration of period k may be written as:

$$p_{n+1} = \frac{p_n x_n f_A + qy(1 + \alpha g_k(n))}{x_n f + y(1 + \alpha g_k(n))}$$

$$x_{n+1} = x_n f + y(1 + \alpha g_k(n)). \tag{2}$$

It is convenient both mathematically and biologically to introduce a per capita migration rate for $x > 0$ given by

$$h(x) \equiv \frac{y}{x},$$

which measures a constant per capita migration per generation relative to the island population size x. Since y is constant, $h(x)$ is a decreasing function of population size, i.e. $h'(x) = -y/x^2 < 0$. After replacing y by $xh(x)$ in equation (2), the transition equations become

$$p_{n+1} = \frac{p_n f_A(p_n, x_n) + qh(x_n)(1 + \alpha g_k(n))}{f(p_n, x_n) + h(x_n)(1 + \alpha g_k(n))}$$

$$x_{n+1} = x_n(f(p_n, x_n) + h(x_n)(1 + \alpha g_k(n))). \tag{3}$$

In equation (3), $f + h(1 + \alpha g_k(n))$ denotes the per capita transition function for the island population. Repeated iteration of equation (3) yields an orbit $\{(p_n, x_n) : n = 0, 1, 2, \ldots\}$ for this two-dimensional, time-dependent dynamical system which is equivalent to equation (2) for $x > 0$. Henceforth, we study the behavior of equation (3).

3. Assumptions for dominance in fitness

When $\alpha = 0$ the phase space for system (3) is the slot in the (p, x)-plane designated by

$$S \equiv \{(p, x) : 0 \leq p \leq 1, 0 < x\}.$$

When $y = 0$ (i.e. $h = 0$), the boundary lines of S, $\{p = 0\}$ and $\{p = 1\}$, represent allele fixation and, therefore, are invariant. If $y > 0$ and $0 < q < 1$, points on these vertical boundaries of S are mapped into the interior of S. Because the dynamical system (3) is time-dependent, different orbits may intersect when plotted in S. Including time as an additional phase variable will remedy this situation. Franke and Selgrade [5] discuss a useful framework for studying this time-periodic dynamical system by considering the corresponding

autonomous dynamical system on the cylinder space defined as the Cartesian product $\mathcal{X}$ of S and the discrete space $\{0, 1, \ldots, k - 1\}$ representing time with the usual product topology, i.e.

$$\mathcal{X} \equiv \{0, 1, \ldots, k - 1\} \times S.$$

$\mathcal{X}$ consists of k copies of S referred to as fibers and orbits of equation (3) move from fiber to fiber in a k-periodic fashion because the time coordinate is taken modulo k (figure 1).

An equilibrium E is an allele frequency $\bar{p}$, $0 \leq \bar{p} \leq 1$, and a population density $\bar{x} > 0$ which remain constant across generations, i.e. $p_n = \bar{p}$ and $x_n = \bar{x}$ for all n. Such an E is said to be *polymorphic* if $0 < \bar{p} < 1$. From equation (3), an equilibrium $E = (\bar{p}, \bar{x})$ must satisfy the following system for all n:

$$\begin{aligned}
\bar{p} &= \bar{p} f_A(\bar{p}, \bar{x}) + qh(\bar{x})(1 + \alpha g_k(n)) \\
1 &= f(\bar{p}, \bar{x}) + h(\bar{x})(1 + \alpha g_k(n)).
\end{aligned} \tag{4}$$

Clearly, the second equation in equation (4) will not be satisfied for all n since g_k depends on n. Hence, equation (3) will have equilibria only if $\alpha = 0$. Although equation (3) with time-dependent immigration will not have equilibria, this dynamical system may have attracting cycles or more general attractors.

The level or degree of dominance with regard to genetic control of fitness has been shown to influence profoundly the properties of equilibria resulting from the joint effects of migration and selection, e.g. see Hedrick [6]. Here we study stable dynamical behavior for two levels of dominance when selection is density-dependent. First, we consider the case where genotypic fitnesses exhibit complete dominance (CD). We assume that the presence of the allele A confers maximal fitness on a genotype. Thus, for all $x > 0$ or all x within an invariant set, we take

$$f_{AA}(x) = f_{Aa}(x) > f_{aa}(x). \tag{CD}$$

With CD allele and mean fitnesses become

$$\begin{aligned}
f_A &= f_{AA} \\
f_a &= p f_{AA} + (1 - p) f_{aa} \\
f &= p(2 - p) f_{AA} + (1 - p)^2 f_{aa}.
\end{aligned} \tag{5}$$

For the second case, we assume that the heterozygote fitness is the average of the homozygote fitnesses, i.e. for all $x > 0$

$$f_{Aa}(x) = (f_{AA}(x) + f_{aa}(x))/2. \tag{ND}$$

In this case the fitnesses are said to be *additive* or to exhibit no dominance (ND). See Falconer and Mackay [4] or Roughgarden [12] for application of this classical concept to selection theory in population genetics. Allele and mean fitnesses become

$$\begin{aligned}
f_A &= p(f_{AA} - f_{aa})/2 + (f_{AA} + f_{aa})/2 \\
f_a &= (1 - p)(f_{aa} - f_{AA})/2 + (f_{AA} + f_{aa})/2 \\
f &= p f_{AA} + (1 - p) f_{aa}.
\end{aligned} \tag{6}$$

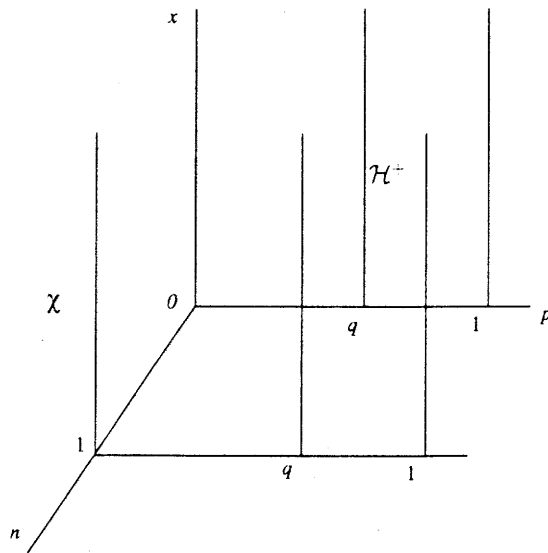In the next section, we show that these dominance properties restrict the positions of attractors for equation (3).

Figure 1.   Phase space $\mathcal{X}$ and region $\mathcal{H}^+$ for period-2 immigration.

4. Attracting regions

Because of these dominance assumptions, the evolutionary behavior of the system is determined by the relative fitnesses of the homozygotes and the frequency of the immigrating allele. We show that if $f_{AA} \geq f_{aa}$ then all attractors are contained within the region where $p \geq q$ and if $f_{aa} \geq f_{AA}$ then all attractors are contained within the region where $p \leq q$.

Biological considerations indicate that if the fitness of the homozygote AA dominates that of the homozygote aa (i.e. $f_{AA} \geq f_{aa}$) and that if in each generation the A allele enters the island population at a frequency q then the frequency of A in the island population should never fall below q if it starts above q and the frequency of A should increase if it starts below q. An analogous statement applies when the fitness of the homozygote aa dominates that of the homozygote AA. These assertions are detailed in the following two results. First, the plane $\{p = q\}$ divides the region $\mathcal{X}$ into two subregions (figure 1):

$$\mathcal{H}^+ \equiv \{(n, p, x) : 0 \leq n \leq k - 1, q \leq p \leq 1, 0 < x\} \quad \text{and}$$

$$\mathcal{H}^- \equiv \{(n, p, x) : 0 \leq n \leq k - 1, 0 \leq p \leq q, 0 < x\}.$$

For any set Λ the topological *interior* and *closure* of Λ are denoted Int Λ and Cl Λ, respectively. A set Λ is *invariant* if for each $(p_0, x_0) \in \Lambda$ then $(p_n, x_n) \in \Lambda$ for all $n \geq 0$. Equilibria, cycles and attractors are examples of invariant sets.

LEMMA 4.1.   *Assume CD or ND for all $x > 0$ and that $0 < q < 1$. If $f_{AA}(x) \geq f_{aa}(x)$ for all $x > 0$ then Int $\mathcal{H}^+$ and $\mathcal{H}^+$ are invariant regions. If $f_{aa}(x) \geq f_{AA}(x)$ for all $x > 0$ then Int $\mathcal{H}^-$ and $\mathcal{H}^-$ are invariant regions.*

Proof. For the assertion about the Int $\mathcal{H}^+$, we show that if $p_n > q$ then $p_{n+1} > q$ for $n \geq 0$. Since

$$p_{n+1} = \frac{p_n f_A + qh(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} = q\left[\frac{(p_n/q)f_A + h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))}\right] \qquad (7)$$

we need to show that the bracketed term in equation (7) is greater than 1. This is equivalent to

$$\frac{p_n}{q}f_A - f > 0 \qquad (8)$$

Since $p_n > q$ and $f_{AA}(x_n) \geq f_{aa}(x_n)$, we have

$$\frac{p_n}{q}f_A - f > f_A - f.$$

Then equation (8) holds because

$$f_A - f = \begin{cases} [f_{AA}(x_n) - f_{aa}(x_n)](1 - p_n)^2 \geq 0 & \text{if (CD) holds} \\ [f_{AA}(x_n) - f_{aa}(x_n)](1 - p_n)/2 \geq 0 & \text{if (ND) holds} \end{cases} \qquad (9)$$

Also, if $p_n < 1$ then clearly $p_{n+1} < 1$. Thus Int $\mathcal{H}^+$ is invariant. If we assume that $p_n \geq q$ then the preceding strict inequalities are weakened, which gives that $p_{n+1} \geq q$, i.e. that $\mathcal{H}^+$ is invariant.

To prove the assertions about $\mathcal{H}^-$ we reverse the preceding inequalities using the assumptions that $p_n < q$ and $f_{aa}(x) \geq f_{AA}(x)$.   □

Notice that $x_n \geq y(1 - \alpha)$ for $n \geq 1$ because of the immigration. Hence, after the first iterate, the inequalities on fitnesses need hold only for $x \geq y(1 - \alpha)$ to obtain inequalities on frequency iterates as summarized in the following corollary.

COROLLARY 4.2.   *Assume CD or ND for all $x > 0$ and that $0 < q < 1$. If $f_{AA}(x) \geq f_{aa}(x)$ for all $x \geq y(1 - \alpha)$ and $q < p_n < 1$ then $q < p_{n+1}$ for all $n \geq 1$. If $f_{aa}(x) \geq f_{AA}(x)$ for all $x \geq y(1 - \alpha)$ and $0 < p_n < q$ then $p_{n+1} < q$ for all $n \geq 1$.*

Also, with similar assumptions on fitness, a solution orbit in the complement of $\mathcal{H}^+$ or $\mathcal{H}^-$ iterates monotonically in p_n toward $\mathcal{H}^+$ or $\mathcal{H}^-$ as follows:

LEMMA 4.3.   *Assume CD or ND for all $x > 0$ and that $0 < q < 1$. If $f_{AA}(x) \geq f_{aa}(x)$ for all $x \geq y(1 - \alpha)$ and $p_n < q$ for $n \geq 1$ then $p_n < p_{n+1}$. If $f_{aa}(x) \geq f_{AA}(x)$ for all $x \geq y(1 - \alpha)$ and $p_n > q$ for $n \geq 1$ then $p_n > p_{n+1}$.*

Proof. For the first assertion we need to establish the inequality

$$p_{n+1} = p_n\left[\frac{f_A + \frac{q}{p_n}h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))}\right] > p_n. \qquad (10)$$

which is equivalent to showing

$$\frac{f_A + (q/p_n)h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} > 1. \tag{11}$$

Clear the denominator, move all terms to the right and substitute genotype fitnesses into equation (11) to get

$$0 > h(x_n)(1 + \alpha g_k(n))\frac{(p_n - q)}{p_n} + \begin{cases} [f_{aa}(x_n) - f_{AA}(x_n)](1 - p_n)^2 & \text{if (CD)} \\ [f_{aa}(x_n) - f_{AA}(x_n)](1 - p_n)/2 & \text{if (ND)} \end{cases} \tag{12}$$

But equation (12) is true when $f_{AA}(x_n) \geq f_{aa}(x_n)$ and $p_n < q$. Reversing the inequalities in equations (10)–(12) proves the second assertion. □

Because of environmental limitations, it is biologically reasonable to assume that the population size x is bounded for all generations. An assumption about genotype fitnesses which will guarantee this is:

There exists $B > 0$ so that $xf_{AA}(x) < B$ *and* $xf_{aa}(x) < B$ for all $x > 0$. (A1)

From (A1), it follows that the genotype fitnesses are bounded and approach zero as $x \to \infty$. In many applications, it is assumed that the fitnesses are decreasing functions of x but that assumption is not needed here. Also (A1) implies that $x_n f(p_n, x_n) \leq B + y(1 + \alpha)$ for all n and hence all solutions to equation (2) are bounded. In fact, if the interval $\mathcal{J} \equiv [y(1 - \alpha), y(1 + \alpha) + B]$ then we have:

LEMMA 4.4. *If equation (3) satisfies (A1) and either CD or ND for all $x > 0$ then each solution (p_n, x_n) is contained in the rectangle $\mathcal{R} \equiv [0, 1] \times \mathcal{J}$ for all $n \geq 1$.*

Since solutions to equation (3) are contained in a compact set $\mathcal{R}$, the next Lemma estimates the rate of increase or decrease of p_n as indicated in Lemma 4.3.

LEMMA 4.5. *Assume (A1) and either CD or ND for all $x > 0$ and $0 < q < 1$. If $f_{AA}(x) > f_{aa}(x)$ for all $x \in \mathcal{J}$ then there is $r > 0$ so that $p_n \leq q$ where $n \geq 1$ implies that $p_{n+1} \geq p_n(1 + r)$. If $f_{aa}(x) > f_{AA}(x)$ for all $x \in \mathcal{J}$ then there is $s > 0$ so that $p_n \geq q$ where $n \geq 1$ implies that $1 - p_{n+1} \geq (1 - p_n)(1 + s)$. Also, r and s are independent of p_n.*

Proof. First assume that $f_{AA}(x) > f_{aa}(x)$ for all $x \in \mathcal{J}$. From equation (3) it follows that

$$p_{n+1} = p_n \left[1 + \frac{f_A - f + ((q/p_n) - 1)h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} \right]. \tag{13}$$

For the fractional expression in equation (13) we wish to minimize the numerator and maximize the denominator. Let $\min_1$ denote $\min_{x \in \mathcal{J}}(f_{AA}(x) - f_{aa}(x))$. Since $(p_n, x_n) \in \mathcal{R}$ for $n \geq 1$ and $p_n \leq q$, when CD holds we have that

$$(1 - q)^2 \min_1 \leq (1 - p_n)^2 (f_{AA}(x_n) - f_{aa}(x_n)) + h(x_n)(1 + \alpha g_k(n))(q - p_n)/p_n$$

$$= f_A - f + h(x_n)(1 + \alpha g_k(n))(q - p_n)/p_n \tag{14}$$

or when ND holds we have that

$$(1 - q)\min_1/2 \leq (1 - p_n)(f_{AA}(x_n) - f_{aa}(x_n))/2 + h(x_n)(1 + \alpha g_k(n))(q - p_n)/p_n$$

$$= f_A - f + h(x_n)(1 + \alpha g_k(n))(q - p_n)/p_n. \tag{15}$$

To bound the denominator note that $x_n \geq y(1 - \alpha)$ so

$$f(p_n, x_n) + h(x_n)(1 + \alpha g_k(n)) \leq f_{AA}(x_n) + \frac{1 + \alpha}{1 - \alpha} \leq \frac{1 + \alpha}{1 - \alpha} + \max_{x \in \mathcal{J}} f_{AA}(x). \tag{16}$$

When CD holds then $r > 0$ is defined by

$$r = \frac{(1 - q)^2\min_1}{((1 + \alpha)/(1 - \alpha)) + \max_{x \in \mathcal{J}} f_{AA}(x)} \tag{17}$$

or when ND holds then $r > 0$ is defined by

$$r = \frac{(1 - q)\min_1/2}{\frac{1+\alpha}{1-\alpha} + \max_{x \in \mathcal{J}} f_{AA}(x)}. \tag{18}$$

Thus from the preceding inequalities it follows that

$$p_{n+1} \geq p_n(1 + r). \tag{19}$$

Now assume that $f_{aa}(x) > f_{AA}(x)$ for all $x \in \mathcal{J}$. Define $v_n = 1 - p_n$ and note that

$$v_{n+1} = \frac{v_n f_a + (1 - q)h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))}.$$

We have the following expression for v_{n+1} similar to equation (13) for p_{n+1}

$$v_{n+1} = v_n\left[1 + \frac{f_a - f + (((1 - q)/v_n) - 1)h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))}\right]. \tag{20}$$

Since $p_n \geq q$ then $v_n \leq 1 - q$. If $\min_2$ denotes $\min_{x \in \mathcal{J}}(f_{aa}(x) - f_{AA}(x))$ then when ND holds we have that

$$q\min_2/2 \leq (1 - v_n)(f_{aa}(x_n) - f_{AA}(x_n))/2 + h(x_n)(1 + \alpha g_k(n))(1 - q - v_n)/v_n$$

$$= f_a - f + h(x_n)(1 + \alpha g_k(n))(1 - q - v_n)/v_n \tag{21}$$

and

$$f(p_n, x_n) + h(x_n)(1 + \alpha g_k(n)) \leq f_{aa}(x_n) + \frac{1 + \alpha}{1 - \alpha} \leq \frac{1 + \alpha}{1 - \alpha} + \max_{x \in \mathcal{J}} f_{aa}(x). \tag{22}$$

If $s > 0$ is defined by

$$s = \frac{q\min_2/2}{\frac{1-\alpha}{1-\alpha} + \max_{x \in \mathcal{J}} f_{aa}(x)}. \tag{23}$$

then from equations (20) to (22) we have

$$1 - p_{n+1} \geq (1 - p_n)(1 + s). \tag{24}$$

This completes the argument.   □

The bounds r and s in Lemma 4.5 are rather crude for estimating the number of generations required to approach an attractor (see the example in Section 6). In part, this is because max's and min's are taken over all $\mathcal{J}$. However, these exponential rates allow us to prove the existence of global attractors.

THEOREM 4.6. *Assume* (A1) *and either CD or ND for all $x > 0$ and that $0 < q < 1$. If $f_{AA}(x) > f_{aa}(x)$ for all $x \in \mathcal{J}$ then equation* (3) *has a global attractor in* Int $\mathcal{H}^+$. *On the other hand, if $f_{aa}(x) > f_{AA}(x)$ for all $x \in \mathcal{J}$ then equation* (3) *has a global attractor in* Int $\mathcal{H}^-$.

Proof. For a solution to equation (3), Lemma 4.4 asserts that $(p_n, x_n) \in \mathcal{R}$ for all $n \geq 1$. By Lemma 4.5, if $f_{AA}(x) > f_{aa}(x)$ and $p_n \leq q$ for all n then p_n grows exponentially. This contradicts the fact that p_n is bounded by 1. Hence there is N so that $p_N > q$. By Corollary 4.2, $p_n > q$ for all $n \geq N$. Hence, the open set $U \equiv (q, 1) \times (y(1 - \alpha), y(1 + \alpha) + B)$ is a trapping region and the intersection of all forward iterates of Cl U is the global attractor.

On the other hand, if $f_{aa}(x) > f_{AA}(x)$ and $p_n \geq q$ for all n then p_n will decrease exponentially by Lemma 4.5, which is not possible. Hence there is N so that $p_n < q$ for all $n \geq N$. Thus the open set $V \equiv (0, q) \times (y(1 - \alpha), y(1 + \alpha) + B)$ is a trapping region and the intersection of all forward iterates of Cl V is the global attractor. $\square$

5. Examples of no dominance (ND)

If ND is assumed, a variety of attractors may occur and variations in allele frequency on the attractor depends on the relationship between the homozygote genotype fitnesses in accordance with Theorem 4.6. Here we discuss several examples where k-periodic immigration is obtained by taking $g_k(n) = \cos(2\pi n/k)$ for $n = 0, 1, 2, \ldots$.

If $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$ then the global attractor is a subset of Int $\mathcal{H}^+$, i.e. $p_n > q$ on the attractor. Let $y = 1$, $q = 0.2$ and take

$$f_{AA}(x) = e^{1.8 - 0.5x} \quad \text{and} \quad f_{aa}(x) = e^{1.0 - 0.5x}. \tag{25}$$

If the immigration is constant ($\alpha = 0$) then for fitnesses (25) the global attractor is the equilibrium at $(p, x) \approx (0.448, 3.54)$, see figure 2(a). If α increases from zero and immigration is 2-periodic then a bifurcation occurs resulting in a stable 2-cycle. Such bifurcations are expected and discussed in Selgrade and Roberds [14] and in Franke and Selgrade [5]. Figure 2(b) depicts this 2-cycle when $\alpha = 0.5$. If the immigration is period-5 then the atractor is a 5-cycle as seen in figure 2(c), (d). Note that in figure 2(c), $q = 0.2$ so $p_n > 0.2$ on the 5-cycle but in figure 2(d), $q = 0.8$ so $p_n > 0.8$.

A chaotic attractor may occur if the larger fitness considered as the per capita transition function for a single population gives a chaotic one-hump map. For instance, take

$$f_{AA}(x) = e^{1-x} \quad \text{and} \quad f_{aa}(x) = e^{3.1 - 0.3x}. \tag{26}$$

Note that $f_{aa}(x) > f_{AA}(x)$ for all $x > 0$ and that map $xf_{aa}(x)$ is a chaotic one-hump map. For our selection-migration model, if $y = 0.1$, $q = 0.92$ and immigration is constant then the global attractor is chaotic, see figure 3(a). When $\alpha = 0.5$ and $k = 2$, the attractor for the resulting 2-periodic immigration consists of two subsets (figure 3(b)) which iterate to each
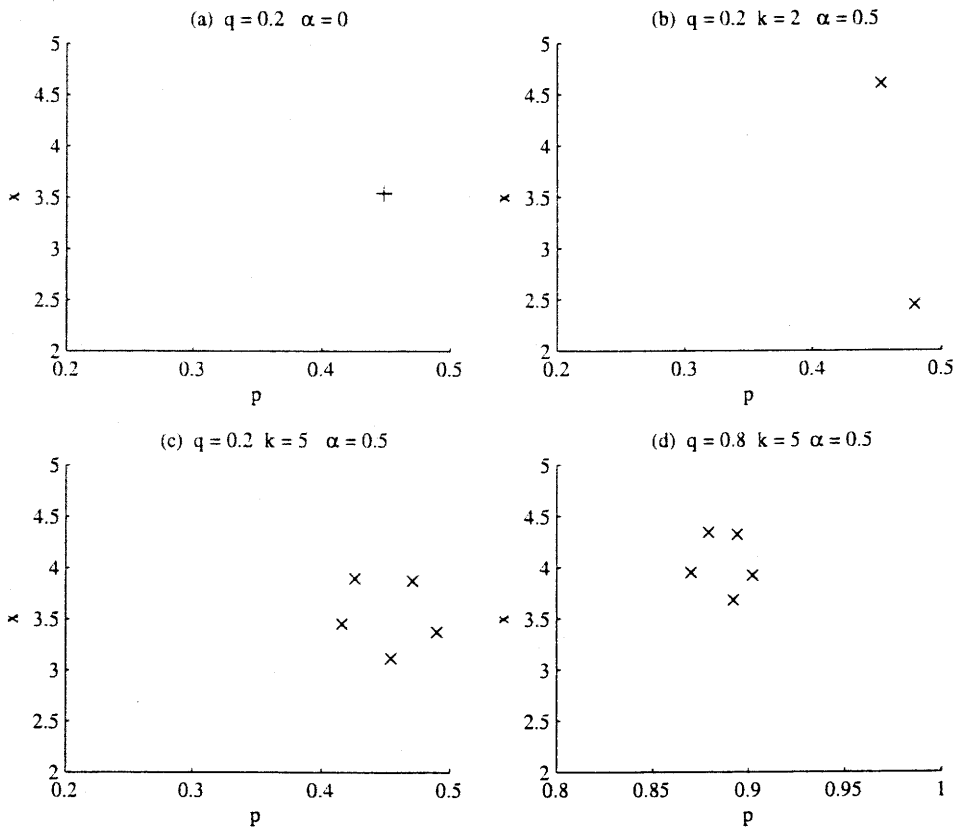
Figure 2. Global attractors for fitnesses (25). + denotes an attracting equilibrium. × denotes a point on an attracting 2- or 5-cycle.
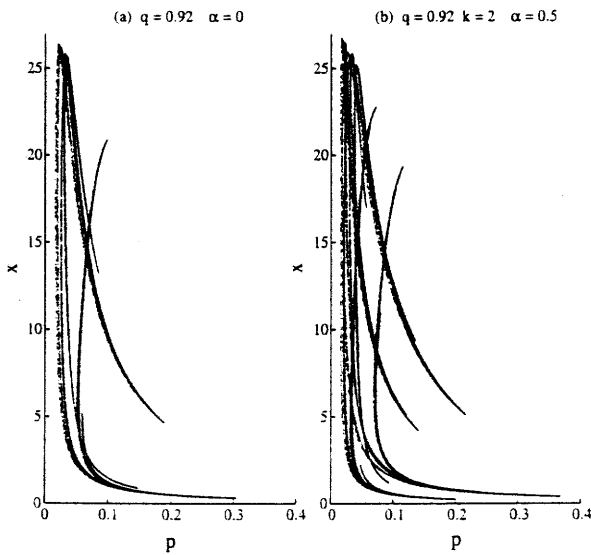

Figure 3. Global, chaotic attractors for fitnesses (26).

other and each is similar to the chaotic attractor in figure 3(a). In more restrictive settings, Franke and Selgrade [5] have shown that each subset of the attractor for the time-dependent system is homeomorphic to the attractor for the time-independent system.

6. Examples of complete dominance (CD) and transgenic immigration

Suppose the transgene A confers a fitness advantage to the genotype which possesses it. Hence, to use this one-island selection-migration model to study the migration of a transgene into a natural population, we assume CD in fitness, i.e. $f_{AA} = f_{Aa} > f_{aa}$. Then the aa genotype represents the natural population. Hence, system (2) may model transgene immigration if a population with large A allele frequency q enters a population consisting only of the aa genotype, i.e. $p_0 = 0$. It follows that

$$p_1 = \frac{qy}{x_0 f_{aa}(x_0) + y} \geq \frac{qy}{y + \max_{x \geq 0} x f_{aa}(x)}. \tag{27}$$

Here we assume that immigration is constant ($\alpha = 0$), not periodic in time. Let $y = 1$, $q = 0.9$ and take

$$f_{AA}(x) = e^{1-x} \quad \text{and} \quad f_{aa}(x) = e^{1-3x}. \tag{28}$$

In this case, since $\max_{x \geq 0} x f_{aa}(x) \approx 0.34$ then equation (27) implies that $p_1 > 0.67$. Using equation (17) of Lemma 4.5, we compute $r \approx 0.002$. Hence, an orbit starting with $p = 0.67$ would require 147 iterates before p_n is larger than $q = 0.9$. However, numerical simulations indicate that an orbit with initial frequency $p_0 = 0$ reaches frequency 0.9 within five iterates. Figure 4 depicts three representative orbits approaching the attracting equilibrium at $(\bar{p}, \bar{x}) = (0.906, 1.80)$.

Thus, after several generations, a transgene exhibiting CD will maintain itself in the natural population with at least the frequency that it enters the population. This will also occur if ND holds but the transgene homozygote fitness, f_{AA}, is always larger than the fitness
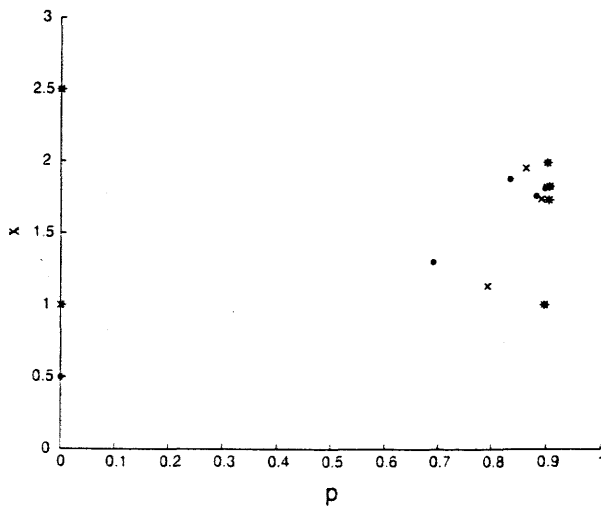

Figure 4. For fitnesses (28), five iterates of three orbits with $p_0 = 0$ approaching the equilibrium $(\bar{p}, \bar{x}) = (0.906, 1.80)$. $x_0 = 0.5$ for (•). $x_0 = 1$ for (×) and $x_0 = 2.5$ for (*).

for the other homozygote, f_{aa}. The example in the next section shows that the location of the attractor is more subtle if homozygote fitness superiority does not hold for all x.

7. Conclusion and future directions

With the homozygote superiority assumed here, we establish the existence of global attractors in regions bounded by the immigrating allele frequency q and we calculate attractor approach rates. However, if the homozygote fitness curves intersect and cross then the hypotheses of Theorem 4.6 are not satisfied. Are there conditions on such fitnesses which will predict the positions of attractors? Consider a ND model with $y = 0.1$, $q = 0.5$, and

$$f_{AA}(x) = e^{1.5-0.15x} \quad \text{and} \quad f_{aa}(x) = e^{3-0.3x}. \tag{29}$$

With these fitnesses and constant immigration ($\alpha = 0$), the population size x remains in the interval $[0, 25]$. From their graphs (figure 5), it is clear that $f_{aa}(x)$ is much larger than $f_{AA}(x)$ for most of the range $0 < x < 10$ and, after crossing at $x \approx 10$, $f_{aa}(x)$ and $f_{AA}(x)$ are almost equal for $10 < x < 25$. Because of apparent fitness superiority of the aa-genotype, one would intuitively suspect that the aa-genotype would dominate the AA-genotype and the global attractor would be located where $p < q = 0.5$. However, numerical simulations indicate that the global attractor is the 2-cycle $\{(p_0, x_0) = (0.5347, 14.85), (p_1, x_1) = (0.6173, 5.5478)\}$ where $p > 0.5$. Thus, the size of the area between the homozygote fitness curves determines neither genotype dominance nor attractor location. Investigating the position of attractors when the homozygote fitness curves cross will be the topic of future studies.

Also, in order to consider more general heterozygote behavior, i.e. not assume that CD or ND holds, it would be useful to consider three-dimensional models which track genotype population numbers like Li [9]. In these models, migration terms may be included, different mating schemes proposed and post- or pre-selection migration investigated.
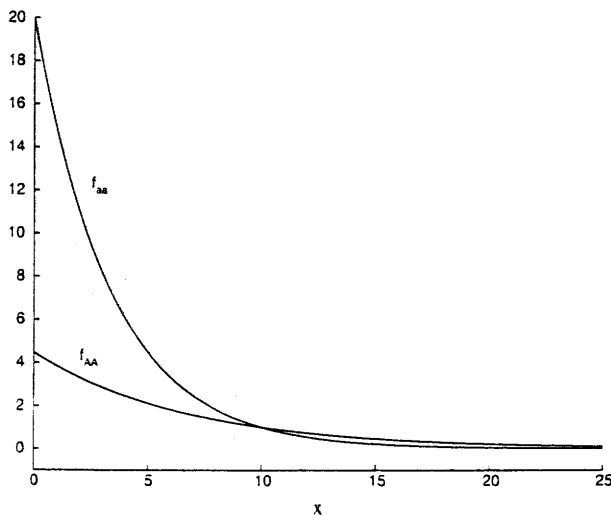

Figure 5. Crossing fitnesses (29)

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