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# EQUILIBRIUM AND NONEQUILIBRIUM ATTRACTORS FOR A DISCRETE, SELECTION-MIGRATION MODEL

*To Paul Waltman on the occasion of his retirement and to the memory of Geoffrey J. Butler.*

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ABSTRACT. This study presents a discrete-time model for the effects of selection and immigration on the demographic and genetic compositions of a population. Under biologically reasonable conditions, it is shown that the model always has an equilibrium. Although equilibria for similar models without migration must have real eigenvalues, for this selection-migration model we illustrate a Hopf bifurcation which produces long-term stable oscillations in allele frequency and population density. The interplay between the selection parameters in the fitness functions and the migration parameters is displayed by using migration parameters to reverse destabilizing bifurcations that occur as intrinsic density parameters are varied. Also, the rich dynamics for this selection-migration model are illustrated by a period-doubling cascade resulting in a pulsating strange attractor.

**1 Introduction** Natural selection and migration can act jointly to shape the demographic and genetic compositions of a population. A number of models have been proposed to study allele frequency dynamics associated with the combined action produced by natural selection and migration. The simplest of these is the one-island or continent-island model in which a single population is the recipient of immigrants from a large nearby population. Effects of selection together with migration in an island model of this type were first reported by Haldane [**8**] and Wright [**28, 29**]. Both obtained equilibrium solutions for allele frequencies in discrete-time models. Their studies did not consider effects

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on population size, but were entirely focused on allele frequency behavior under constant selection. In this setting, they demonstrated that equilibrium allele frequencies are primarily influenced by the strength of migration compared to selection plus the degree of dominance for genotype fitnesses (Hedrick [**11**]). Similar results were obtained by Nagylaki [**16**] for weak selection in a continuous-time model of comparable form.

The value of concurrently studying the effect of natural selection on genetic composition and on population size for obtaining a better understanding of evolutionary behavior has been pointed out by Roughgarden [**19**] and Ginzburg [**7**]. A key feature of methods used to investigate such joint behavior is that population size is treated both as a variable of primary interest and as a factor that affects individual fitness. Because of its effect on fitness, population size influences genotype frequencies in populations and thus allele frequencies. In this paper (also see Roberds and Selgrade [**18**]), we take an additional step toward understanding complex evolutionary dynamics by introducing migration effects into the study of density-dependent selection. We analyze allele frequency and population size dynamics resulting from the combined effects of migration and density-dependent selection in a discrete, one-island migration model.

Section 2 presents the model and discusses historical background. Analysis of equilibria is carried out in Section 3. In particular, it is shown that the model always has a polymorphic equilibrium under biologically reasonable assumptions. Equilibria for the model without migration must have real eigenvalues [**22**]. However, with migration, eigenvalues may be complex and we illustrate Hopf bifurcation in Section 4, which produces long-term stable oscillations in allele frequency and population density. In Section 5, we exhibit the rich dynamics for this selection-migration model by discussing a period-doubling cascade which results in a pulsating strange attractor. Finally, we show that destabilizing bifurcations that occur as intrinsic density parameters are varied may be reversed by varying migration parameters. This emphasizes the interplay between the selection parameters in the fitness functions and the migration parameters.

**2 Model ackground** A simple setting for studying allele frequency variation consists of a diploid population with two alleles, $A$ and $a$, at a single autosomal locus. Hence, the population consists of individuals with one of three genotypes, $AA$, $Aa$, or $aa$. Let $p$ denote the frequency of the $A$ allele, where $0 \leq p \leq 1$, and hence $1 - p$ is the frequency of the

$a$ allele. Evolutionary pressures due to natural selection determine an average per capita replacement rate or *fitness* $f_{ij}$ 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 $f_A \equiv p f_{AA} + (1-p) f_{Aa}$ and $f_a \equiv p f_{Aa} + (1-p) f_{aa}$. Accordingly, the population mean fitness $f$ is given by $f \equiv p f_A + (1-p) f_a$. In the original theory developed by Fisher [**4**], Haldane [**9**] and Wright [**28**], migration was ignored and genotype fitnesses were constants. Assuming random mating, the following difference equation describes a discrete-time model where changes in allele frequency $p$ take place from one generation to the next:

$$p' = \frac{p\, f_A(p)}{f(p)} \tag{1}$$

Here $p'$ denotes allele frequency in the next generation. Repeated iteration of (1) produces an orbit denoted by $\{p_n : n = 0, 1, 2, ...\}$ that represents the evolution of allele frequency over time. For this case, Fisher's fundamental theorem asserts that mean fitness $f$ increases along orbits, i.e., the population evolves to increase mean fitness. For a more detailed discussion see Roughgarden [**19**].

More recent developments involve dynamics produced by demographic effects acting under the influence of genetic factors. In models constructed to investigate these dynamics, genotype fitness is assumed to vary as a function of population size and two-dimensional systems of equations have been used to track concurrent changes in allele frequency $p$ and population size $x$. The following system of difference equations describes the appropriate discrete-time model:

$$\begin{aligned} p' &= \frac{p\, f_A(p,x)}{f(p,x)} \\ x' &= x\, f(p,x)\,. \end{aligned} \tag{2}$$

Here $p'$ and $x'$ represent allele frequency and population size in the next generation and system (2) is said to model density-dependent selection. Properties of equilibria have been investigated in both this discrete-time model and the analogous continuous-time differential equation model. Analyses of the system of difference equations (2) revealed that a stable equilibrium maximizes population size along the curve defined by mean fitness equals one and occurs only in the presence of heterozygote superiority in fitness at equilibrium (see Asmussen and Feldman [**3**], Roughgarden [**19**], Asmussen [**2**], or Selgrade and Namkoong [**22**]). Similar behavior was found for the analogous system of differential equations, except that in this system, a stable equilibrium maximizes population size along the zero mean fitness curve (e.g., see Levin and Udovic [**14**], Ginzburg [**6, 7**] or Selgrade and Namkoong [**22, 20**]). Although the system of differential equations admits no periodic solutions (Selgrade and Namkoong [**22**]), cyclic behavior including period-doubling cascades that lead to chaos have been observed for the difference equation analogue (see Asmussen [**1**] or van Coller and Namkoong [**27**]).

Adding migration to the discrete-time model produces even more diverse stable nonequilibrium behavior. The one-island model that we study here has an immigration component in which the number of immigrants is proportional to the size of the island population in each generation and allele frequency in the immigrating population is constant. An immigration rate proportional to population size may occur in a natural biological setting if the migrants are attracted by pheromones released by the island population. Activities in the island population may also result in a sequence of events which causes immigration to increase with population size (the simplest increasing function being a proportionality). For example, Tonkyn [**26**] discusses a population of phloem-feeding aphids where insect feeding stimulates the plant's production of phloem which, in turn, attracts more aphids (immigrants). Density proportionate immigration allows us to obtain bounds for polymorphic equilibria in terms of immigration rate and to investigate Hopf bifurcation. The development in Roberds and Selgrade [**18**] includes a more general immigration term but the generality complicates the mathematical analysis without providing additional conceptual insight.

For the one-island migration model, let $x$ denote the size of the island population and $p$ represent the frequency of the $A$ allele in this island population. In each generation following selection, assume a number of individuals directly proportional to the island population immigrate to the island from a nearby continental population or collection of populations. Then the number of migrants per generation is given by $m\,x$ where $m$, $0 \leq m < 1$, is the constant per capita immigration rate. Following immigration, random mating is assumed to take place yielding Hardy-Weinberg proportions in the population of zygotes that form the next generation. In the population of migrants, let the allele frequency for $A$ be represented by the constant $q$ where $0 \leq q \leq 1$. Then counting alleles and numbers of individuals, we obtain the following system of difference equations [**18**] which describes the changes in allele frequency and population size that take place between generations:

$$\begin{aligned} p' &= \frac{p\, f_A(p,x) + q\, m}{f(p,x) + m} \\ x' &= x\,(f(p,x) + m)\,. \end{aligned} \tag{3}$$

Notice that when $m = 0$, this system reduces to the system (2) for density-dependent selection.

**3 Analysis of equilibria** The phase space for system (3) is the slot in the $(p,x)$-plane given by

$$\mathcal{H} \equiv \{(p,x) : 0 \le p \le 1, 0 \le x\}\,.$$

When $m = 0$, the boundary lines of $\mathcal{H}$, $\{p = 0\}$ and $\{p = 1\}$, represent allele fixation and are invariant. However, if $m > 0$ then this is not necessarily true. In fact, for $0 < q < 1$, points on the boundary of $\mathcal{H}$ iterate into the interior of $\mathcal{H}$. A polymorphic equilibrium $E = (\overline{p}, \overline{x})$ is an allele frequency $\overline{p}$, $0 < \overline{p} < 1$, and population density $\overline{x} \neq 0$ which do not change from generation to generation. Hence, the coordinates of $E$ satisfy the system:

$$\begin{aligned} p &= p\, f_A(p,x) + q\, m \\ 1 &= f(p,x) + m. \end{aligned} \tag{4}$$

In order to determine the stability of $E$ we need the derivative matrix, $D(E)$, of the right side of (3) evaluated at $E$:

$$D(E) = \begin{bmatrix} \begin{array}{l} f_A - \overline{p}(f_A - f_a) \\ +\overline{p}(1-\overline{p})\Big(\frac{\partial f_A}{\partial p} - \frac{\partial f_a}{\partial p}\Big) \end{array} & \overline{p}(1-\overline{p})\Big(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\Big) \\ \overline{x}\,\frac{\partial f}{\partial p} & 1 + \overline{x}\,\frac{\partial f}{\partial x}\,. \end{bmatrix} \tag{5}$$

$E$ is asymptotically stable if both eigenvalues, $\lambda_1$ and $\lambda_2$, of (5) are inside the unit circle.

Because of the detrimental effects of population crowding, we assume that each genotype fitness $f_{ij}$ where $i, j = A, a$, is a decreasing function of the population density $x$, i.e., $\partial f_{ij}/\partial x < 0$. Using the terminology of ecology, we refer to such a function $f_{ij}$ as a *pioneer* fitness function (see Selgrade and Namkoong [**21**]). For instance, exponential (see Moran [**15**] and Ricker [**17**]), rational or Beverton-Holt (see Hassell and Comins [**10**]), and linear (see Selgrade and Roberds [**23, 24**]) functions are used in the modeling literature as pioneer fitnesses. Henceforth, we assume that each genotype fitness is pioneer for all $(p,x) \in \mathcal{H}$, although this may be unrealistic for small $x$. It follows that for all $(p,x) \in \mathcal{H}$ we have $\partial f_A/\partial x < 0$ and $\partial f/\partial x < 0$. Thus, the curves determined by (4)

$$\begin{aligned} \mathcal{C}_A &\equiv \{(p,x) : p\,[f_A(p,x) - 1] + q\,m = 0\} \quad \text{and} \\ \mathcal{C} &\equiv \{(p,x) : f(p,x) + m = 1\} \end{aligned}$$

may be considered as the graphs of $x$ as functions of $p$, which will be denoted by $\tilde{x}_A(p)$ and $\tilde{x}(p)$, respectively. Clearly, at a point $(p,x) \in \mathcal{C}$ we have $f(p,x) \leq 1$, and at a point $(p,x) \in \mathcal{C}_A$ we have $f_A(p,x) \leq 1$. When $qm > 0$, along $\mathcal{C}_A$ we have $-1 \leq f_A - 1 < 0$ so

$$p = \frac{q\,m}{1 - f_A} \geq q\,m \tag{6}$$

and, hence, the function $\tilde{x}_A(p)$ is defined only for $p \geq qm$. From the implicit function theorem it follows that

$$\frac{d\tilde{x}_A}{dp} = \frac{1 - f_A - p(\partial f_A/\partial p)}{p(\partial f_A/\partial x)} \qquad \text{and} \qquad \frac{d\tilde{x}}{dp} = \frac{-\partial f/\partial p}{\partial f/\partial x}\,. \tag{7}$$

The polymorphic equilibria of (3) are the points of intersection of $\mathcal{C}_A$ and $\mathcal{C}$. When $m = 0$, it is reasonable to assume that for each fixed $p$ there is a population density such that the population equilibrates, i.e., for each $p$ there is an $x > 0$ so that $f(p,x) = 1$ or, equivalently, $f(p,0) > 1$ since $\partial f/\partial x < 0$. Hence, for $m > 0$ we have $f(p,0) + m > 1$ for all $p$, which implies that $\mathcal{C}$ lies above the $p$-axis and separates $\mathcal{H}$ into a lower and an upper region. Orbits that remain below $\mathcal{C}$ asymptotically approach $\mathcal{C}$ from below. Similarly, orbits remaining above $\mathcal{C}$ approach $\mathcal{C}$ from above. However, orbits can jump from above $\mathcal{C}$ to below $\mathcal{C}$ and vice versa.

If the genotype fitnesses depend on both frequency and density then the dynamical behavior of (3) even when $m = 0$ is quite general, e.g., see Roughgarden [**19**]. The mean fitness $f$ may not increase on orbits as is the case for constant genotype fitnesses (see Kingman [**13**]). Also, the point of maximum density along the curve where mean fitness equals one, i.e. $\mathcal{C}$, may not be a stable equilibrium as is the case for density-dependent genotype fitnesses (see Roughgarden [**19**]). In fact, Selgrade and Namkoong [**20**] present an example of frequency-dependent fitnesses with a globally, asymptotically stable interior equilibrium which is not the maximum along $\mathcal{C}$.

In order to obtain some general results on equilibrium existence and stability, we make the following four assumptions on each genotype fitness $f_{ij}$ where $i, j = A, a$:

(H1) $\partial f_{ij}/\partial x < 0$, i.e., crowding.
(H2) For each $p$ there is an $x > 0$ which depends on $p$ so that $f(p, x) = 1$.
(H3) $f_{ij}$ is independent of the allele frequency $p$.
(H4) $f_{ij}(x)$ approaches 0 if and only if $x \to \infty$.

(H1) and (H2) have been introduced earlier and (H4) enhances the crowding effect.

By differentiating the expression

$$f(p, x) = p^2 f_{AA} + 2p(1-p) f_{Aa} + (1-p)^2 f_{aa}$$

we see that

$$\frac{\partial f}{\partial p} = 2(f_A - f_a)\,. \tag{8}$$

From (8), it follows that the critical points along $\mathcal{C}$ are precisely the points where the allele fitnesses are equal. Also, since $f$ is quadratic in $p$, we observe that for each $x$ there are at most two values of $p$ where the horizontal line determined by $x$ meets $\mathcal{C}$. Hence $\mathcal{C}$ has at most one local maximum and one local minimum for $0 < p < 1$. The following result regarding the occurrence of equilibria as critical points along $\mathcal{C}$ is somewhat similar to the case of no migration where interior equilibria always occur at critical points of $\mathcal{C}$, e.g., see Roughgarden [**19**] or Selgrade and Namkoong [**22**].

**Theorem 1.** *Assume that* $m > 0$ *and* $0 < q < 1$ *and that* (H1)–(H4) *hold for each genotype fitness* $f_{ij}$ *where* $i, j = A, a$. *The point* $Q \equiv (q, \tilde{x}(q))$ *is an equilibrium of* (3) *if and only if* $Q$ *is a critical point of* $\mathcal{C}$, *the curve where mean fitness equals* $1 - m$. *At such an equilibrium* $Q$, *the genotype fitnesses:*

(i) *exhibit heterozygote superiority* ($f_{Aa} > f_{AA}, f_{aa}$) *and* $Q$ *is a local maximum of* $\mathcal{C}$,
(ii) *exhibit heterozygote inferiority* ($f_{Aa} < f_{AA}, f_{aa}$) *and* $Q$ *is a local minimum of* $\mathcal{C}$, *or*

(iii) *exhibit neutrality* ($f_{Aa} = f_{AA} = f_{aa}$).

*If* $-2 < \tilde{x}(q)\,(\partial f/\partial x)$ *then* $Q$ *is locally asymptotically stable in cases* (i) *and* (iii). *In addition, for case* (ii), *if* $f_{AA} + f_{aa} - 2f_{Aa} < m/(q - q^2)$ *then* $Q$ *is locally asymptotically stable.*

*Proof.* With $m > 0$ and $0 < q < 1$, for an equilibrium $E = (\overline{p}, \overline{x})$, we obtain

$$0 = 0.5\,\overline{p}\,(1-\overline{p})\,\frac{\partial f}{\partial p} + m\,(q - \overline{p})\,, \tag{9}$$

using both equations in (4) and equation (8). Eq. (9) implies that $E$ is a critical point along $\mathcal{C}$ if and only if $\overline{p} = q$. Also, the fitnesses $f$, $f_A$, and $f_a$ all have the value $1 - m$ at the equilibrium $Q = (q, \overline{x})$. Hence, the genotype fitnesses have three possible orderings at $x = \overline{x}$:

(i) $f_{Aa} > 1 - m > f_{AA}, f_{aa}$ (heterozygote superiority);
(ii) $f_{Aa} < 1 - m < f_{AA}, f_{aa}$ (heterozygote inferiority); or
(iii) $f_{Aa} = f_{AA} = f_{aa} = 1 - m$ (neutrality).

Since $\partial f/\partial p = 0$ at $Q$, the derivative $D(Q)$ given by (5) is upper triangular with eigenvalues

$$\lambda_1 = 1 - m + q(1-q)[f_{AA} + f_{aa} - 2f_{Aa}] \quad \text{and} \quad \lambda_2 = 1 + \overline{x}\,\frac{\partial f}{\partial x}\,. \tag{10}$$

For case (iii), clearly $0 < \lambda_1 < 1$. For cases (i) and (ii), to obtain information about $\lambda_1$ we solve the equations for the allele fitnesses equal to $1-m$ to represent $q$ in terms of the genotype fitnesses at $x = \overline{x}$ giving

$$q = \frac{1 - m - f_{Aa}}{f_{AA} - f_{Aa}} = \frac{1 - m - f_{aa}}{f_{Aa} - f_{aa}}\,. \tag{11}$$

From (11) compute that

$$1 - m = \frac{f_{Aa}^2 - f_{AA}f_{aa}}{2f_{Aa} - f_{AA} - f_{aa}} \tag{12}$$

which lies between 0 and 1 since $0 < m < 1$. If the heterozygote is superior (i), we multiply both sides of (12) by 2 and observe that at $x = \overline{x}$

$$2\,(1-m) = \frac{(2f_{Aa}^2 - 2f_{AA}f_{aa})}{(2f_{Aa}^2 - f_{Aa}f_{AA} - f_{Aa}f_{aa})}\,f_{Aa} > f_{Aa}\,.$$

Hence

$$0 < 2f_{Aa} - f_{AA} - f_{aa} < 4\,(1-m) - f_{AA} - f_{aa} < 4\,(1-m)\,. \tag{13}$$

When the heterozygote is superior, the fact that $q(1-q) \leq 1/4$ and (13) imply that $0 < \lambda_1 < 1$. When the heterozygote is inferior and $f_{AA} + f_{aa} - 2f_{Aa} < m/(q-q^2)$ then clearly $0 < \lambda_1 < 1$. In both cases, with $\lambda_1$ in the stable range, $Q = (q, \overline{x})$ has a stable manifold with a horizontal tangent line at $Q$. With the additional assumption that $-2 < \overline{x}\,(\partial f/\partial x)$, the eigenvalue $\lambda_2$ is also in the stable range and, therefore, $Q = (q, \overline{x})$ is locally stable. In addition, the concavity of $\mathcal{C}$ at $Q = (q, \overline{x})$ may be found by differentiating (7) which gives

$$\frac{d^2\tilde{x}}{dp^2} = \frac{2\,[2f_{Aa} - f_{AA} - f_{aa}]}{\partial f/\partial x}\,.$$

Hence, heterozygote superiority implies that $Q$ is a local maximum along $\mathcal{C}$ and heterozygote inferiority implies that $Q$ is a local minimum. $\square$

If the heterozygote is inferior (ii) and there is no migration ($m = 0$), then

$$\lambda_1 = 1 + \overline{p}(1-\overline{p})\,[f_{AA} + f_{aa} - 2f_{Aa}] > 1$$

so the equilibrium is unstable. However, if $m > 0$, then from (10) $\lambda_1 < 1$ if

$$f_{AA} + f_{aa} - 2f_{Aa} \,<\, \frac{m}{q\,(1-q)}\,.$$

In fact, here we present an example of an asymptotically stable equilibrium where the heterozygote is inferior. Take $m = 0.4$, $q = 0.75$ and genotype fitnesses given by:

$$f_{AA} = e^{3-\,x}\,, \quad f_{Aa} = e^{2.4-0.88956\,x} \quad \text{and} \quad f_{aa} = e^{1.6-0.5\,x} \quad .$$

The equilibrium $Q = (q, \overline{x}) \approx (0.75, 3.4607)$ satisfies (ii) and has eigenvalues $\lambda_1 \approx 0.6926$ and $\lambda_2 \approx -0.9087$. Numerical studies indicate that $Q$ is globally stable.

In general, an equilibrium $E = (\overline{p}, \overline{x})$ may occur along $\mathcal{C}$ where $\overline{p} \neq q$ and, hence, at a point which is not a critical point of $\mathcal{C}$. Here we show that there is at least one equilibrium in the interior of $\mathcal{H}$. This result is stronger than a similar result in Roberds and Selgrade [**18**].

**Theorem 2.** *Assume that* $m > 0$ *and* $0 < q < 1$ *and that* (H1)–(H4) *hold for each genotype fitness* $f_{ij}$ *where* $i, j = A, a$. *Then* (3) *has at least one equilibrium* $E = (\overline{p}, \overline{x})$ *where* $q\,m < \overline{p} < q\,m + 1 - m$. *If* $\overline{p} = q$ *then* $E$ *is a critical point of* $\mathcal{C}$. *If* $\overline{p} \neq q$ *then* $E$ *will only occur along an increasing segment of* $\mathcal{C}$ *with* $q < \overline{p} < q\,m + 1 - m$ *or along a decreasing segment of* $\mathcal{C}$ *with* $q\,m < \overline{p} < q$.

*Proof.* Note that $\mathcal{C}_A$ is defined for $qm < p \leq 1$ and has a vertical asymptote at $p = q\,m$. This second property is true because as $p$ approaches $q\,m$ from the defining equation for $\mathcal{C}_A$ we see that $f_A(p, x)$ must approach 0 and, hence, $x \to \infty$ as a consequence of (H4). Also, $\mathcal{C}_A$ meets the line $\{p = 1\}$ at a value for $x$ such that

$$f_{AA}(x) = 1 - q\,m > 1 - m\,.$$

But since $f_{AA}(x)$ is decreasing, this value for $x$ is less than the value for $x$ where $\mathcal{C}$ meets the line $\{p = 1\}$, i.e., where $f_{AA} = 1 - m$. Hence, $\mathcal{C}_A$ and $\mathcal{C}$ cross at some $\overline{p}$, where $q\,m < \overline{p} < 1$ as in Figure 1.

By subtracting the two equations in (4), for $E = (\overline{p}, \overline{x})$ we obtain

$$f_a = 1 - \frac{m\,(1-q)}{1-\overline{p}} \; < \; 1\,.$$

Hence, it follows that

$$\overline{p} = 1 - \frac{m\,(1-q)}{1-f_a} \; < \; 1 - m\,(1-q) = q\,m + 1 - m\,.$$

Theorem 1 asserts that if $\overline{p} = q$ then $E$ will occur at a critical point along $\mathcal{C}$. Hence we assume that $\overline{p} \neq q$. Then from (8), since $f_A \neq f_a$ at $E = (\overline{p}, \overline{x})$, either $f_A > 1 - m > f_a$ or $f_A < 1 - m < f_a$. In the former case, $E$ occurs where $\mathcal{C}_A$ crosses $\mathcal{C}$ along an increasing segment of $\mathcal{C}$ since $\partial f / \partial p > 0$. Also in this case, the determining equation for $\mathcal{C}_A$ gives

$$\overline{p} = \overline{p}\,f_A + q\,m > \overline{p}\,(1-m) + q\,m = \overline{p} + m\,(q - \overline{p})\,,$$

which implies that $\overline{p} > q$. In the case where $f_A < 1 - m < f_a$, a similar argument indicates that $E$ occurs along a decreasing segment of $\mathcal{C}$ where $\overline{p} < q$. Thus the positions of the local extrema of $\mathcal{C}$ and $q$ determine intervals along $\mathcal{C}$ where equilibria may occur. □

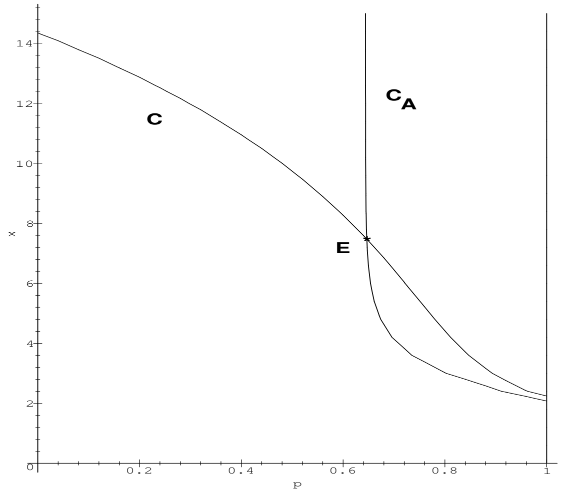

FIGURE 1: Curves $\mathcal{C}_A$ and $\mathcal{C}$ for fitnesses in (15).

**4 Attracting invariant curve** In the case of no migration, interior equilibria always occur at critical points of $\mathcal{C}$, e.g., see Roughgarden [**19**] or Selgrade and Namkoong [**22**]. Hence, $\partial f/\partial p = 0$ and the matrix $D(E)$ in (5) is upper triangular, so Hopf bifurcation cannot occur because the eigenvalues of $D(E)$ are always real. This no longer holds with immigration.

In order for the eigenvalues of $E$ to be complex, the characteristic equation must have a negative discriminant, i.e.,

$$[\operatorname{tr} D(E)]^2 - 4 \det D(E) < 0 ,$$

where tr and det denote the trace and determinant of a matrix, respectively. For the discriminant to be negative, it is necessary that the off-diagonal terms of $D(E)$ have opposite sign. From (5) and (7), we see that the sign of the lower left entry of $D(E)$ is determined by the slope of $\mathcal{C}$ and the sign of the upper right entry is the sign of

$$\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x} = \overline{p}\, f'_{AA}(\overline{x}) + (1 - 2\,\overline{p})\, f'_{Aa}(\overline{x}) - (1 - \overline{p})\, f'_{aa}(\overline{x})\,. \tag{14}$$

By choosing the fitness for the homozygote $aa$ larger at $x = 0$ and decreasing more slowly than the fitness for the homozygote $AA$ and by choosing an intermediate heterozygote fitness, it is possible to have

$\mathcal{C}$ decreasing and (14) positive. In this case Theorem 2 guarantees an equilibrium with $q\,m < \overline{p} < q$. Specifically, we use exponential fitnesses of the form:

$$f_{AA} = e^{1-x}\,, \quad f_{Aa} = e^{1.9-0.9\,x} \quad \text{and} \quad f_{aa} = e^{3.1-0.3\,x} \quad . \tag{15}$$

We fix $m = 0.7$ and we allow our parameter $q$ to vary from 0.85 to 0.99. The curves $\mathcal{C}_A$ and $\mathcal{C}$ intersect as in Figure 1. Numerically, we observe a Hopf bifurcation for $q$ between 0.9 and 0.92. Using the software *Maple*, for $q = 0.9$ we find that $E \approx (0.632, 7.721)$ and its eigenvalues are $\lambda_\pm \approx 0.654 \pm 0.754\,i$, so $|\lambda_\pm| \approx 0.998$. For $q = 0.92$, we have that $E \approx (0.647, 7.463)$ and its eigenvalues are $\lambda_\pm \approx 0.696 \pm 0.755\,i$ giving $|\lambda_\pm| \approx 1.027$. The invariant curve is an attractor, enlarges as $q$ increases (see Figure 2), and coalesces with a homoclinic loop when $q \approx 0.9996$. The equilibrium $B = (\overline{p}, \overline{x}) \approx (0.9985, 2.3452)$ determining this homoclinic loop appears at the point forming at the lower right corners of the invariant curves as $q$ increases toward 0.9996 (see Figure 2). The homoclinic loop is the weak “unstable” manifold for $B$ because $B$ has an eigenvalue of 1 in the direction of this manifold. However, as an invariant set this homoclinic loop is attracting. As $q$ increases through $q \approx 0.9996$, the degenerate equilibrium $B$ splits into a saddle point equilibrium and a stable equilibrium via a saddle-node bifurcation. The loop attractor is preserved and is a heteroclinic loop consisting of the unstable manifold of the saddle and both equilibria for $0.9996 < q < 1$. When $q = 1$, the stable node reaches the invariant line $\{p = 1\}$ and becomes the attractor as the loop is broken.

**5 Pulsating strange attractor** Another significant difference between the situations where $m > 0$ and where $m = 0$ for an equilibrium $E = (\overline{p}, \overline{x})$ may be illustrated by the case of fitness neutrality, i.e., $f_{Aa}(\overline{x}) = f_{AA}(\overline{x}) = f_{aa}(\overline{x})$ . Assume neutrality and $m = 0$. Since each genotype fitness must be 1 at equilibrium, both equations in (4) are satisfied for all $p$, $0 \le p \le 1$. Hence, the horizontal line $\{x = \overline{x}\}$ is a set of degenerate equilibria where $\lambda_1 = 1$. If $m > 0$ then each fitness $f_{ij} = 1 - m$, $\lambda_1 = 1 - m < 1$, and the line $\{x = \overline{x}\}$ is still invariant. In fact, from (3) it is clear that $\overline{p} = q$ so a neutral equilibrium must occur at $E = (q, \overline{x})$. The line $\{x = \overline{x}\}$ is part of the stable manifold of $E$ because orbits of points $(p, \overline{x})$ limit on $E$, since for $p < q$ we have that $p < p' < q$ and for $p > q$ we have $q < p' < p$. The stability of $E$ is determined by $\lambda_2$.

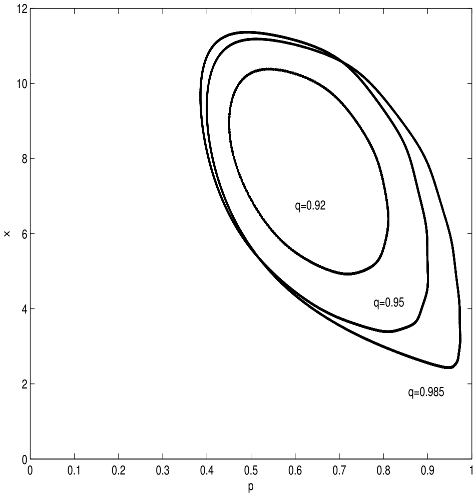

FIGURE 2: Attracting invariant curves for fitnesses (15) with $m = 0.7$.

Consider linear genotype fitnesses given by:

$$(16)\ f_{AA} = 4 - 3.2\,x/4\,, \quad f_{Aa} = 2 - 1.2\,x/4 \quad \text{and} \quad f_{aa} = 3 - 2.2\,x/4\,.$$

Notice that each $f_{ij}(4) = 0.8$. So, if $m = 0.2$, for each $q$ the point $E_q = (q, 4)$ is a neutral equilibrium. For small $q$ this equilibrium is stable but loses stability via a period-doubling bifurcation as $q$ increases through $(5 + \sqrt{10})/15 \approx 0.5441$, where $\lambda_2 = -1$. As $q$ continues to increase, a period-doubling cascade occurs which results in the strange attractor at $q = 0.95$ depicted in Figure 3.

This is an example of a *pulsating attractor* also observed by Franke and Yakubu [**5**] in a 4-dimensional model for the competition between two populations, each with two size classes. The attractor in Figure 3 contains an unstable 5-cycle whose unstable manifold determines the five primary appendages which extend away from the main body of the attractor. When an orbit within the attractor passes close to the 5-cycle, the orbit must track the unstable manifold of the cycle. Since an arbitrary orbit within the attractor only occasionally passes close to the 5-cycle, the orbit exhibits a pulsing behavior to an observer over time. The main body of the attractor lies between $p = 0.77$ and $p = 0.95$ and the bottom appendage extends to $p = 0.1$. Hence, there is considerable variation in allele frequency within this attractor.

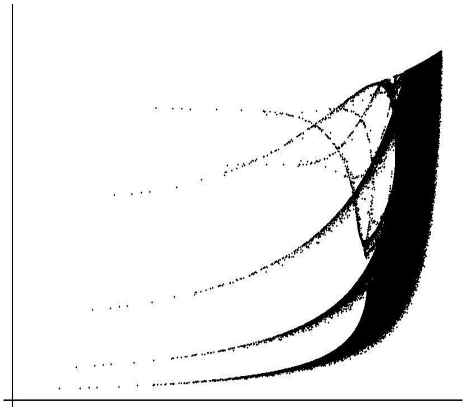

FIGURE 3: A pulsating attractor for fitnesses (16) with $q = 0.95$ and $m = 0.2$ is pictured in the $(p, x)$-plane. The attractor extends along the horizontal $p$-axis from $p \approx 0.1$ to $p \approx 0.95$ and along the vertical $x$-axis from $x \approx 0.1$ to $x \approx 5.4$.

## 6 Migration to reverse destabilizing bifurcations

Varying selection parameters such as growth rates of genotype fitnessses may cause and an attracting equilibrium to become unstable. If the resulting attractor has the allele frequency variable $p$ assuming values on the new attractor less than the allele frequency of the original stable equilibrium, then one may surmise that immigration which introduces more of the $A$ allele into the island population may restabilize the equilirium.

Here we discuss an example where migration of the $A$ allele into our island population restabilizes population equilibrium. Consider the following fitnesses where the homozygote $AA$ is larger at $x = 0$ and decreases more rapidly than the other two genotype fitnesses:

$$f_{AA} = e^{2.1 - x}, \quad f_{Aa} = e^{1.9 - 0.904\,x} \quad \text{and} \quad f_{aa} = e^{1.1 - b\,x} \quad . \tag{17}$$

For (3) without migration ($m = 0$), Selgrade and Roberds [**24**] prove that increasing the parameter $b$ through the value $b \approx 0.526$ results in loss of equilibrium stability via a period-doubling bifurcation. From numerical simulations, it is clear that for $b > 0.526$ the stable equilibrium is replaced by a stable 2-cycle with frequencies for the $A$ allele smaller than the equilibrium frequency. For example, if $b = 0.53$ then there is an unstable equilibrium at $(\overline{p}, \overline{x}) \approx (0.899, 2.10)$ and a stable 2-cycle varying between $(p_1, x_1) \approx (0.840, 1.71)$ and $(p_2, x_2) \approx (0.847, 2.487)$.

To compensate for this decrease in $A$ allele frequency we increase the migration parameter $m$ from zero and observe a reversal of the period-doubling bifurcation. For example, if $b = 0.53$ and we allow migration into the island with a small rate $m = 0.05$ and large allele frequency $q = 0.9$ then the stable 2-cycle is replaced by a stable equilibrium at $(\overline{p}, \overline{x}) \approx (0.888, 2.153)$. Hence, migration can be used to restabilize population equilibrium. The period-doubling bifurcation curve in the $(b, m)$-plane may be obtained by using *Maple* to solve the equilibrium equations (4) with the following eigenvalue equation

$$\operatorname{tr} D(E) + \det D(E) = -1\,. \tag{18}$$

Figure 4 depicts this bifurcation curve for $0.4 < b < 0.75$ and $0 < m < 0.07$.

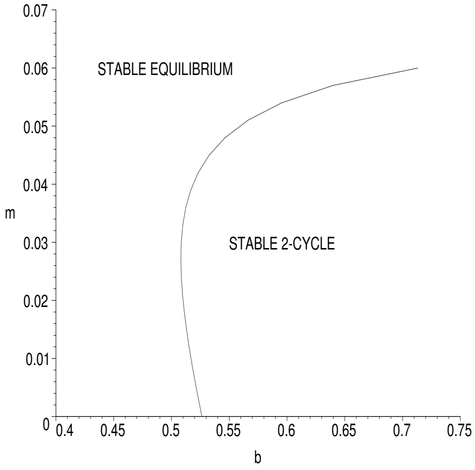

FIGURE 4: Period-doubling bifurcation curve in the parameter space, i.e., the $(b, m)$-plane, for fitnesses (17) with $q = 0.9$.

The nonmonotone nature of this bifurcation curve indicates that for certain fixed values of $b$ near $b = 0.52$, as $m$ increases from zero the attractor changes from an equilibrium to a 2-cycle and then back to an equilibrium. Such "bubbling" behavior was noticed by L. Stone [**25**] in 1-dimensional ecological models. We fix $b = 0.524$ and increase $m$ from zero to 0.06 to observe a bubble in the bifurcation diagram where $x$ is graphed against $m$, see Figure 5. Hence, for a small range of the parameter $b$ from $b \approx 0.51$ to $b \approx 0.526$, increasing the migration parameter $m$ actually destabilizes and then restabilizes the equilibrium.

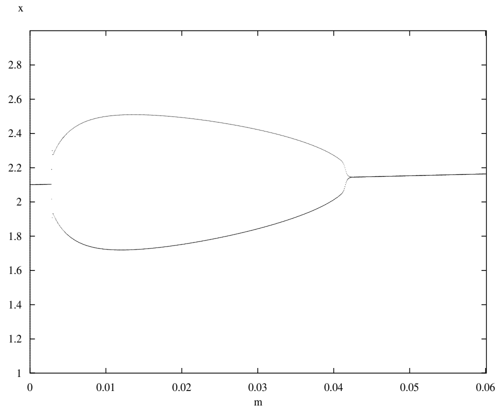

FIGURE 5: Bifurcation curve in the $(m, x)$-plane showing fixed point and 2-cycle attractors (a bubble) for fitnesses (17) with $q = 0.9$ and $b = 0.524$.

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