Dynamical analysis of density-dependent selection in a discrete one-island migration model

James H. Roberds [a,*], James F. Selgrade [b]

[a] *USDA Forest Service, Southern Research Station, Southern Institute of Forest Genetics, Harrison Experimental Forest, 23332 Hwy. 67, Saucier, MS 39574, USA*

[b] *Department of Mathematics, North Carolina State University, Raleigh, NC 27695-8205, USA*

Abstract

A system of non-linear difference equations is used to model the effects of density-dependent selection and migration in a population characterized by two alleles at a single gene locus. Results for the existence and stability of polymorphic equilibria are established. Properties for a genetically important class of equilibria associated with complete dominance in fitness are described. The birth of an unusual chaotic attractor is also illustrated. This attractor is produced when migration causes chaotic dynamics on a boundary of phase space to bifurcate into the interior of phase space, resulting in bistable genetic polymorphic behavior. © 2000 Published by Elsevier Science Inc. All rights reserved.

Keywords: Selection; Migration; Genotype; Density-dependence; Bifurcation

1. Introduction

The combined effects of natural selection and migration can significantly influence the genetic composition and demographic properties of populations. Of particular interest in evolutionary theory are ways that these processes concurrently act to maintain genetic polymorphisms and regulate population growth. The simplest migration model developed to investigate genetic dynamics resulting from the joint action of these two evolutionary forces is the one-island or continent-island model. In migration behavior of this form, immigrants in each generation are contributed to a single population by a large nearby population or collection of populations. Initial studies on the joint effects of selection and migration in this context were deterministic

*Corresponding author. Tel.: +1-228 832 2747; fax: +1-228 832 0130.

E-mail addresses: roberds@datasync.com (J.H. Roberds), selgrade@math.ncsu.edu (J.F. Selgrade).

treatments and concentrated on allele frequency equilibrium behavior in a constant selection setting [1–3].

Recently, Selgrade and Roberds [4] used this migration model to investigate dynamical behavior for island populations undergoing density-dependent selection. Again the approach was deterministic but both allele frequency and population dynamics were studied by employing a system of two-dimensional difference equations similar in form to the system commonly used to study density-dependent selection in the absence of migration, e.g., see [5–7]. In Selgrade and Roberds [4], the migration rate was included in these equations as a density-dependent factor, with the number of immigrants in each generation being treated as a constant proportion of the island population size. The genetic model analyzed consisted of a single locus with two alleles and genotypic fitnesses which were declining functions of population size. Conditions for the existence of polymorphic equilibria in this system were determined and characteristics of these equilibria explored and contrasted with results obtained when migration does not occur. In addition, some features of bifurcation behavior were illustrated and a novel strange attractor for this system was described.

In this paper, we continue the exploration of dynamics resulting from the interaction of density-dependent selection and migration which was begun in [4]. We report results for a more comprehensive migration treatment that includes both density-dependent and constant immigration. An additional class of equilibria associated with complete dominance in fitness is studied and conditions for local stability are described. Finally, we illustrate an unusual chaotic attractor that results when migration causes chaotic dynamics to bifurcate from a boundary location into the interior of phase space resulting in bistable genetic polymorphic behavior.

2. The model

We consider an island population of diploid individuals that undergoes density-dependent selection. Individual fitnesses are assumed to be controlled by genotypes at a single autosomal locus having two alleles, A and a, and thus the population consists of individuals with genotypes AA, Aa or aa at this locus. Selection is considered to occur only in the island population. In our treatment, x represents island population size or density and p denotes frequency of the A allele in the island population prior to selection, with $0 \leqslant p \leqslant 1$. Genotypic fitnesses in the island population are represented by f_{AA}, f_{Aa}, and f_{aa} and are assumed to be non-negative per capita growth functions of x. Allelic fitnesses are defined by $f_A \equiv pf_{AA} + (1-p)f_{Aa}$ and $f_a \equiv pf_{Aa} + (1-p)f_{aa}$. Clearly then the population mean fitness is given by $f \equiv pf_A + (1-p)f_a$. Following selection in each generation, suppose g gametes are contributed to the island population by immigration from a continental population or collection of populations. Let the frequency q of the A allele in the population of migrant gametes be constant over generations with $0 \leqslant q \leqslant 1$. If random mating occurs following migration, the number of gametes that unite to produce zygotes in the next generation is given by

$$2p^2 f_{AA}x + 4p(1-p)f_{Aa}x + 2(1-p)^2 f_{aa}x + g.$$

Furthermore, the number of gametes carrying the A allele is seen to be

$$2p^2 f_{AA}x + 2p(1-p)f_{Aa}x + qg.$$

Therefore, the frequency of allele A in the next generation is

$$\frac{p^2 f_{AA}x + p(1-p)f_{Aa}x + qg/2}{p^2 f_{AA}x + 2p(1-p)f_{Aa}x + (1-p)^2 f_{aa}x + g/2}.$$

Hence we have the following system of difference equations that describes changes in allele frequency and population size between generations:

$$p' = \frac{pxf_A + qy}{xf + y},$$
$$x' = xf + y. \tag{1}$$

Here, $y = g/2$ is the number of additional zygotes in the next generation produced as a consequence of immigration and p' and x' represent allele frequency and population size in the next generation. When $y = 0$, this system clearly is identical to the system previously studied for density-dependent selection, e.g., see [7].

The equations displayed in (1) depict changes produced by postselection migration. A comparable system of equations has been developed that describes changes for a preselection migration model. This latter system differs from (1) in form and its dynamics will be investigated in future research.

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

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

which measures the per capita migration per generation relative to the island population size x. It is biologically reasonable to assume that h(x) is a non-increasing function of population size, i.e., h'(x) ⩽ 0. There are two standard examples of migration in this form. The simplest case occurs when the same amount of migration takes place in each generation so that y is constant and $h'(x) = -y/x^2 < 0$. The second type occurs when the amount of migration increases linearly with x in each generation as discussed in [4]. Here $y = mx$, where m, $0 \leqslant m < 1$, is a constant. Immigration proportional to population size may occur in a biological setting if migrants are attracted by pheromones released by the island population. Furthermore, activities in the island population may lead to a sequence of events which causes immigration to increase with population size. Tonkyn [8] discusses such a situation involving phloem-feeding aphids where the feeding activity of attacking aphids stimulates an increase in the flow of phloem sap to feeding sites, which ultimately may attract more aphids (immigrants). In this case although the number of migrants is increasing as x increases, the per capita migration rate $h(x) = m$ is constant. With our approach, both these types of migration are included.

After replacing y by $xh(x)$ in (1), the transition equations become

$$p' = \frac{pf_A + qh}{f \cdot + \cdot h},$$
$$x' = x(f + h). \tag{2}$$

Since (1) and (2) are equivalent for x > 0, henceforth we study (2).

3. Properties of equilibria

The phase space for system (2) is the slot in the (p, x)-plane designated by

$$\mathscr{H} \equiv \{(p,x) : 0 \leqslant p \leqslant 1,\ 0 \leqslant x\}.$$

When $y = 0$ (i.e., $h = 0$), the boundary lines of $\mathscr{H}$, $\{p = 0\}$ and $\{p = 1\}$, represent allele fixation and, therefore, are invariant. If $y > 0$ (i.e., $h > 0$) then this is not usually the case. In fact, for $0 < q < 1$, points on the boundary of $\mathscr{H}$ are mapped via (2) into the interior of $\mathscr{H}$. If $q = 0$ then the line $\{p = 0\}$ is invariant, but points on the line $\{p = 1\}$ are mapped into the interior of $\mathscr{H}$. If $q = 1$ then the line $\{p = 1\}$ is invariant, but points on the line $\{p = 0\}$ are mapped into the interior of $\mathscr{H}$. Repeated iteration of (2) yields an orbit which we denote as $\{(p_n, x_n) : n = 0, 1, 2, \ldots\}$.

An equilibrium E is an allele frequency $\bar{p}, 0 \leqslant \bar{p} \leqslant 1$, 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 (2), an equilibrium $E = (\bar{p}, \bar{x})$ satisfies the system:

$$\begin{aligned} p &= p f_A + q h, \\ 1 &= f + h. \end{aligned} \tag{3}$$

To determine the local stability of $E = (\bar{p}, \bar{x})$ we need the Jacobian matrix, $D(E)$, of the right side of (2)

$$D(E) = \begin{bmatrix} f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right) & \bar{p}(1 - \bar{p})\left(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\right) + h'(x)(q - \bar{p}) \\ \bar{x}\frac{\partial f}{\partial p} & 1 + \bar{x}\left(\frac{\partial f}{\partial x} + h'(x)\right) \end{bmatrix}, \tag{4}$$

E is stable if both eigenvalues, λ_1 and λ_2, of (4) lie inside the unit circle.

The detrimental effects of population crowding can lead to a reduction in fitness. Thus, we assume that genotype fitnesses, f_{ij} where $i, j = $ A, a, are decreasing functions of the population density x, i.e., $\partial f_{ij}/\partial x < 0$. Borrowing from ecology, we refer to such functions f_{ij} as *pioneer* fitness functions [9]. Exponential (see [10]), rational (see [1 1]), and linear (see [12,13]) functions have been used as pioneer fitnesses in modeling research. Henceforth, we assume that genotype fitnesses are of pioneer type for all $(p, x) \in \mathscr{H}$. This assumption implies certain geometric properties for the functions in (3). For all $(p, x) \in \mathscr{H}$ we have $\partial f_A/\partial x < 0$ and $\partial f/\partial x < 0$. Since $h'(x) \leqslant 0$, the implicit function theorem asserts that the curves defined by (3)

$$\mathscr{C}_A \equiv \{(p,x) : p[f_A(p,x) - 1] + qh(x) = 0\} \quad \text{and} \quad \mathscr{C} \equiv \{(p,x) : f(p,x) + h(x) = 1\}$$

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. We compute that

$$\frac{d\tilde{x}_A}{dp} = \frac{1 - f_A - p(\partial f_A/\partial p)}{p(\partial f_A/\partial x) + qh'} \tag{5}$$

and

$$\frac{d\tilde{x}}{dp} = \frac{-(\partial f/\partial p)}{(\partial f/\partial x) + h'}, \tag{6}$$

Since we assume that population fertility and survival are high at low density, we have $f(p, x) > 1$ for small x. This can be guaranteed by assuming $f_{ij}(p, 0) > 1$ for all p where $i, j = A, a$. Hence, for small x, we have

$$f(p,x) + h(x) > f(p,x) > 1.$$

Also, as a consequence of crowding, we assume that each $f_{ij}(p, x)$ approaches zero as x gets large. Furthermore, we assume that h(x) is a constant less than 1 (for the case that $y = mx$) or approaches zero as x becomes large. It follows that for each value of p there is an x so that $f(p,x) + h(x) = 1$. Hence, for each p, $0 \leqslant p \leqslant 1$, the function $\tilde{x}(p)$ exists and the curve $\mathscr{C}$ separates $\mathscr{H}$ into two subsets. A similar argument may be applied to the function $\tilde{x}_A(p)$. First, note that for small x we have $f_A(p, x) > 1$ so

$$p[f_A(p,x) - 1] + qh(x) > 0.$$

If both $f_A(p,x)$ and h(x) approach zero as x gets large then, for each $p > 0$, the quantity $p[f_A(p,x) - 1] + qh(x)$ becomes negative as x gets large. Consequently, for each $p > 0$, the function $\tilde{x}_A(p)$ exists. Notice that as $p \to 0$ the function $\tilde{x}_A(p)$ approaches infinity because $h(x)$ must approach zero for the equation defining $\mathscr{C}_A$ to be satisfied. In the case, where $y = mx$ and so $h = m < 1$, Selgrade and Roberds [4] show that $\tilde{x}_A(p)$ exists only for $p > qm$ and has a vertical asymptote at $p = qm$.

In addition, for $0 < q < 1$, at $p = 1$ we obtain the inequality

$$f(1,x) + h(x) = f_{AA}(1,x) + h(x) > f_{AA}(1,x) + qh(x) = f_A(1,x) + qh(x). \tag{7}$$

Since both sides of inequality (7) are decreasing functions of x, it follows that $\tilde{x}(1) > \tilde{x}_A(1)$. Hence, the curve $\mathscr{C}_A$ is above the curve $\mathscr{C}$ near $p = 0$ or near $p = qm$ (when $h = m$) and the curve $\mathscr{C}_A$ is below $\mathscr{C}$ at $p = 1$. Therefore, these curves must cross at least once. We have established the following result:

Theorem 3.1 (Existence of a polymorphic equilibrium). *Fix $0 < q < 1$. Assume that each genotype fitness f_{ij} where $i, j = A, a$ is decreasing in x with $f_{ij}(p, 0) > 1$ for all p and that $f_{ij}(p, x) \to 0$ as $x \to \infty$. Assume that $h'(x) \leqslant 0$ and that either h is a constant less than 1 or $h(x) \to 0$ as $x \to \infty$. Then (2) has at least one polymorphic equilibrium $E = (\bar{p}, \bar{x})$, i.e., $0 < \bar{p} < 1$.*

In the case, where $h(x) = m$, a constant, Selgrade and Roberds [4] obtain precise bounds for $\bar{p}$ of the form

$$qm < \bar{p} < qm + 1 - m.$$

4. Density-dependent behavior

In the remaining sections, we assume that genotypic fitnesses f_{ij} where $i, j = A, a$, are independent of the allele frequency p. Taking the derivative of

$$f(p,x) = p^2 f_{AA}(x) + 2p(1 - p)f_{Aa}(x) + (1 - p)^2 f_{aa}(x) \tag{8}$$

with respect to p produces

$$\frac{\partial f}{\partial p} = 2(f_A - f_a). \tag{9}$$

It follows from (6) and (9) that critical points along $\mathscr{C}$ are points where the allele fitnesses are equal and, because f is quadratic in p, there are at most two values of p where the horizontal line determined by x meets $\mathscr{C}$. Clearly then $\mathscr{C}$ has at most one local maximum and one local minimum for $0 < p < 1$.

Now we assume that $0 < q < 1$. Multiplying the second equation in (3) by p and subtracting from the first equation in (3) gives

$$p(1-p)[f_A(p,x) - f_a(p,x)] = h(x)(p-q). \tag{10}$$

Hence from (9), at an equilibrium $E = (\bar{p}, \bar{x})$, we obtain

$$0.5\bar{p}(1-\bar{p})\frac{\partial f}{\partial p} = h(\bar{x})(\bar{p}-q), \tag{11}$$

which indicates that a polymorphic equilibrium is a critical point along $\mathscr{C}$ if and only if $\bar{p} = q$, i.e., the allele frequency at equilibrium equals the allele frequency in the migrating population. From (10), we see that the fitnesses f, f_A, and f_a all have the same value $1 - h(\bar{x})$ at $E = (q, \bar{x})$ and $0 < 1 - h(x) < 1$ because of (3). Therefore, the genotype fitnesses have three possible orderings at $x = \bar{x}$:

  (i) $f_{Aa}(\bar{x}) > 1 - h(\bar{x}) > f_{AA}(\bar{x}), f_{aa}(\bar{x})$ (heterozygote superiority);
  (ii) $f_{Aa}(\bar{x}) < 1 - h(\bar{x}) < f_{AA}(\bar{x}), f_{aa}(\bar{x})$ (heterozygote inferiority); or
  (iii) $f_{Aa}(\bar{x}) = f_{AA}(\bar{x}) = f_{aa}(\bar{x}) = 1 - h(\bar{x})$ (neutrality).
  The derivative $D(E)$ given by (4) may be rewritten as

$$\begin{bmatrix} 1 - h + q(f_{AA} - f_{Aa}) & q(1-q)\left(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\right) \\ 0 & 1 + \bar{x}\left(\frac{\partial f}{\partial x} + h'\right) \end{bmatrix}. \tag{12}$$

Clearly the eigenvalues of (12) are $\lambda_1 = 1 - h + q(f_{AA} - f_{Aa})$ and $\lambda_2 = 1 + \bar{x}((\partial f/\partial x) + h')$. To obtain bounds for λ_1, we set the allele fitnesses equal to $1 - h$ and solve for q in terms of the genotype fitnesses at $x = \bar{x}$ giving

$$q = \frac{1 - h - f_{Aa}}{f_{AA} - f_{Aa}} = \frac{1 - h - f_{aa}}{f_{Aa} - f_{aa}}. \tag{13}$$

From (13) we see that $\lambda_1 = 2(1-h) - f_{Aa}$ and that

$$1 - h = \frac{f_{Aa}^2 - f_{AA}f_{aa}}{2f_{Aa} - f_{AA} - f_{aa}}, \tag{14}$$

From (14) we find that

$$f_{Aa}[2(1-h) - f_{Aa}] = f_{AA}[1 - h - f_{aa}] + (1-h)f_{aa}. \tag{15}$$

If the heterozygote is superior in fitness (i) then the right side of (15) is positive and we conclude that $f_{Aa} < 2(1-h)$. Thus, with (13) we have

$$0 < \lambda_1 = 2(1-h) - f_{Aa} < 1 - h < 1. \tag{16}$$

Furthermore, if $-2 < \bar{x}(\partial f/\partial x) + h')$ then $-1 < \lambda_2 < 1$ and $E \simeq (q, \bar{x})$ is locally asymptotically stable. The concavity of $\mathscr{C}$ at E is found by differentiating (6) with respect to p which yields

$$\frac{\mathrm{d}^2\tilde{x}}{\mathrm{d}p^2} = \frac{2[2f_{Aa} - f_{AA} - f_{aa}]}{(\partial f/\partial x) + h'},$$

Hence, heterozygote superiority in fitness implies that E is a local maximum along $\mathscr{C}$ and heterozygote inferiority implies that E is a local minimum. These conclusions agree with those in [7,14] for the no migration case, i.e., $h = 0$.

An important difference occurs between the cases $h = 0$ and $h > 0$ when the heterozygote is inferior (ii). If $h = 0$ then $\lambda_1 > 1$, which implies that $E = (q, \bar{x})$ is unstable. On the other hand, if $h > 0$ then it is possible to choose genotype fitnesses so that $\lambda_1 < 1$. Selgrade and Roberds [4] provide an example of density-dependent migration with a globally stable equilibrium at which heterozygote inferiority occurs.

The preceding discussion establishes the following result.

Theorem 4.1. *Assume $0 < h < 1, 0 < q < 1$, and that each genotype fitness $f_{ij}(x)$ where $i, j = A, a$ is a decreasing function of x with $f_{ij}(0) > 1$. The point $E = (q, i(q))$ is an equilibrium of (2) if and only if E is a critical point of $\mathscr{C}$. At such an equilibrium E, the genotype fitnesses exhibit:*
   (i) *heterozygote superiority (E is a local maximum of $\mathscr{C}$),*
   (ii) *heterozygote inferiority (E is a local minimum of $\mathscr{C}$), or*
   (iii) *neutrality ($\mathscr{C}$ is a horizontal line).*
In addition, if $-2 < \tilde{x}(q) ((\partial f/\partial x) + h'(\tilde{x}(q)))$ then E is locally asymptotically stable in cases (i) *and* (iii).

5. Complete dominance in fitness at equilibrium

The degree of dominance with respect to genetic control of fitness has been shown to be an important determinant of allele frequency equilibrium behavior resulting from the joint effects of gene migration and constant selection, see [15]. In this section, we explore some properties of equilibrium behavior when selection is density-dependent and when genotypic fitnesses exhibit complete dominance at equilibrium (see Eq. (17)). Equilibria of this type do not exist for pure density-dependent selection (no migration) or for density-dependent selection with migration when $\bar{p} = q$. At equilibrium in these cases, the heterozygote fitness must be either superior or inferior to the homozygote fitnesses or else all genotypes must have equal fitness (see [7] and Theorem 4.1 in Section 4). Here we assume that allele A is dominant to allele a and thus

$$f_{AA}(\bar{x}) = f_{Aa}(\bar{x}) > f_{aa}(\bar{x}), \tag{17}$$

where $E = (\bar{p}, \bar{x})$ is a polymorphic equilibrium. Such an ordering of the genotype fitnesses at E is consistent with conditions given in Theorem 3.1 for the existence of a polymorphic equilibrium. As a consequence of (17), at E we have $f_A = f_{AA}$ which implies with (9) that

$$\frac{\partial f}{\partial p} = 2(1 - \bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) > 0. \tag{18}$$

Hence, from (18) and (11) it follows that $\bar{p} > q$. Using the fact that $1 - 2p(1 - p) \geq 0.5$ with (4) and (18), we conclude that the upper left entry $d_{11}(E)$ of the derivative matrix $D(E)$ may be re-written in terms of genotype fitnesses and lies between 0 and 1, i.e.,

$$0 < d_{11}(E) \equiv f_{AA}(\bar{x}) - 2\bar{p}(1 - \bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) < 1. \tag{19}$$

A tedious computation shows that the determinant of $D(E)$ is

$$\begin{aligned}
\det[D(E)] &= f_{AA}(\bar{x}) - 2\bar{p}(1 - \bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + 2\bar{x}\bar{p}(1 - \bar{p})f_{aa}(\bar{x})f'_{AA}(\bar{x}) + \bar{x}(1 \\
&\quad - \bar{p})^2 f_{AA}(\bar{x})f'_{aa}(\bar{x}) + \bar{x}\bar{p}^2 f_{AA}(\bar{x})f'_{AA}(\bar{x}) + 2\bar{x}q(1 - \bar{p})f_{aa}(\bar{x})h'(\bar{x}) + \bar{x}[1 - 2q(1 \\
&\quad - \bar{p})]f_{AA}(\bar{x})h'(\bar{x}).
\end{aligned} \tag{20}$$

Since the only positive term in (20) is the first term and since $f_{AA}(\bar{x}) < 1$ because of (17) and (3), we have established the following result.

Lemma 5.1.   *If $E = (\bar{p}, \bar{x})$ is a polymorphic equilibrium exhibiting complete dominance, i.e., $f_{AA}(\bar{x}) = f_{Aa}(\bar{x}) > f_{aa}(\bar{x})$, then*

   det *$[D(E)] < 1$.*

A consequence of Lemma 5.1 is that if the eigenvalues of $D(E)$ are complex then E is a stable focus. Hence, a Hopf bifurcation cannot occur at an equilibrium exhibiting complete dominance.

Additional properties of the eigenvalues, λ_1 and λ_2, of $D(E)$ may be obtained from the determinant and trace of $D(E)$. The product $\lambda_1\lambda_2$ is given by (20), and from (4) and (19) the trace of $D(E)$ may be written as

$$\lambda_1 + \lambda_2 = d_{11}(E) + 1 + \bar{x}\bar{p}(2 - \bar{p})f'_{AA}(\bar{x}) + \bar{x}(1 - \bar{p})^2 f'_{aa}(\bar{x}) + \bar{x}h'(\bar{x}). \tag{21}$$

Subtracting (21) from (20) and rearranging terms gives

$$\begin{aligned}
(1 - \lambda_1)(1 - \lambda_2) &= \bar{x}\{2\bar{p}(1 - \bar{p})[f_{aa}(\bar{x}) - 1]f'_{AA}(\bar{x}) + (1 - \bar{p})^2[f_{AA}(\bar{x}) - 1]f'_{aa}(\bar{x}) + \bar{p}^2[f_{AA}(\bar{x}) \\
&\quad - 1]f'_{AA}(\bar{x}) + [f_{AA}(\bar{x}) - 1]h'(\bar{x}) + 2q(1 - \bar{p})[f_{aa}(\bar{x}) - f_{AA}(\bar{x})]h'(\bar{x})\}.
\end{aligned} \tag{22}$$

Since $f_{aa}(\bar{x}) < f_{AA}(X) < 1$, the right side of (22) is positive. Lemma 5.1 and (22) guarantee that if the eigenvalues of $D(E)$ are real then they must both be less than 1. Hence, an equilibrium with non-negative eigenvalues is always a stable node. Lemma 5.1 also implies that complex eigen-values have moduli less than 1. Furthermore, since $(1 - \lambda_1)(1 - \lambda_2) > 0$ and since $\lambda_1 + \lambda_2 = 1 + \lambda_1\lambda_2 - (1 - \lambda_1)(1 - \lambda_2)$, we have the following result.

Proposition 5.2. *If $E = (\bar{p}, \bar{x})$ is a polymorphic equilibrium exhibiting complete dominance, then real eigenvalues of $D(E)$ are less than 1 and complex eigenvalues are inside the unit circle. In addition,*

   trace *$[D(E)] < 1 +$ det $[D(E)]$.*

More general stability results cannot be obtained without lower bounds on the eigenvalues of $D(E)$. However, we are able to derive inequalities relating quantities associated with the matrix $D(E)$ which, when satisfied, are equivalent to the eigenvalues lying inside the unit circle. As in Theorem 4.1, it is important to control the size of the term

$$\bar{x}\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right] = \text{trace}\,[D(E)] - 1 - d_{11}, \tag{23}$$

and so our conditions involve bounds for this term. Using (23) and Proposition 5.2, we obtain the following upper bound:

Lemma 5.3. *If* $E = (\bar{p}, \bar{x})$ *is a polymorphic equilibrium exhibiting complete dominance, then*

$$\bar{x}\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right] < \det[D(E)] - d_{11}(E).$$

Our inequalities are summarized in the following theorem.

Theorem 5.4. *Assume that* $E = (\bar{p}, \bar{x})$ *is a polymorphic equilibrium exhibiting complete dominance. Then the eigenvalues of* $D(E)$ *are inside the unit circle if and only if*

$$-1 < \det D(E) \text{ and} \tag{24a}$$

$$-2 - \det D(E) - d_{11}(E) < \bar{x}\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right]. \tag{24b}$$

In addition, bounding intervals associated with the type of eigenvalues are as follows:
  (i) *If* $0 < \det D(E)$ *then*
   (a) *both eigenvalues are negative if and only if*

$$-2 - \det D(E) - d_{11}(E) < \bar{x}\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right] \lessgtr -1 - 2\sqrt{\det D(E)} - d_{11}(E),$$

   (b) *both eigenvalues are complex if and only if*

$$-1 - 2\sqrt{\det D(E)} - d_{11}(E) < \bar{x}\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right] < -1 + 2\sqrt{\det D(E)} - d_{11}(E), \text{ or}$$

   (c) *both eigenvalues are positive if and only if*

$$-1 + 2\sqrt{\det D(E)} - d_{11}(E) \leqslant \bar{x}\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right] < \det D(E) - d_{11}(E).$$

  (ii) *If* $-1 < \det D(E) < 0$ *then the eigenvalues have opposite signs.*

Proof. Assume that (24a) and (24b) hold. Transposing all the terms in (24b) to the right side of the inequality and rewriting in terms of the eigenvalues, we obtain

$$0 < a_1 + \lambda_2 + 1 + \lambda_1\lambda_2 = (1 + \lambda_1)(1 + \lambda_2).$$

Because of (24a), we conclude that real eigenvalues are greater than -1. Then Proposition 5.2 implies that all eigenvalues lie inside the unit circle.

Proving the necessity of (24) involves the inequalities of (i) and (ii) in a natural way. For instance, the eigenvalues of $D(E)$ being complex is equivalent to the square of the trace being less than four times the determinant. This inequality is equivalent to those of (i), (b). Then (24a) and (24b) follow easily. The remainder of the argument is similar. □

Recall that without migration the eigenvalues of a polymorphic equilibrium are always real. Here we present an example of a polymorphic equilibrium exhibiting dominance with complex eigenvalues and, hence, this equilibrium is a stable focus. Consider density-dependent immigration, i.e., $y = mx$, where $m = 0.7$ and g = 0.1 with exponential genotypic fitnesses of the form $f_{ij} = e^{a_{ij} - b_{ij} x}$, where $a_{ij}, b_{ij} > 0$. Following van Coller and Namkoong [16], in this and subsequent examples, we choose b values consistent with genotypic carrying capacities K_{ij} smaller than or equal to 10. This results in small population sizes which easily can be simulated and graphed on a scale with allele frequency. However, values may be suitably scaled to achieve any carrying capacity (hence, any population size) since $K_{ij} = a_{ij}/b_{ij}$ for exponential fitnesses and $K_{ij} = (a_{ij} - 1)/b_{ij}$ for linear fitness functions. Specifically, we study the genotypic fitnesses:

$$f_{AA}(x) = f_{Aa}(x) = e^{2.2-0.7x} \quad \text{and} \quad f_{aa}(x) = e^{1-x}. \tag{25}$$

For (25), $f_{AA}(x) > f_{aa}(x)$ for all x. A unique polymorphic equilibrium occurs at $E \approx (0.215, 3.706)$ and its eigenvalues are $0.322815 \pm 0.41017\%$. Numerical simulations indicate that this equilibrium is globally, asymptotically stable. The inequalities of Theorem 5.4 (i) (b) are obtained by computing the quantities $d_{11}(E) \approx 0.4692$, det $D(E) \approx 0.27245$, and $\partial f/\partial x \approx 0.22228$. Hence, we have

$$-1 - 2\sqrt{\det D(E)} - d_{11}(E) < \bar{x}\frac{\partial f}{\partial x} < -1 + 2\sqrt{\det D(E)} - d_{11}(E) - 2.51314$$
$$< -0.82377 < -0.42526.$$

As g increases, the right bound in this inequality and the term $\bar{x}(\partial f/\partial x)$ move closer together and coalesce at g ≈ 0.69 as the equilibrium becomes a stable node. Then the inequalities of (i) (c) in Theorem 5.4 apply and are computed below for g = 0.7 where $E \approx (0.724, 4.758)$.

$$-1 + 2\sqrt{\det D(E)} - d_{11}(E) < \bar{x}\frac{\partial f}{\partial x} < \det D(E) - d_{11}(E) - 1.0177 < -1.0014 < -0.1945.$$

Examples can be constructed where both eigenvalues of E are negative. Take density-dependent immigration with $y = mx$ where g = 0.05 and allele fitnesses:

$$f_{AA}(x) = f_{Aa}(x) = e^{7-2x} \quad \text{and} \quad f_{aa}(x) = e^{3-3x}. \tag{26}$$

If $m = 0.6$ then there is an unstable equilibrium $E \approx (0.2597, 3.5614)$ with eigenvalues $\lambda_1 \approx -0.1462$ and $\lambda_2 \approx -1.521$. This system has an attracting two-cycle and another attractor consisting of three arcs. Attractors of a similar nature are illustrated in Fig. 3. As m increases, a reverse period-doubling bifurcation occurs resulting in a stable node at $m = 0.62$. Here the inequalities of Theorem 5.4 (i) (a) are satisfied. For $m > 0.64$ the eigenvalues become complex. For values of m between 0.6 and 0.645, two attractors exist.

We conclude this section with an example of a system with a saddle point equilibrium exhibiting dominance but where the system has a strange attractor. Our example has density-dependent immigration, where $m = 0.2$ and g = 0.75 with linear allele fitnesses of the form $f_{ij} = a_{ij} - b_{ij}x$ with $a_{ij} > 1$ and $b_{ij} > 0$ such that

$$f_{AA}(x) = f_{Aa}(x) = 3.8 - 0.8x \quad \text{and} \quad f_{aa}(x) = 3 - 0.65x. \tag{27}$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all x. A polymorphic equilibrium occurs at $E \approx (0.791, 3.737)$ with eigenvalues $\lambda_1 = 0.7307$ and $\lambda_2 = -1.9674$. The strange attractor for this system is depicted in Fig. 1.
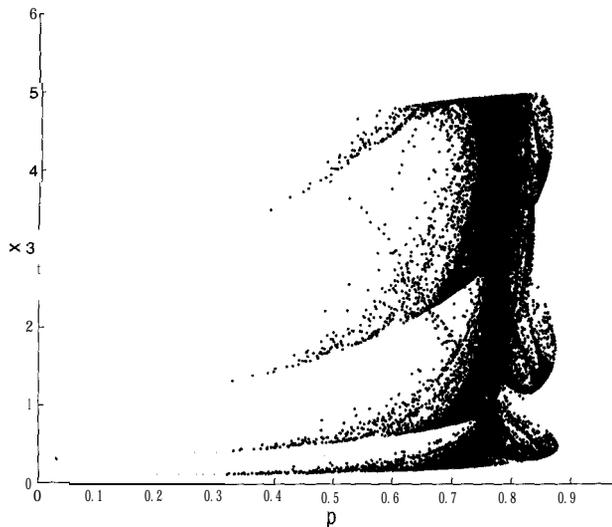
Fig. 1. Strange attractor for (27) with $m = 0.2$ and $q = 0.75$.

6. Bistability and a chaotic attractor

Here we present an example which illustrates the richness of the dynamical behavior for this selection-migration model and which demonstrates the interplay between selection parameters and migration parameters. Consider exponential allele fitnesses of the form

$$f_{AA}(\mathbf{x}) = e^{1-bx}, \quad f_{Aa}(x) = e^{0.5-x} \quad \text{and} \quad f_{aa}(x) = e^{3-0.3x}. \tag{28}$$

The parameter b measures the selective pressure of population density on the AA genotype. Increasing b decreases the fitness of the AA genotype. We take $y = mx$ so the migration parameters are the migration rate m and the frequency q of the A allele in the migrant pool. Increasing either migration parameter will increase the numbers of *AA* genotype in future generations. If $b = 0.15$, $m = 0.03$ and $q = 0.95$ then a surprising polymorphic bistability occurs. There is an asymptotically stable equilibrium ('*' in Fig. 2) with allele frequency p slightly less than 1 and a chaotic attractor resembling a fish-hook with allele frequency in the range $0 < p < 0.35$, see Fig. 2. The domains of attraction are separated by the stable manifold of a saddle point at $p \approx 0.768$. The fish-hook attractor is the unstable manifold of a saddle point $(\bar{p}, \bar{x}) \approx (0.029, 9.907)$. Hence there are three polymorphic equilibria although two of these are unstable.

The mathematical origins of these attractors are quite interesting. The fish-hook attractor bifurcates from the line $\{p = 0\}$ as m increases from zero. When $m = 0$ the line $\{p = 0\}$ is invariant and the dynamical behavior of (1) on this line is given by iterating the map

$$g(x) \equiv x f_{aa}(x) = x e^{3-0.3x}. \tag{29}$$

This map is a one-hump map with its critical point at $x = \frac{10}{3}$ and unstable fixed points (equilibria) at $x = 0$ and $x = 10$. The map is chaotic on the attracting interval $[g^2(\frac{10}{3}), g(\frac{10}{3})] \approx [0.3057, 24.630]$, which is the unstable manifold of the nonzero equilibrium (e.g., see [17]). As m becomes positive, the line $\{p = 0\}$ loses its invariance, and the attractor bifurcates into the interior of $\mathscr{H}$ and forms
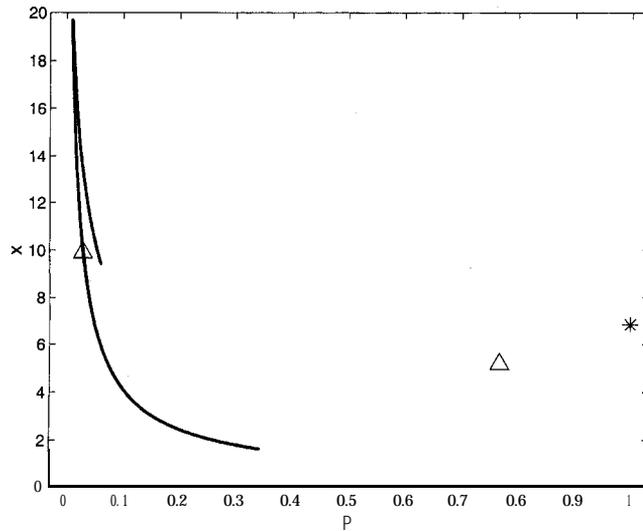
Fig. 2. Fish-hook attractor and three polymorphic equilibria for $b = 0.15$, $m = 0.03$ and $q = 0.95$. △ denotes a saddle point and ∗ denotes a stable focus.

a fish-hook by spreading apart the fold which occurs at its maximum. The equilibrium △ ≈ $(0.029, 9.907)$ in Fig. 2 is the continuation, as m increases to 0.03, of the equilibrium at $(0, 10)$ for $m = 0$ and the fish-hook is the unstable manifold of △. As m continues to increase, first the fish-hook attractor becomes disconnected (Fig. 3(a)) and then a reverse period-doubling cascade occurs resulting in the attracting two-cycle denoted by '+' in Fig. 3(b) and, finally, resulting in the stable node when $m = 0.15$ pictured in Fig. 3(c). This node and the remaining saddle annihilate
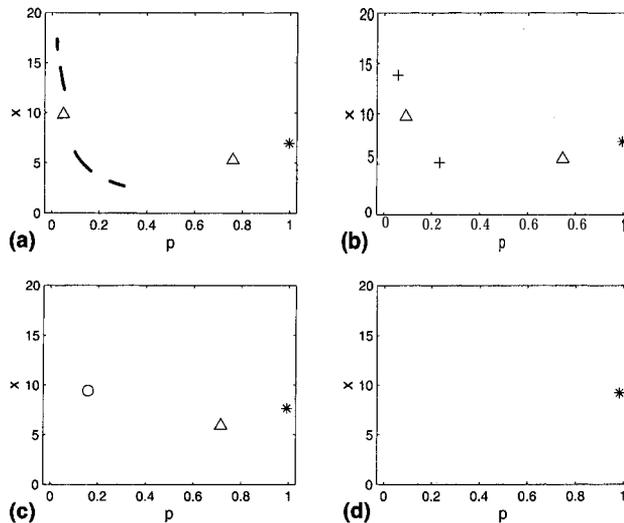

Fig. 3. Sequence of attractors as m increases. + denotes a point on a two-cycle. △ denotes a saddle point, ∗ denotes a stable focus and o denotes a stable node: (a) $m = 0.05$; (b) $m = 0.09$; (c) $m = 0.15$; (d) $m = 0.34$.

each other in a saddle-node bifurcation when $m \approx 0.305$ and the focus becomes globally, asymptotically stable (Fig. 3(d)). Notice that Fig. 3(c) depicts two stable polymorphic equilibria, i.e., '∗' is a stable focus and 'o' is a stable node.

Although this sequence of attractors seems unrealistic biologically, it does have a reasonable biological interpretation. Without migration $(m = 0)$, solutions to Eq. (1) approach allele fixation except for a polymorphic saddle point and its stable manifold. On the line $\{p = 0\}$, the behavior is chaotic because when density is small the *aa* fitness is large and decreases rapidly as density increases. Hence, if density is small during a generation then there tends to be a large increase in population for the next generation. But the fitness at large density results in a significant drop in population in the subsequent generation. These two effects cause unstable fluctuations in population density from one generation to the next. On the line $\{p = 1\}$, there is a stable equilibrium because the AA fitness is not large when $x = 0$ and decreases slowly as a function of x when $b = 0.15$. Since $q = 0.95$, the migrants have AA genotype predominantly. With small migration, the dynamical behavior is affected only slightly, see Figs. 2 and 3(a). However, as m increases, the presence of additional numbers of AA genotype diminishes the chaotic influence of the *aa* genotype on the total population until a balance is reached. For $0.143 < m < 0.305$, the system exhibits bistable equilibrium behavior, i.e., there is a stable node where the *aa* genotype dominates and a stable focus where the AA genotype dominates (Fig. 3(c)). As m continues to increase, the chaotic influence of the *aa* genotype is overwhelmed by the stabilizing effect of the AA genotype and a single globally stable, polymorphic equilibrium is maintained with large A frequency (Fig. 3(d)).

Increasing b, which is the crowding parameter for the AA genotype, has an effect on the dynamical behavior which is opposite that for increasing m. The domain of attraction of the fish-hook becomes larger as the saddle moves toward the stable focus, which becomes a node (Fig. 4). As b continues to increase, the stable node and saddle coalesce and annihilate each other in a saddle-node bifurcation at $b \approx 1.2$. For larger values of b, the fish-hook is a global attractor.
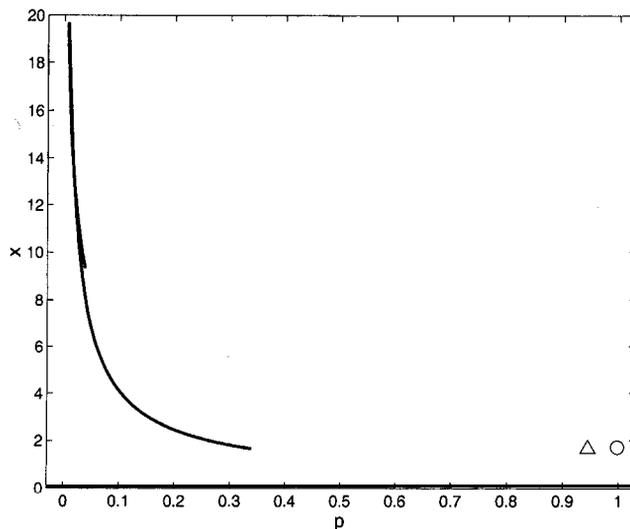

Fig. 4. Attractors for $b = 0.6$, $m = 0.03$ and $q = 0.95$. When b increases further, saddle △ and node o coalesce.

Decreasing q results in a similar saddle-node bifurcation since the stabilizing effect of the AA genotype is being diminished, e.g., if $b = 0.6$ and $m = 0.03$ then the saddle-node bifurcation occurs at $q \approx 0.665$.

7. Summary

We explore dynamical behavior resulting from the interplay of density-dependent selection and migration in a discrete, one-island, migration model. In this model, fitness is assumed to be under the control of a single gene locus with two alleles and the phase variables are allele frequency p in the island population and island population density x. Genotypic fitnesses are taken to be decreasing functions of x and, in each generation, migration into the island population takes place following selection. Allele frequency in the population of migrants is assumed constant over generations.

A per capita immigration rate, h(x), is defined relative to the island population and is assumed to be a non-increasing function of x. Thus two common types of immigration are included, immigration that is constant in each generation and immigration that is proportional to x in each generation. Under natural crowding assumptions on the genotypic fitnesses and on h(x), we prove that at least one polymorphic equilibrium exists. If genotypic fitnesses are independent of p and f represents mean fitness then the polymorphic equilibrium occurs at a critical point along the curve defined by $f + h = 1$ if and only if allele frequency at equilibrium equals that in the migrating population.

Stability properties of equilibria which exhibit complete dominance in fitness are also investigated. We show that if an equilibrium of this type has complex eigenvalues then it is asymptotically stable and, hence, cannot undergo Hopf bifurcation. Conditions for local stability are established in terms of quantities that can be determined from the derivative matrix at equilibrium.

Finally, we present an example which illustrates the rich dynamical behavior that is associated with the occurrence of migration. Without migration, the only polymorphic equilibrium in this example is unstable. At fixation of one allele, say A, there is a stable equilibrium. But at fixation of the other allele, say a, fitness decreases rapidly as density increases which results in density varying chaotically over generations. With even the slightest immigration, the resulting dynamical behavior exhibits polymorphic bistability because a chaotic fish-hook attractor coexists with a stable polymorphic equilibrium. If the immigrating population consists predominantly of the AA genotype then, as immigration increases, the stabilizing influence of the AA genotype diminishes the chaotic influence of the *aa* genotype. The sequence of bifurcations occurring in this example has both biological and mathematical interest.

With respect to biological implications, our results suggest that immigration broadens the range of genetic behavior associated with stable genetic polymorphisms when density-dependent selection occurs. Furthermore, our examples displaying chaotic attractors demonstrate that such higher level attractors must be considered as possible mechanisms for maintaining genetic polymorphisms in populations subject to density-dependent selection and migration. In this regard, our final example illustrates a way by which strictly demographically associated chaotic behavior can be modified by the action of immigration so as to yield genetic polymorphisms.

Acknowledgements

References

[1] J.B.S. Haldane, A mathematical theory of natural and artificial selection. VI. Isolation, Proc. Cambridge Philos. Soc. 26 (1930) 220.

[2] S. Wright, Evolution in Mendelian populations, Genetics 16 (1931) 97.

[3] S. Wright, Evolution and the Genetics of Populations, II: The Theory of Gene Frequencies, University of Chicago, Chicago, 1969.

[4] J.F. Selgrade, J.H. Roberds, Dynamical behavior for a discrete, one-island, migration model with density-dependent selection, submitted.

[5] M.A. Asmussen, M.W. Feldman, Density dependent selection I: A stable feasible equilibrium may not be attainable, J. Theor. Biol. 64 (1977) 603.

[6] J. Roughgarden, Theory of Population Genetics and Evolutionary Ecology: An Introduction, MacMillan, New York, 1979.

[7] J.F. Selgrade, G. Namkoong, Dynamical behavior for population genetics models of differential and difference equations with nonmonotone fitness, J. Math. Biol. 30 (1992) 815.

[8] D.W. Tonkyn, Predator-mediated mutualism: theory and tests in the homoptera, J. Theor. Biol. 118 (1986) 15.

[9] J.F. Selgrade, G. Namkoong, Stable periodic behavior in a pioneer-climax model, Nat. Res. Modeling 4 (1990) 215.

[10] W.E. Ricker, Stock and recruitment, J. Fish. Res. Bd. Can. 11 (1954) 559.

[11] M.P. Hassell, H.N. Comins, Discrete time models for two-species competition, Theor. Popul. Biol. 9 (1976) 202.

[12] J.F. Selgrade, J.H. Roberds, Lumped-density population models of pioneer-climax type and stability analysis of Hopf bifurcations, Math. Biosci. 135 (1996) 1.

[13] J.F. Selgrade, J.H. Roberds, Period-doubling bifurcations for systems of difference equations and applications to models in population biology, Nonlin. Anal.: Th. Meth. Appl. 29 (1997) 185.

[14] J. Roughgarden, Resource partitioning among competing species − a coevolutionary approach, Theor. Popul. Biol. 9 (1976) 388.

[15] P.W. Hedrick. Genetics of Populations, Science Books International, Boston, 1983.

[16] L. van Coller, G. Namkoong, Periodic polymorphisms with density-dependent selection, Genet. Res. 70 (1997) 45.

[17] R.L. Devaney, An Introduction to Chaotic Dynamical Systems, Benjamin/Cummings, Menlo Park, CA, 1986.