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# Convergence to constant equilibrium for a density-dependent selection model with diffusion

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**Abstract.** We consider the classical single locus two alleles selection model with diffusion where the fitnesses of the genotypes are density dependent. Using a theorem of Peter Brown, we show that in a bounded domain with homogeneous Neumann boundary conditions, the allele frequency and population density converge to a constant equilibrium lying on the zero population mean fitness curve. The results agree with the case without diffusion obtained by Selgrade and Namkoong. Frequency and density dependent selection is also considered.

**Key words:** Density dependent — Constant equilibrium — Diffusion — Contracting rectangles — Maximum principles — Frequency dependent

## 1. Introduction

The purpose of this paper is to study the asymptotic behavior of solutions to the following system of reaction-diffusion equations

$$\begin{cases} p_t = p_{xx} + (\eta_A - \eta_a)p(1-p) \\ N_t = N_{xx} + \eta N \end{cases} \tag{1.1}$$

in the domain $[a, b] \times [0, \infty)$ subject to the following boundary and initial conditions

$$\begin{cases} p_x(a, t) = p_x(b, t) = 0 \\ N_x(a, t) = N_x(b, t) = 0 \\ p(x, 0) = p_0(x), \quad N(x, 0) = N_0(x). \end{cases} \tag{1.2}$$

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In the above equations, $p$ represents the frequency of an allele $A$ in a single-locus two alleles model and $N$ represents the size of the population. The functions $\eta_A$, $\eta_a$ and $\eta$ represent the fitnesses of allele $A$, allele $a$ and the population respectively. They are given by

$$\begin{cases} \eta_A = p\eta_{AA} + (1-p)\eta_{Aa}, \quad \eta_a = p\eta_{Aa} + (1-p)\eta_{aa}, \quad \text{and} \\ \eta = p\eta_A + (1-p)\eta_a \end{cases} \tag{1.3}$$

where $\eta_{AA}$, $\eta_{Aa}$, $\eta_{aa}$ are the fitnesses of the three genotypes, $AA$, $Aa$ and $aa$ in the population. These fitness functions in general may depend on $x$, $t$, $p$ or $N$. However in this paper, except for the last section, we shall assume that they are a function of $N$ only (density dependent). Note that $\eta = p^2\eta_{AA} + 2p(1-p)\eta_{Aa} + (1-p)^2\eta_{aa}$.

Without diffusion, that is without the terms $p_{xx}$ and $N_{xx}$, (1.1) is a special case of the continuous time, multi-alleles selection model in [3], p. 191. The dynamics of that model, with the assumption that the fitnesses of all genotypes are density dependent, have been studied by Ginzburg [4]. In the two alleles case, Selgrade and Namkoong studied the model allowing the fitnesses to depend on both $p$ and $N$ [7]. Roughgarden considered a discrete-time version of the two-alleles model in [9], also without diffusion. Hadeler proved the global stability of spatially homogeneous solutions of the multi-alleles selection model with diffusion in [5]. Hadeler's method is by constructing a Lyapunov functional which is different from the approach in this paper.

In the absence of diffusion, when $\eta_{AA}$, $\eta_{Aa}$ and $\eta_{aa}$ are density dependent and $\eta_N < 0$, Selgrade and Namkoong showed that the system of o.d.e. has no periodic solution and that the solution of the o.d.e. evolves to maximize, locally, the population size lying on the curve $\eta = 0$ [1]. These facts can be proved by applying the Poincaré-Bendixson theorem and by showing that the eigenvalues of the linearized matrix at an equilibrium point, which occurs at a local maximum of the curve $\eta = 0$, are both negative.

Suppose now we assume that the population lives in a homogeneous habitat and that individuals in the population diffuse randomly. Then the obvious question is whether the results of Selgrade and Namkoong are still valid. The purpose of this paper is to show that the answer is yes if we assume only density dependent fitnesses and that the population lives in a bounded region with no flux boundary conditions. For simplicity, we assume that the bounded region is the interval $[a, b]$ and that random diffusion is modelled by second derivative in $x$.

This paper is organized into five sections. For the rest of this section, we show that simply adding $p_{xx}$ and $N_{xx}$ to the o.d.e. is only an approximation to the true model. We also provide some justification to the study of (1.1). In the next section, we state our hypotheses and summarize the different cases to be considered in (2.3). In Sect. 3, we collect the mathematical results which we need to prove our theorem. The statement of the theorem and proofs are given in Sect. 4. In Sect. 5, we consider the frequency and density dependent case where the techniques in Sect. 4 are still applicable.

Let $2n$ be the total number of allele $A$ in the population and suppose that all the individuals in the population diffuse at the same (unit) rate. Then if we think of $\eta_A$ and $\eta$ as per capita growth rates of allele $A$ and the population, we have

$$\begin{cases} n_t = n_{xx} + \eta_A n \\ N_t = N_{xx} + \eta N. \end{cases} \tag{1.4}$$

Since $p = n/N$, a simple calculation shows that

$$\begin{cases} p_t = p_{xx} + (\eta_A - \eta_a)p(1-p) + 2(\log N)_x p_x \\ N_t = N_{xx} + \eta N. \end{cases} \tag{1.5}$$

Except for the last term in the first equation, (1.5) is just (1.1). On the other hand, let $(p, N)$ be a solution to (1.1) and (1.2). We can prove later that $(p, N)$ converges uniformly in $[a, b]$ to a constant so that $(p, N)$ satisfies (1.5) at least approximately for large time.

## 2. Hypotheses

For notational convenience, we define $\eta_1 = \eta_{AA}$, $\eta_2 = \eta_{Aa}$, $\eta_3 = \eta_{aa}$. We assume the following about the functions $\eta_i$, $\eta_A - \eta_a$ and $\eta$.

$$\begin{aligned} &\text{(i)}\ \eta_i(N) \in C^1[0, \infty); \\ &\text{(ii)}\ \eta_i(0) > 0 \text{ and there exists } K_i > 0 \text{ such that} \\ &\qquad \eta_i(N) > 0 \text{ on } [0, K_i) \text{ and } \eta_i(N) < 0 \text{ for } N > K_i; \\ &\text{(iii)}\ (\eta_A - \eta_a) < 0 \text{ for small } N \text{ and } (\eta_A - \eta_a) > 0 \\ &\qquad \text{for large } N; \\ &\text{(iv)}\ (\eta_A - \eta_a)_N > 0; \\ &\text{(v)}\ \eta_N < 0. \end{aligned} \tag{2.1}$$

*Remark* 2.1. Conditions (iii)–(v) say that allele $A$ (allele $a$) is more fit in a large (small) population and the average fitness of the population decreases when the population size increases.

From conditions (iv) and (v) and the implicit function theorem, there exist two functions $\hat{N}$ and $\tilde{N}$ such that $\eta(p, \hat{N}(p)) = 0$ and $(\eta_A - \eta_a)(p, \tilde{N}(p)) = 0$ for $0 \le p \le 1$. Let $\Gamma_1$ and $\Gamma_2$ be the graphs of these functions in $Q = \{(p, N) \mid 0 \le p \le 1$ and $N \ge 0\}$. Let $\beta_0 = (0, K_3)$, $\beta_1 = (1, K_1)$ denote the endpoints of $\Gamma_1$, $\gamma_0$, $\gamma_1$ denote the left and right-hand endpoints of $\Gamma_2$. We assume the following about $\Gamma_1$ and $\Gamma_2$.

If $\Gamma_1 \ne \Gamma_2$, then $\Gamma_1$ and $\Gamma_2$ intersect no more than once in the interior of $Q$ and any intersection must be nontangential. (2.2)

Assuming $\Gamma_1 \ne \Gamma_2$, there are then four cases to consider:

*Case* 1. $\Gamma_1$ is above $\Gamma_2$.

*Case* 2. $\Gamma_1$ is below $\Gamma_2$.

*Case* 3. $\Gamma_1$ intersects $\Gamma_2$ once with $\beta_0 > \gamma_0$ and $\beta_1 < \gamma_1$.

*Case* 4. $\Gamma_1$ intersects $\Gamma_2$ once with $\beta_0 < \gamma_0$ and $\beta_1 > \gamma_1$.

From the definition of $\hat{N}$, we have $\hat{N}'(p) = -\eta_p/\eta_N$. Since $\eta_p = 2(\eta_A - \eta_a)$, the function $\hat{N}$ is monotone increasing in Case 1 and monotone decreasing in Case 2. Also $\hat{N}'(p) = 0$ at the point where $\Gamma_1$, $\Gamma_2$ intersect. From (2.2), $\hat{N}$ has at most one extremum. The point of intersection of $\Gamma_1$ and $\Gamma_2$ is a local maximum of $\hat{N}$ in Case 3 and a local minimum of $\hat{N}$ in Case 4.

There is also a relationship between the $K_i$'s and the shape of $\Gamma_1$. Suppose $K_3 < K_2 < K_1$. Then Case 2 cannot occur since in that case $\hat{N}$ is decreasing and $\hat{N}(0) = K_3$, $\hat{N}(1) = K_1$. If $N < K_3$, $\eta = p^2\eta_1 + 2p(1-p)\eta_2 + (1-p)^2\eta_3$ is positive for $0 \leq p \leq 1$ so that $\hat{N}$ cannot have a minimum in (0, 1). This eliminates Case 4. If $N > K_1$, then $\eta$ is negative for $0 \leq p \leq 1$ and this eliminates Case 3. Therefore, if $K_3 < K_2 < K_1$, we are in Case 1. Similarly, if $K_3 > K_2 > K_1$, we are in Case 2. We call these two cases the (heterozygote) intermediate case. If $K_3 < K_2$, $K_1 < K_2$, then we are in Case 3 or the (heterozygote) superior case and if $K_2 < K_3$, $K_2 < K_1$, we are in Case 4 or the (heterozygote) inferior case. Note that (0, 0), (1, 0), $\beta_0$ and $\beta_1$ are the boundary equilibria of (1.1) in all four cases. Internal equilibrium, denoted by $(p^*, N^*)$, exists for Case 3 and 4 where $\Gamma_1$ and $\Gamma_2$ intersect. We summarize the situation below.

*Case* 1. $\Gamma_1$ lies above $\Gamma_2$; $K_3 \leq K_2 < K_1$ or $K_3 < K_2 \leq K_1$;
$\Gamma_1$ is increasing; no internal equilibrium; only $\beta_1$ is stable.

*Case* 2 $\Gamma_1$ lies below $\Gamma_2$; $K_3 \geq K_2 > K_1$ or $K_3 > K_2 \geq K_1$;
$\Gamma_1$ is decreasing; no internal equilibrium; only $\beta_0$ is stable. (2.3)

*Case* 3. $\Gamma_1$ intersects $\Gamma_2$ at an internal equilibrium $(p^*, N^*)$; $K_3 < K_2$, $K_1 < K_2$;
$\Gamma_1$ has a maximum at $(p^*, N^*)$ which is stable. All the four boundary equilibria are unstable.

*Case* 4. $\Gamma_1$ intersects $\Gamma_2$ at an internal equilibrium $(p^*, N^*)$; $K_3 > K_2$, $K_1 > K_2$;
$\Gamma_1$ has a minimum at $(p^*, N^*)$ which is unstable. The boundary equilibria $\beta_0$ and $\beta_1$ are stable while (0, 0), (1, 0) are unstable.

There is also the special case when $K_1 = K_2 = K_3 = K$. Then $(\eta_A - \eta_a) = 0$ or $\eta = 0$ can only be satisfied by $N = K$ because of (2.1) (iv) and (v). We regard this as

*Case* 5. $\Gamma_1 = \Gamma_2$ which coincides with the line $N = K$; $K_1 = K_2 = K_3 = K$.
Every point on the line $N = K$ is an equilibrium point.

## 3. Mathematical preliminaries

The following lemma follows easily from the maximum principle [10, Thm. 10.1].

**Lemma 3.1.** *Let $u(x, t)$, $v(x, t)$ satisfy the inequalities*

$$u_t - u_{xx} - f(x, t, u) \geq v_t - v_{xx} - f(x, t, v) \text{ in } (a, b) \times (0, T)$$

$$u(x, 0) \geq v(x, 0) \text{ in } [a, b]$$

$$u_\nu(x, t) \geq v_\nu(x, t) \text{ for } x = a, b, t > 0.$$

*where $u_\nu$, $v_\nu$ denote differentiation in an outward normal direction. Then $u \geq v$.*

*If* $u(x,0)>v(x,0)$ *for* $x$ *in an open subinterval of* $(a,b)$, *then* $u>v$ *in* $[a,b]\times(0,T]$.

**Lemma 3.2** (Existence). *Let* $0\leqslant p_0(x)\leqslant 1$ *and* $0\leqslant N_0(x)\leqslant M$ *be nontrivial. Then the system* (1.1) *and* (1.2) *admits a unique bounded nonnegative solution* $p(x,t)$, $N(x,t)$ *in* $[a,b]\times[0,\infty)$. *Furthermore,* $0<p(x,t)<1$ *in* $[a,b]$ *for* $t>0$.

*Proof.* We may assume that $M$ is so large that the line $N=M$ is above the curves $\eta=0$ and $\eta_A-\eta_a=0$. Since $\eta$ is negative above $\eta=0$, the region $Q'=\{(p,N)\mid 0\leqslant p\leqslant 1, 0\leqslant N\leqslant M\}$ is an invariant rectangle for (1.1). First half of the lemma follows from [10, Theorem 14.11] and $(p,N)\in Q'$ for all $t\geqslant 0$. Let $a(x,t)=(\eta_A-\eta_a)(1-p)$. Then $p_t-p_{xx}-a(x,t)p=0$. From Lemma 3.1 with $u=p$, $v=0$ and $f(x,t,p)=a(x,t)p$, we have $p>0$ on $[a,b]\times(0,\infty)$. Similarly $p<1$. The proof of Lemma 3.2 is complete.

The following is taken from Exercise 7, p. 127 of Henry's book [6].

**Lemma 3.3.** *Suppose* $\Omega=[a,b]$, $f\colon\mathbb{R}\to\mathbb{R}$ *is* $C^1$, $f(0)=0$, $f(u)/u$ *is strictly monotone for* $u>0$ *and* $\overline{\lim}_{u\to\infty} f(u)/u<0$. *Then any solution* $u\geqslant 0$ *of* $u_t=u_{xx}+f(u)$ *in* $\Omega\times\mathbb{R}^+$ *with* $u=0$ *on* $\partial\Omega$ *(or* $\partial u/\partial\nu+hu=0$ *on* $\partial\Omega$, *given* $h\geqslant 0$*) will tend to a nonnegative equilibrium. If the linearization about* $u=0$ *has no positive eigenvalues, then* $u(\cdot,t)\to 0$ *as* $t\to\infty$. *Otherwise,* $u$ *tends to the unique positive equilibrium solution, or* $u\equiv 0$.

**Corollary.** *In Lemma* 3.3, *suppose* $f(u)/u$ *is decreasing for* $u>0$ *so that there exists* $K>0$ *such that* $f(u)>0$ *on* $(0,K)$, $f(u)<0$ *for* $u>K$. *Let* $u$ *satisfy the boundary conditions* $u_x(x,t)=0$ *for* $x=a$, $b$ *and* $t>0$. *Then* $\lim_{t\to\infty} u(x,t)=K$ *uniformly on* $[a,b]$.

**Lemma 3.4.** *Let* $p(x,t)$, $N(x,t)$ *be the nonnegative, nontrivial solutions of* (1.1) *and* (1.2). *Let* $K_+=\max(K_1,K_2,K_3)$, $K_-=\min(K_1,K_2,K_3)$. *Then given* $\varepsilon>0$, *there exists* $T>0$ *such that* $K_--\varepsilon\leqslant N(x,t)\leqslant K_++\varepsilon$ *for* $t\geqslant T$ *and* $x\in[a,b]$.

*Proof.* We only prove the right inequality, the proof of the left inequality is similar. Let $g(N)=\max(\eta_1,\eta_2,\eta_3)$. Then clearly $\eta(N)\leqslant g(N)$ for $N\geqslant 0$. We can construct an $f$ that satisfies the conditions in the corollary of Lemma 3.3 with $K_+<K<K_++\varepsilon$ and $g(N)N\leqslant f(N)$. Then $N_t-N_{xx}-\eta N\geqslant N_t-N_{xx}-f(N)$ in $[a,b]\times[0,\infty)$. Let $\bar{N}$ be the solution to $\bar{N}_t-\bar{N}_{xx}-f(\bar{N})=0$ in $[a,b]\times[0,\infty)$, $\bar{N}(x,0)=N(x,0)$ on $[a,b]$ and $\bar{N}_x(x,t)=0$ for $x=a$, $b$ and $t>0$. Then according to the corollary of Lemma 3.3, $\bar{N}$ converges uniformly to $K$ as $t\to\infty$. Therefore, given $\varepsilon>0$, there exists $T>0$ such that for $t\geqslant T$, $\bar{N}\leqslant K_++\varepsilon$. From Lemma 3.1 with $u=\bar{N}$, $v=N$, we have $N\leqslant\bar{N}$. Therefore $N\leqslant\bar{N}\leqslant K_++\varepsilon$ on $[a,b]\times[T,\infty)$. The proof of Lemma 3.4 is complete.

The following theorem is taken from Theorem 2.3 of Brown's paper [2] which deals with the system

$$u_t=Du_{xx}+F(u)\ \text{in}\ \Omega\times\mathbb{R}^+ \tag{3.1}$$

where $u=(u_1,\ldots,u_m)$, $F\colon\mathbb{R}^m\to\mathbb{R}^m$ is a smooth function, $D=\operatorname{diag}(d_1,\ldots,d_m)$, $d_i>0$ for each $i$, and $\Omega=\mathbb{R}$ or $[a,b]$. When $\Omega=[a,b]$, we assume that $u_x(x,t)=0$ for $x=a$, $b$ and $t>0$. Also, $u(x,0)=u_0(x)$ is a bounded function defined on $\Omega$.

**Theorem 3.5.** *Let $F$ be smooth and assume there is an isolated critical point $u^*$ of $F$, i.e. $F(u^*)=0$. Assume that there exists a one-parameter family of rectangles $\Sigma(\tau)=\{u\in\mathbb{R}^m \mid a(\tau)\le u\le A(\tau)\}$, $\tau\in[0,1]$ with $\Sigma(1)=\{u^*\}$, $\Sigma(\tau)$ contracting for $\tau\in[0,1)$ and where $a(\tau)$ and $A(\tau)$ are continuous with $a(\tau)$ increasing and $A(\tau)$ decreasing.*

Then if $u(x,t)$ is a solution to the Cauchy problem mentioned above satisfying $u(x,T)\in\Sigma(0)$ for all $x\in\Omega$ and some $T\ge 0$, then $\lim_{t\to\infty} u(x,t)=u^*$, uniformly for $x\in\Omega$.

*Remark* 3.1. Contracting in the above theorem means that the vector field $F(u)$ points strictly into $\Sigma(\tau)$ for $u$ belonging to the boundary of $\Sigma(\tau)$.

The following is taken from Theorem 14.17 of Smoller's book [10].

**Theorem 3.6.** *Consider* (3.1) *with $\Omega=[a,b]$, $u_x(x,t)=0$ for $x=a,b$ and $t>0$, $u(x,0)=u_0(x)$. Assume that* (3.1) *admits a bounded invariant region $\Sigma$ and that $u_0(x)\in\Sigma$ for all $x\in\Omega$. Let $\sigma=\lambda d-C$ where $\lambda>0$ is the principal eigenvalue of $-\partial^2/\partial x^2$ on $\Omega$ with homogeneous Neumann boundary conditions, $d=\min\{d_i;\, i=1,\dots,m\}$ and $C=\max\{|dF_u|: u\in\Sigma\}$. $dF_u$ is the Jacobian matrix of $F$ at $u$. If $\sigma>0$, then there exist positive constants $C_1$, $C_2$ such that $|u(x,t)-\bar u(t)|\le C_1 e^{-\sigma t}$ uniformly for $x$ in $[a,b]$, $|g(t)|\le C_2 e^{-\sigma t}$ for $t>0$ where $\bar u(t)=1/|\Omega|\int_\Omega u(x,t)\,dx$ and $g(t)=d\bar u/dt-F(\bar u)$.*

## 4. Theorem and proofs

We show in this section that the solutions to (1.1) and (1.2) with appropriate initial conditions, converge uniformly to the stable constant equilibrium for Cases 1 through 4 of our model. Case 5 has to be treated differently. Recall that Cases 1 through 5 are described in (2.3).

**Theorem 4.1.** *Let $(p,N)$ be a nontrivial bounded solution to* (1.1), (1.2). *Then in*

*Case* 1. $\lim_{t\to\infty}(p,N)=(1,K_1)$ *uniformly on* $[a,b]$.

*Case* 2. *If $\Gamma_2$ is above the line $N=K_3$ or if $p(x,0)<\tilde p$ in $[a,b]$, where $\tilde p$ is the smallest positive root to the equation $(\eta_A-\eta_a)(p,K_3)=0$, then $\lim_{t\to\infty}(p,N)=(0,K_3)$ uniformly on $[a,b]$.*

*Case* 3. *Let $(p^*,N^*)$ be the internal equilbrium and suppose $\gamma_0<K_1$ where $\gamma_0$ is the left-hand endpoint of $\Gamma_2$. Suppose also that there exist $\varepsilon>0$ and a curve $\Gamma$ in $Q'=\{(p,N)|0\le p\le 1,\ 0\le N\le M\}$ such that $\Gamma$ is increasing, lies between $\Gamma_1$ and $\Gamma_2$ and passes through the points $(\varepsilon,K_1-\varepsilon)$, $(p^*,N^*)$ and $(1-\varepsilon,K_2+\varepsilon)$. Then $\lim_{t\to\infty}(p,N)=(p^*,N^*)$ uniformly on $[a,b]$.*

*Case* 4 (Threshold behavior). *Let $(p^*,N^*)$ be the internal equilibrium. Suppose there exist $\varepsilon>0$ and $\Gamma$ that lies between $\Gamma_1$ and $\Gamma_2$ for $p^*+\varepsilon\le p\le 1$, $\Gamma$ increases from the point $(p^*+\varepsilon,K_2-\varepsilon)$ to $\beta_1=(1,K_1)$ and $p_0(x)\ge p^*+\varepsilon$ on $[a,b]$. Then $\lim_{t\to\infty}(p,N)=(1,K_1)$ uniformly on $[a,b]$. However, if $(p_0(x),N_0(x))$ is sufficiently close to $(0,K_3)$, then $\lim_{t\to\infty}(p,N)=(0,K_3)$ uniformly on $[a,b]$.*

*Case* 5. *Let $\lambda$ be the principal eigenvalue of the operator $-\partial^2/\partial x^2$ on $[a, b]$ with homogeneous Neumann boundary conditions. Let $f = (\eta_A - \eta_a)p(1-p)$, $g = \eta N$ and $\bar{C} = \max\{|f_p|, |f_N|. |g_p|, |g_N|: 0 \leq p \leq 1, 0 \leq N \leq M\}$. Suppose $\lambda > 4\bar{C}$. Then* $\lim_{t\to\infty}(p, N) = (\tilde{p}, K)$ *uniformly in $[a, b]$ for some constant $\tilde{p}$.*

*Proof.* From Lemmas 3.2 and 3.4, we may assume that there exists $\varepsilon > 0$ such that $\varepsilon \leq p_0(x) \leq 1-\varepsilon$ and $K_- - \varepsilon \leq N_0(x) \leq K_+ + \varepsilon$ on $[a, b]$. From Theorem 3.5, it suffices to show that there exists a family of contracting rectangles $\Sigma(\tau)$, decreasing to the constant equilibrium such that $(p_0(x), N_0(x)) \in \Sigma(0)$. We do so by defining the appropriate $\Sigma(\tau)$ in each case. For convenience, we define $f(p, N) = (\eta_A - \eta_a)p(1-p)$ and $g(p, N) = \eta N$.

*Case* 1. From (2.3), there exists a curve $\Gamma$ in $Q'$ such that $\Gamma$ is between $\Gamma_1$ and $\Gamma_2$, $\Gamma$ is increasing, $\varepsilon$ defined above is so small that $(\varepsilon, K_3 - \varepsilon)$ lies on $\Gamma$ and finally, the right-hand endpoint of $\Gamma$ equals $\beta_1 = (1, K_1)$. Let $A(\tau) = (1, \tau K_1 + (1-\tau)M)$ and $a(\tau)$ lies on $\Gamma$ such that $a(0) = (\varepsilon, K_3 - \varepsilon)$, $a(\tau)$ increases to $a(1) = \beta_1$ as $\tau \uparrow 1$. Let $\Sigma(\tau) = \{(p, N) | a(\tau) \leq (p, N) \leq A(\tau)\}$ for $0 \leq \tau \leq 1$. Then $\Sigma(\tau)$ is a family of rectangles in $Q'$ decreasing to $\Sigma(1) = \beta_1$ as $\tau \uparrow 1$. For each $0 \leq \tau < 1$, since the upper and lower sides of $\Sigma(\tau)$ lie on opposite sides of $\Gamma_1$ and the left side of $\Sigma(\tau)$ lies above $\Gamma_2$, $\Sigma(\tau)$ is a contracting rectangle except for the right side that lies on $p = 1$. There, $f = 0$ and $(f, g)$ points toward $\beta_1$. Brown's theorem can be extended to cover this case. Since $\varepsilon \leq p_0(x) \leq 1$ and $K_3 - \varepsilon \leq N_0(x) \leq M$, we have $(p_0(x), N_0(x)) \in \Sigma(0)$ on $[a, b]$. Our result then follows from Theorem 3.5.

*Case* 2. We first assume that $\Gamma_2$ is above the line $N = K_3$. By continuity, we may assume that $\Gamma_2$ is above the line $N = K_3 + \varepsilon$ where $\varepsilon$ is defined at the beginning of the proof and is sufficiently small. Since $\Gamma_1$ is decreasing, there exists a curve $\Gamma$ such that $\Gamma$ lies between $\Gamma_1$ and $\Gamma_2$, $\Gamma$ is increasing, the left-hand endpoint of $\Gamma$ is $\beta_0 = (0, K_3)$ and $(1-\varepsilon, K_3 + \varepsilon)$ lies on $\Gamma$. Let $A(\tau)$ lie on $\Gamma$ for $0 \leq \tau \leq 1$, $A(0) = (1-\varepsilon, \ K_3 + \varepsilon)$, $A(\tau)$ decreases to $A(1) = \beta_0$ as $\tau \uparrow 1$. Let $a(\tau) = (0, \tau K_3 + (1-\tau)(K_1 - \varepsilon))$ and $\Sigma(\tau) = \{(p, N) | a(\tau) \leq (p, N) \leq A(\tau)\}$ for $0 \leq \tau \leq 1$. We also choose $A(\tau)$ such that the lower right corner of the rectangle $\Sigma(\tau)$ lies below $\Gamma_1$. Then $\Sigma(\tau)$ is a contrcting rectangle (except on the left side) and $\Sigma(\tau)$ decreases to $\Sigma(1) = (0, K_3)$ as $\tau \uparrow 1$. Also $(p_0, N_0) \in \Sigma(0)$. Our result then follows from Theorem 3.5. For the second half of Case 2, we observe that $\Gamma_2$ is above $\Gamma_1$ on the interval $[0, \tilde{p}]$. A proof similar to the first half would yield the desired result.

*Case* 3. We assume that $K_1 < K_3$, this being the more difficult case to prove. Note that $\gamma_1$, the right-hand endpoint of $\Gamma_2$, is above $K_2$ since $(\eta_A - \eta_a)(1, K_2) = \eta_1(K_2) < 0$. Similarly $K_2 > N^*$. Let $A(\tau)$ lie on $\Gamma$ for $0 \leq \tau \leq 1$ and decreases from $A(0) = (1-\varepsilon, K_2 + \varepsilon)$ to $A(1) = (p^*, N^*)$ as $\tau \uparrow 1$. Similarly, let $a(\tau)$ lie on $\Gamma$ for $0 \leq \tau \leq 1$ and increases from $a(0) = (\varepsilon, K_1 - \varepsilon)$ to $a(1) = (p^*, N^*)$. We also choose $A(\tau)$ and $a(\tau)$ such that the rectangle $\Sigma(\tau) = \{(p, N) | a(\tau) \leq (p, N) \leq A(\tau)\}$ has its lower right-hand corner lie below $\Gamma_1$. Then it is easy to see that $\Sigma(\tau)$ is contracting for $0 \leq \tau < 1$, $\Sigma(1) = (p^*, N^*)$ and $(p_0, N_0) \in \Sigma(0)$. Our result then follows from Theorem 3.5. One way to guarantee the existence of $\Gamma$ in the hypotheses of the theorem is for $\Gamma_2$ to be increasing. This happens for example if $\eta_1+\eta_3-2\eta_2<0$ on $[0, M]$. Note that if $\gamma_0$ is above $K_1$ and $K_1<K_3$, then contracting rectangles cannot be constructed since $(f, g)$ will be pointing outward on the left-side below $\Gamma_2$. (See Fig. 1).

*Case* 4. Without loss of generality, we assume that $K_1<K_3$. Note that since $\eta(p, K_2)>0$ for all $p$, $K_2<N^*$. Also $\gamma_1<K_2$. Now let $A(\tau)=(1, \tau K_1+(1-\tau)(K_3+\epsilon))$ and $a(\tau)$ lie on $\Gamma$, $a(\tau)$ increases from $a(0)=(p^*+\varepsilon, K_2-\varepsilon)$ to $a(1)=(1, K_1)$ as $\tau\uparrow 1$. Let $\Sigma(\tau)=\{(p, N)|a(\tau)\leq (p, N)\leq A(\tau)\}$. Then $\Sigma(\tau)$ is a contracting rectangle (except on the right side) for each $0\leq\tau<1$ and decreases to $\Sigma(1)=(1, K_1)$ as $\tau\uparrow 1$. Also $(p_0(x), N_0(x))\in\Sigma(0)$ from our hypotheses. The first half of Case 4 follows from Theorem 3.5. The proof of the second half is the same. Sufficiently close means $(p_0, N_0)$ belong to a rectangle that lie under $\Gamma_2$ and contains $\beta_0=(0, K_3)$ on its left side. Note that $\Gamma_2$ is decreasing if $\eta_1+\eta_3-2\eta_2>0$.

*Case* 5. All points on the line $N=K$ are equilibrium points. The solutions to (1.1) without diffusion increases and turn left below $N=K$, decreases and turn right above $N=K$. From Lemma 3.4, $N$ converges to $K$ uniformly on $[a, b]$. From Theorem 3.6 and our hypotheses, to show that $p$ converges to some value $\tilde{p}$ it suffices to show that the spatial average $\bar{p}$ approaches a constant. Note that the norm of the matrix $dF_u$ is no greater than $4\bar{C}$ by Schwarz's inequality. Since $d\bar{p}/dt=(1-\bar{N}/K)\varphi(x, t)+g(t)$ where $|\varphi(x, t)|$ is bounded and $|g(t)|\leq C_2 e^{-\sigma t}$, it suffices to show that $\bar{N}$ converges to $K$ sufficiently fast so that $|1-\bar{N}/K|$ is integrable. Let $\eta_+(N)=\max\{\eta_1(N), \eta_2(N), \eta_3(N)\}$ on $[0, \infty)$. Then $\eta_+>0$ on $[0, K)$, $\eta_+<0$ on $(K, \infty)$. Also $\eta\leq\eta_+$ and $0=N_t-N_{xx}-\eta N\geq N_t-N_{xx}-\eta_+ N$. Let $\gamma, \beta>0$ satisfy $N(x, 0)\leq K+\gamma$ on $[a, b]$ and $\delta-\beta>0$ where $\delta>0$ is chosen so that $\eta_+(N)\leq\delta(1-N/K)$ on $[0, K+\gamma]$. Then $w=(K+\gamma e^{-\beta t})$ satisfies $w_t-w_{xx}-\eta_+ w\geq 0$, $w_x=0$ and $w(x, 0)\geq N(x, 0)$. The first inequality follows from the fact that $-\eta_+(w)w\geq-\eta_+(w)K\geq\delta\gamma e^{-\beta t}$. Therefore, Lemma 3.1 implies that $N-K\leq\gamma e^{-\beta t}$. Similarly we can show that $-\gamma' e^{-\beta' t}\leq N-K$ so that $N$, and

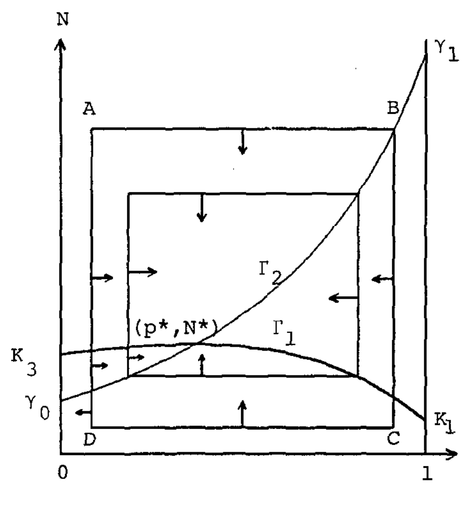


**Fig. 1.** Initially, $DC$ has to be below $K_1$. If $\gamma_0>K_1$, then part of $AD$ will be below $\Gamma_2$ so that $\Sigma(0)$ cannot be contracting

hence $\bar{N}$, converges to $K$ exponentially. The proof of Case 5 is complete and so is Theorem 4.1.

## 5. Frequency and density dependent selection

In this section, we shall examine the possibility of extending the results in Sect. 4 to the case when $\eta_1$, $\eta_2$, $\eta_3$ are both frequency and density dependent. Consider the reaction-diffusion equations (1.1) subject to the boundary and initial conditions (1.2). We continue to assume conditions (2.1) except that we replace (2.1)(i) by $\eta_i(p, N) \in C^1([0, 1]\times[0, \infty))$ and (2.1)(ii) by $\eta_i(p, 0) > 0$ and $\eta_i(p, M) < 0$ for some $M > 0$. Of course (1.3) is still valid.

Let $Q'$ be defined as before. Then $Q'$ is an invariant rectangle so that solutions of (1.1), (1.2) with initial data in $Q'$ exist for all $t > 0$ and lie in $Q'$. From (2.1)(iv) and (v), $\hat{N}(p)$ and $\tilde{N}(p)$ are defined on [0, 1]. Let $\Gamma_1, \Gamma_2$ be their graphs and let $\beta_0, \beta_1$ be the endpoints of $\Gamma_1$, $\gamma_0$, $\gamma_1$ be the endpoints of $\Gamma_2$ in $Q'$. Since $\eta_p \neq 2(\eta_A - \eta_a)$, we cannot say anything about the monotonicity of $\Gamma_1$. We continue to assume (2.2) so that we have the four cases listed right after (2.2). In Cases 3 and 4, let $(p^*, N^*)$ be the intersection of $\Gamma_1, \Gamma_2$ inside $Q'$. It is clear that $\beta_0, \beta_1, (0, 0)$, and $(1, 0)$ are the boundary equilibria in all four cases and $(p^*, N^*)$ is the internal equilibrium in Cases 3 and 4. The stability properties of these equilibria (assuming no diffusion) remain the same as in the frequency independent case. Thus $\beta_1$ is stable in Case 1, $\beta_0$ is stable in Case 2, $(p^*, N^*)$ is stable in Case 3 and $\beta_0, \beta_1$ are stable in Case 4. Lemmas 3.1, 3.2 and Theorem 3.5 are results taken from elsewhere and will not be affected by our new assumptions. Lemma 3.4 is still valid if we replace $K_+$, $K_-$ by $K_+ = \max\{\hat{N}(p)|0 \leq p \leq 1\}$ and $K_- = \min\{\hat{N}(p)|0 \leq p \leq 1\}$. The proof is very similar to that given in Sect. 3.

We are now ready to examine the results of Cases 1 through 4 of Theorem 4.1. The idea is to find a family of contracting rectangles $\Sigma(\tau) = \{(p, N)|a(\tau) \leq (p, N) \leq A(\tau)\}$ in $Q'$, $0 \leq \tau \leq 1$, such that $(p_0, N_0) \in \Sigma(0)$ and $\Sigma(1)$ equals to the desired stable equilibrium. $\Sigma(\tau)$ is contracting if the left side lies above $\Gamma_2$, the right side lies below $\Gamma_2$ and the top and bottom of $\Sigma(\tau)$ lies on opposite sides of $\Gamma_1$. Since $\Gamma_1$ and $\Gamma_2$ are not monotone, there is no general way of constructing $\Sigma(\tau)$ like the frequency independent case and the fact that $(p_0, N_0) \in \Sigma(0)$ generally becomes an additional hypothesis on the initial data. We discuss the four cases briefly below.

In Case 1, suppose $\beta_1$ is the maximum point of $\Gamma_1$ (i.e. $K_+$ occurs at $p = 1$). Then one can construct an increasing curve $\Gamma$ between $\Gamma_1$ and $\Gamma_2$ such that its right hand endpoint is $\beta_1$. The left hand endpoint $(= a(0))$ should be extended as close to the $p = 0$ axis as possible. Then one can choose $a(\tau)$ to lie on $\Gamma$ and $A(\tau)$ to lie on the $p = 1$ axis above $\beta_1$ for $0 \leq \tau \leq 1$, both converging to $\beta_1$ as $\tau \uparrow 1$. In Case 2, suppose $\beta_0$ is the maximum point of $\Gamma_1$. Then the method used in the second half of Case 2 of Theorem 4.1 may be employed to construct $\Sigma(\tau)$. Case 3 is perhaps the most difficult case since the internal equilibrium $(p^*, N^*)$ need not be a local maximum of $\Gamma_1$. All one can say is that $\Gamma_2$ is increasing at $(p^*, N^*)$ and if $\Gamma_1$ is also increasing there, then one can construct locally an increasing curve $\Gamma$ between $\Gamma_1$ and $\Gamma_2$ that passes through $(p^*, N^*)$. Then one can construct $\Sigma(\tau)$ at $(p^*, N^*)$. If $\Gamma_1$ has a very negative slope at $(p^*, N^*)$, then the construction of $\Sigma(\tau)$, even locally, may not be possible. Finally in Case 4, suppose $\beta_1$ is the maximum point of $\Gamma_1$ for $p^* \leq p \leq 1$, then one can construct an increasing curve $\Gamma$ between $\Gamma_1$ and $\Gamma_2$ with right hand endpoint at $\beta_1$. One can then construct $\Sigma(\tau)$ as in the frequency independent case.

## References


1. Aronson, D. G., Weinberger, H. F.: Nonlinear diffusion in population genetics, combustion and nerve propagation. In: Goldstein, J. (ed.) Partial differential equations and related topics. (Lect. Notes Math., vol. 446, pp. 5–49) Berlin Heidelberg New York: Springer 1975
2. Brown, P. N.: Decay to uniform states in ecological interactions. SIAM J. Appl. Math. **38**, 22–37 (1980)
3. Crow, J. F., Kimura, M.: An introduction to population genetics theory. Minneapolis: Burgess 1970
4. Ginzburg, L. R.: The equilibrium and stability for *n* alleles under the density-dependent selection. J. Theor. Biol. **68**, 545–550 (1977)
5. Hadeler, K.P.: Diffusion in Fisher's population model. Rocky Mt. J. Math. **11**, 39–45 (1981)
6. Henry, D: Geometric theory of semilinear parabolic equations (Lect. Notes Math., vol 840) Berlin Heidelberg New York: Springer 1981
7. Namkoong, G. Selgrade, J. F.: Frequency-dependent selection in logistic growth models. Theor. Popul. Biol. **29**, 64–86 (1986)
8. Protter, M. H., Weinberger, H. F.: Maximum principles in differential equations. Englewood Cliffs: Prentice-Hall 1967
9. Roughgarden, J.: Theory of population genetics and evolutionary ecology: an introduction. New York: Macmillan 1979
10. Smoller, J.: Shock waves and reaction-diffusion equations. (Grundlehren der mathematischem Wissenschaften, vol. 258) Berlin Heidelberg New York: Springer 1983
11. Selgrade, J. F., Namkoong, G.: Dynamical behavior of differential equation models of frequency- and density-dependent populations. J. Math. Biol. **19**, 133–146 (1984)


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