The retreat of the less fit allele in a population-controlled model for population genetics

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Abstract

It is shown that the solutions of a single-locus diploid model with population control for the spatial and temporal interaction of the three genotypes approach a constant-density equilibrium in which only the more fit allele is present, provided the density dependent birth rate and fitnesses have certain properties. The speed at which this phenomenon spreads is at least as great as that of the linearization of the corresponding Fisher equation. A larger upper bound for this speed is also obtained.

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1 Introduction.

This work is concerned with the interaction between genotypes of a diploid species which only differ by the presence or absence of two possible alleles a and A at a single genome site. We are interested in the long-time evolution of the spatial densities of the three genotypes aa, aA, and AA. The populations are distributed on the spatial habitat, which is the n-dimensional Euclidean space. We shall use the notation

$\rho_1(\mathbf{x}, t)$=spatial density of the aa homozygotes at $\mathbf{x}$ at time t;

$\rho_2(\mathbf{x}, t)$=spatial density of the aA heterozygotes at $\mathbf{x}$ at time t;

$\rho_3(\mathbf{x}, t)$=spatial density of the AA homozygotes at $\mathbf{x}$ at time t.

A classical model for the evolution of a monoecious population under the assumption of random gamete formation and pairing and random migration is the system

$$
\begin{aligned}
\left\{\frac{\partial}{\partial t} - \nabla^2\right\} \rho_1 &= \frac{B[\rho_1 + \frac{1}{2}\rho_2]^2}{\rho_1 + \rho_2 + \rho_3} - D_1\rho_1 \\
\left\{\frac{\partial}{\partial t} - \nabla^2\right\} \rho_2 &= \frac{2B[\rho_1 + \frac{1}{2}\rho_2][\frac{1}{2}\rho_2 + \rho_3]}{\rho_1 + \rho_2 + \rho_3} - D_2\rho_2 \qquad (1.1) \\
\left\{\frac{\partial}{\partial t} - \nabla^2\right\} \rho_3 &= \frac{B[\frac{1}{2}\rho_2 + \rho_3]^2}{\rho_1 + \rho_2 + \rho_3} - D_3\rho_3.
\end{aligned}
$$

For the sake of obtaining a simple model, we have assumed that the birth rate B and the migration properties do not depend on the genotype, while the death rates D_1, D_2, and D_3 do. The unit of length has been chosen to make the diffusivity due to random migration equal to 1. The nonlinear terms on the right come from the fact that the rate at which a gametes are formed per unit area is $B[\rho_1 + \frac{1}{2}\rho_2]$ while A gametes are formed at the rate $B[\frac{1}{2}\rho_2 + \rho_3]$. These rates imply that the fraction of all gametes being produced at $(\mathbf{x}, t)$ which are of type a is $[\rho_1 + \frac{1}{2}\rho_2]/[\rho_1 + \rho_2 + \rho_3]$.

We shall be concerned with the so-called **heterozygote intermediate** case, which is defined by the inequalities

$$D_1 \geq D_2 \geq D_3 > 0 \text{ and } D_1 > D_3. \qquad (1.2)$$

That is, the AA homozygote is fitter than the aa homozygote, and the fitness of the aA heterozygote lies between those of the homozygotes.

The purpose of the present work is to investigate the long-time behavior of a class of solutions of a system of the form (2.3) in which the total population density $\rho := \rho_1 + \rho_2 + \rho_3$ is kept under control by replacing the birth rate B and the fitnesses $B - D_i$ by suitable functions of ρ. Theorem 2.1 will show that if these functions satisfy certain inequalities, and if the initial values of the densities represent the perturbation through invasion or mutation of an equilibrium state in which the fitter allele A is absent, then the total

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population density lies between two positive constants, and the density vector $(\rho_1(\mathbf{x}, t), \rho_2(\mathbf{x}, t), \rho_3(\mathbf{x}, t))$ converges to a constant equilibrium $(0, 0, K_3)$ in which the allele a is absent, and $K_3 > 0$. Moreover, there is an easily computed positive number c_- with the property that if $c < c_-$, then the convergence is uniform on the sets $\{(\mathbf{x}, t) : |\mathbf{x}| \leq ct\}$. That is, the new final state spreads at least as quickly as any speed below c_-.

Theorem 4.1 gives an upper bound c_+ for the speed of spreading of the set where the solution is close to the equilibrium. However, $c_+ > c_-$, so that our results do not prove the existence of an asymptotic spreading speed for the problem (2.3).

When the densities are independent of the space variable $\mathbf{x}$ so that no net migration occurs, our model is a special case of equation (4) of chapter XV in the book of Kostitzin [6]. The convergence of $(\rho_1(t), \rho_2(t), \rho_3(t))$ to $(0, 0, K_3)$ for spatially independent solutions was stated in this book.

We note that our equations are for the spatial densities ρ_i of the genotypes rather than gene fractions, which are ratios of these densities. The reason is that we wish to model the random migration of individuals of the three genotypes, which leads to diffusion equations for these densities, but not for their ratios. The derivation of the equation of R. A. Fisher [3] for the case $D_2 = [D_1 + D_3]/2$ and its extension to other cases formally yields the Fisher equation

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} U = U(1 - U)[(D_1 - D_2)(1 - U) + (D_2 - D_3)U]. \qquad (1.3)$$

The formal derivation depends on the assumption that the gene fraction

$$u := \frac{\frac{1}{2}\rho_2 + \rho_3}{\rho_1 + \rho_2 + \rho_3}. \qquad (1.4)$$

satisfies a diffusion equation. This assumption is physically flawed, because while population densities diffuse, ratios do not. Mathematically, this flaw is reflected in the fact that when the diffusion operator, which is of second order in $\mathbf{x}$, is applied to a ratio, the chain rule yields not just a linear combination of the results of applying the operator to the numerator and to the denominator, but also a multiple of the scalar product of the gradients of the numerator and denominator. This cross-differentiation term is missing from the Fisher equation. While it is shown in the Appendix of [1] that if the differences in the fitnesses are small, U is a good approximation to u for a sizable but limited time, the relation of the long-time behaviors of U and u is unclear. That is, the long-time behavior of the system (1.1) needs to be be studied directly.

It was recently shown by P. Souplet and M. Winkler [8, 9] that if all the parameters in (1.1) are constant and if the inequalities (1.2) are satisfied, then any solution in which the allele A is initially present has the property that the gene fraction u defined by (1.4) converges to one, uniformly on every bounded $\mathbf{x}$-set. That is, the fitter allele drives the less fit one out of the population. In the ecologically interesting case in which the fitnesses $B - D_i$ are all positive, the proof in [8, 9] consists of showing that all three population

densities diverge exponentially to infinity, but that the rate of divergence of ρ_3 is greater than that of the other two densities. As was pointed out in [9], the fact that the population densities approach infinity shows that the model with constant parameters is unrealistic. More specifically, while such a model might provide a good approximation when the time is not too large, it was noted by T. R. Malthus [7] that faith in the accuracy of such a model for extremely long times can result in unrealistic predictions.

In the case of population ecology it was shown independently by Lotka and Volterra that the population can be kept under control by making the fitness a decreasing linear function of the population density. We shall show that in the population genetic problem the population can be kept under control by making B and the three fitnesses $B - D_i$ be decreasing functions of the total population density ρ, and we shall study the large-time asymptotics of solutions of the resulting system (2.3).

Our main result, Theorem 2.1, and the lemmas which are used to establish it are presented in Section 2. Section 3 examines the special case in which the birth rates and the fitnesses are logistic functions. It is shown that the conditions of Theorem 2.1 can be satisfied by choosing the coefficients in the logistic functions in a proper order. Theorem 4.1, which gives an upper bound for how quickly the convergence to $(0, 0, K_1)$ can spread in space, is stated in Section 4. Section 5 discusses some possible extensions of our results. All proofs are given in the Appendix, which is Section 6.

2 The takeover by the fitter allele of a system with population control.

We begin by writing the system (1.1) in a simpler form. The algebraic identities

$$
\begin{aligned}
[\rho_1 + \tfrac{1}{2}\rho_2]^2 &= [\rho_1 + \rho_2 + \rho_3]\rho_1 + \tfrac{1}{4}\rho_2^2 - \rho_1\rho_3 \\
2[\rho_1 + \tfrac{1}{2}\rho_2][\tfrac{1}{2}\rho_2 + \rho_3] &= [\rho_1 + \rho_2 + \rho_3]\rho_2 - 2[\tfrac{1}{4}\rho_2^2 - \rho_1\rho_3] \qquad (2.1) \\
[\tfrac{1}{2}\rho_2 + \rho_3]^2 &= [\rho_1 + \rho_2 + \rho_3]\rho_3 + \tfrac{1}{4}\rho_2^2 - \rho_1\rho_3.
\end{aligned}
$$

show that if one defines the function

$$
h := \frac{\tfrac{1}{4}\rho_2^2 - \rho_1\rho_3}{\rho_1 + \rho_1 + \rho_3}, \qquad (2.2)
$$

then the system can be written in the form

$$
\begin{aligned}
\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \rho_1 &= [B - D_1]\rho_1 + Bh \\
\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \rho_2 &= [B - D_2]\rho_2 - 2Bh \qquad (2.3) \\
\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \rho_3 &= [B - D_3]\rho_3 + Bh.
\end{aligned}
$$

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Remarks. 1. Unlike the usual model for the population of three interacting species, this system involves not only the three fitnesses $B - D_i$, but also the per capita birth rate B.

2. The definition (2.2) of h shows that $h = 0$ if and only if the Hardy-Weinberg law is satisfied.

We shall study a system of the form (2.3) in which the birth rate B and the death rates D_i are functions of the total population density

$$\rho := \rho_1 + \rho_2 + \rho_3 \tag{2.4}$$

with certain properties. Because one can expect the per capita birth rate B to decrease and the death rates D_i to increase with increased crowding, we shall always assume that **the fitnesses $B(\rho) - D_i(\rho)$ are decreasing functions of ρ.**

We first observe that if the allele A is initially absent so that $\rho_2(\mathbf{x}, 0) \equiv \rho_3(\mathbf{x}, 0) \equiv 0$, then because the system (2.3) contains no mechanism for in-migration or mutation, $\rho_2 \equiv \rho_3 \equiv 0$ for $t > 0$. In this case, the definition (2.2) shows that $h \equiv 0$, so that the first equation of the system (2.3) becomes

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \rho_1 = [B(\rho_1) - D_1(\rho_1)]\rho_1. \tag{2.5}$$

This is a single equation of the type studied by Lotka, Volterra, and others to model the growth and spread of a single species. (See, e.g., [1, 2, 10].) If $\alpha > 0$ and $B(\alpha) - D_1(\alpha) \neq 0$, the solution of (2.5) with the constant initial value α, is given implicitly by the equation

$$\int_\alpha^{\rho_1} \frac{d\sigma}{[B(\sigma) - D_1(\sigma)]\sigma} = t.$$

If $B(\rho_1) - D_1(\rho_1) > 0$ for all positive ρ_1, this shows that ρ_1 must approach infinity with t. Hence, as in Malthus [7], the equation (2.5) is an unrealistic predictor for long-time behavior. If $B(\rho_1) - D_1(\rho_1) < 0$ for all positive ρ_1, then ρ approaches zero as $t \to \infty$, and the same is true of all bounded solutions of (2.5), which means that the aa monoculture is not viable. We conclude that since $B(\rho) - D_1(\rho)$ is a decreasing function of ρ, the only interesting model of this kind is one in which $B(\rho) - D_1(\rho)$ changes sign at some value $K_1 > 0$. In this case, any solution of (2.5) with $\rho_1(\mathbf{x}, 0)$ bounded, non-negative, and not identically zero converges to the constant K_1, uniformly on every bounded set, as $t \to \infty$. The constant K_1 is called the **carrying capacity** of the habitat for the aa monoculture.

In a similar vein, we consider the special case in which $\rho_1(\mathbf{x}, 0) \equiv \rho_2(\mathbf{x}, 0) \equiv 0$, to find a solution $(0, 0, \rho_3(\mathbf{x}, t))$, where ρ_3 satisfies the scalar equation

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \rho_3 = [B(\rho_3) - D_3(\rho_3)]\rho_3. \tag{2.6}$$

As in the case of the above equation (2.5), we find the this model is of interest only under the assumption that there is a $K_3 > 0$ such that the decreasing

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function $B(\rho) - D_3(\rho)$ is zero at K_3. Then K_3 is the carrying capacity of the habitat for the AA monoculture.

If $D_1(K_1) > D_3(K_1)$, then $B(K_1) - D_3(K_1) = D_1(K_1) - D_3(K_1) > 0$. Since $B - D_3$ is decreasing,
$$K_3 > K_1.$$
The same argument also shows that if the heterozygote intermediate condition (1.2) is valid at $\rho = K_1$ and $\rho = K_3$, then there is a K_2 with

$$K_1 \leq K_2 \leq K_3 \text{ and } B(K_2) - D_2(K_2) = 0,$$

Since the system (2.3) has no solution of the form $(0, \rho_2(\mathbf{x}, t), 0)$ with $\rho_2 \not\equiv 0$, it is difficult to assign a biological meaning to K_2.

Finally, we observe that the constant vectors $(K_1, 0, 0)$ and $(0, 0, K_3)$ are equilibria of the system (2.3).

We are primarily interested in the situation in which, until shortly before $t = 0$, the population consisted entirely of aa homozygotes, with its density ρ_1 everywhere equal to the carrying capacity K_1. Then A alleles appeared, either through mutation or through invasion. In both of these processes, ρ_1 is not increased, while ρ_2 and ρ_3 are not decreased. If the mutation or invasion is not too large, we can expect that

$$
\begin{aligned}
& K_1 \leq \rho_1(\mathbf{x}, 0) + \rho_2(\mathbf{x}, 0) + \rho_3(\mathbf{x}, 0) \leq K_3, \\
& \tfrac{1}{2}\rho_2(\mathbf{x}, 0) + \rho_3(\mathbf{x}, 0) \not\equiv 0, \text{ and} \qquad (2.7)\\
& \rho_1(\mathbf{x}, 0) - \rho_3(\mathbf{x}, 0) \leq K_1.
\end{aligned}
$$

We shall establish the convergence of a large class of solutions of (2.3) with such initial conditions to the equilibrium $(0, 0, K_3)$ under some simple conditions on the birth and death rate functions. We begin with a known proposition, which gives elementary assumptions about the functions $B(\rho)$ and D_i under which the inequality $K_1 \leq \rho \leq K_3$ for the initial conditions implies the same inequality for all $t > 0$.

Proposition 2.1. *Suppose that for some constants $K_1 > 0$ and $K_3 > K_1$ the functions $B(\rho)$, $D_1(\rho)$, $D_2(\rho)$, and $D_3(\rho)$ are continuously differentiable and non-negative on the interval $K_1 \leq \rho \leq K_3$, and that*

$$B(K_1) - D_i(K_1) \geq 0 \text{ and } B(K_3) - D_i(K_3) \leq 0 \text{ for } i = 1, 2, 3. \qquad (2.8)$$

Then the inequalities

$$K_1 \leq \rho_1(\mathbf{x}, 0) + \rho_2(\mathbf{x}, 0) + \rho_3(\mathbf{x}, 0) \leq K_3,$$

for the initial values of a solution of the system (2.3) imply that

$$K_1 \leq \rho_1(\mathbf{x}, t) + \rho_2(\mathbf{x}, t) + \rho_1(\mathbf{x}, t) \leq K_3 \text{ for all } \mathbf{x} \text{ and all } t \geq 0. \qquad (2.9)$$

The proof of this Proposition and all other proofs will be presented in the Appendix, which is Section 6.

Remark. Proposition 2.1 shows that as long as the initial values of the total population density ρ lie between K_1 and K_3, this density remains bounded below by K_1 and above by K_3, so that the population is controlled and kept from extinction. It also implies that the corresponding solution of the system depends only on the properties of the restriction of the functions $B(\rho)$ and $D_i(\rho)$ to the interval $[K_1, K_3]$.

We shall show below that the following hypotheses permit one to show that a solution whose initial values satisfy the conditions (2.7) converge to the equilibrium $(0, 0, K_3)$ and to find a lower bound for the speed at which this convergence spreads in space.

Hypotheses 2.1. *i. The constants K_1, K_2, and K_3 satisfy the inequalities*

$$0 < 3K_1 < K_2 < K_3. \tag{2.10}$$

ii. The birth rate $B(\rho)$ and the death rates $D_1(\rho), D_2(\rho)$, and $D_3(\rho)$ are continuously differentiable on the interval $[K_1, K_3]$, and have the following properties.

$$B(K_i) - D_i(K_i) = 0 \text{ and } B'(\rho) - D_i'(\rho) < 0$$
$$\text{for } i = 1, 2, 3 \text{ and } K_1 \le \rho \le K_3. \tag{2.11}$$

iii.

$$D_1(\rho) \ge D_2(\rho) \ge \tfrac{1}{2}[D_1(\rho) + D_3(\rho)] \text{ for } K_1 \le \rho \le K_3, \tag{2.12}$$

iv.

$$D_3(\rho) > 0 \text{ for } K_1 \le \rho \le K_3. \tag{2.13}$$

Remark. The inequalities (2.12) imply that $D_1 \ge D_2 \ge D_3$, and the inequalities (2.11) imply that $D_1(\rho) > D_3(\rho)$, so that the heterozygote intermediate conditions (1.2) are satisfied for $K_1 \le \rho \le K_3$.

Our main result is the the following theorem.

Theorem 2.1. *Let the Hypotheses 2.1 be satisfied. Let $(\rho_1(\mathbf{x}, t), \rho_2(\mathbf{x}, t), \rho_3(\mathbf{x}, t))$ be any non-negative solution of the system (2.3) whose initial values are continuous and satisfy the inequalities (2.7).*

Then for any c with

$$c < c_- := 2\sqrt{D_1(K_1) - D_2(K_1)} \tag{2.14}$$

the solution has the properties

$$\lim_{t \to \infty} \left[\max_{|\mathbf{x}| \le ct} \rho_1(\mathbf{x}, t) \right] = 0,$$

$$\lim_{t \to \infty} \left[\max_{|\mathbf{x}| \le ct} \rho_2(\mathbf{x}, t) \right] = 0, \text{ and} \tag{2.15}$$

$$\lim_{t \to \infty} \left[\max_{|\mathbf{x}| \le ct} |K_3 - \rho_3(\mathbf{x}, t)| \right] = 0.$$

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We shall prove Theorem 2.1 by using Proposition 2.1 and a sequence of lemmas. All proofs will be presented in the Appendix (Section 6). The proofs will be based on a form of the maximum principle often called a Phragmén-Lindelöf principle, which works, as here, when the habitat is unbounded. A simple version of this principle will be stated and proved as Proposition 6.1 at the beginning of the Appendix.

We begin with a bound for the difference $\rho_1 - \rho_3$.

Lemma 2.1. *Assume that the conditions of Theorem 2.1 are satisfied. Then*

$$\rho_1(\mathbf{x}, t) - \rho_3(\mathbf{x}, t) \leq K_1 \text{ for all } t \geq 0. \tag{2.16}$$

Because (2.13) says that the continuous function $D_3(\rho)$ is strictly positive on the closed interval $[K_1, K_3]$, we see that

$$\delta := \min_{K_1 \leq \rho \leq K_3} D_3(\rho) > 0. \tag{2.17}$$

The next lemma gives a decaying uniform upper bound for the nonlinear function h defined in equation (2.2). We note that it does not give a lower bound for h.

Lemma 2.2. *Let the conditions of Theorem 2.1 be satisfied, and let h be defined by (2.2). Then*

$$h(\mathbf{x}, t) \leq \max\{\sup_{\mathbf{x}} h(\mathbf{x}, 0), 0\} e^{-\delta t}, \tag{2.18}$$

where δ is defined by (2.17).

We now obtain a spreading result for the density

$$q := 2\rho_3 + \rho_2 \tag{2.19}$$

of the allele A.

Lemma 2.3. *Assume that the conditions of Theorem 2.1 are satisfied. Then for any number*

$$c < c_- := 2\sqrt{D_1(K_1) - D_2(K_1)} \tag{2.20}$$

the inequality

$$\liminf_{t \to \infty} \left[\min_{|\mathbf{x}| \leq ct} q(\mathbf{x}, t) \right] \geq K_2 - K_1 \tag{2.21}$$

is valid.

We are now ready to prove the first statement of Theorem 2.1.

Lemma 2.4. *Let the conditions of Theorem 2.1 be satisfied. Then there are positive constants M_1 and $\hat{\alpha}$ such that*

$$\max_{|\mathbf{x}| \leq ct} \rho_1(\mathbf{x}, t) \leq M_1 e^{-\hat{\alpha} t}. \tag{2.22}$$

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Lemmas 2.2 and 2.4 also yield the second statement of Theorem 2.1.

Lemma 2.5. *Assume that the conditions of Theorem 2.1 are satisfied. For any $c < c_-$ there is an $M_2 > 0$ such that*

$$\max_{|\mathbf{x}| \leq ct} \rho_1(\mathbf{x}, t)] \leq M_2 e^{-\frac{1}{2}\hat{\alpha}t},$$

where $\hat{\alpha}$ is the constant in Lemma 2.4.

The last lemma gives the last statement of Theorem 2.1.

Lemma 2.6. *Let the conditions of Theorem 2.1 be satisfied. Then for any*

$$c < c_-$$

there are an M_3 and an $\bar{\alpha}$ with

$$0 < \bar{\alpha} \leq \tfrac{1}{2}\hat{\alpha} \tag{2.23}$$

such that

$$\max_{|\mathbf{x}| \leq ct} |K_3 - \rho_3(\mathbf{x}, t)| \leq M_3 e^{-\bar{\alpha}t}. \tag{2.24}$$

We observe that Lemmas 2.4, 2.5, and 2.6 immediately imply the statements (2.15) of Theorem 2.1.

Since the asymptotic spreading speed of the Fisher equation (1.3) is bounded below by the spreading speed $2\sqrt{D_1 - D_2}$ of its linearization about $U = 0$, we see that these lower bounds coincide if we take D_1 and D_2 in the latter formula to be the values $D_1(K_1)$ and $D_2(K_1)$ of the death rates of (2.3) at the unstable equilibrium $(K_1, 0, 0)$.

3 An example with logistic functions.

In order to find an explicit system for which the Hypotheses 2.1 are satisfied, we first choose constants

$$0 < 3K_1 < K_2 < K_3,$$

so that Hypothesis 2.1.i is satisfied. We choose the restrictions of the birth rate and death rates to the interval $[K_1, K_3]$ in the form

$$
\begin{aligned}
B(\rho) &= \beta[1 - (\rho/J)] \\
D_i(\rho) &= \beta[1 - (\rho/J)] - \gamma_i[1 - (\rho/K_i)] \text{ for } i = 1, 2, 3.
\end{aligned}
\tag{3.1}
$$

so that the birth rate and the fitnesses are Verhulst logistic functions. All parameters are positive. These functions clearly satisfy Hypothesis 2.1.ii.

The definitions of the D_i in (3.1) show that (2.12) can be written in the form

$$\gamma_1[1-(\rho/K_1)] \le \gamma_2[1 - (\rho/K_2)]$$
$$\le \tfrac{1}{2}\{\gamma_1[1 - (\rho/K_1)] + \gamma_3[1 - (\rho/K_3)]\} \text{ for } K_1 \le \rho \le K_3. \tag{3.2}$$

Because all the functions are linear, these inequalities are true on the interval $[K_1.K_3]$ if and only if they are true at the end points. By setting $\rho = K_1$, we obtain the inequalities

$$0 \le \gamma_2[1 - (K_1/K_2)] \le \tfrac{1}{2}\gamma_3[1 - (K_1/K_3)].$$

We can satisfy this by choosing any positive γ_2, and choosing any γ_3 such that

$$\gamma_3 \ge 2\gamma_2[1 - (K_1/K_2)]/[1 - (K_1/K_3)]. \tag{3.3}$$

By setting $\rho = K_3$ in (3.2) and dividing by the negative number $\tfrac{1}{2}[1 - (K_3/K_1)]$, we find the inequalities

$$\gamma_2[(K_3/K_2)-1]/[(K_3/K_1)-1] \le \gamma_1 \le 2\gamma_2[(K_3/K_2)-1]/[(K_3/K_1)-1]. \tag{3.4}$$

Thus Hypothesis 2.1.iii is satisfied whenever γ_2 is any positive number, γ_1 satisfies (3.4), and γ_3 satisfies (3.3).

The remaining Hypothesis 2.1.iv takes the form

$$\beta[1 - (\rho/J)] - \gamma_3[1 - (\rho/K_3)] > 0 \text{ for } K_1 \le \rho \le K_3.$$

As above, the function is linear, so that we only have to satisfy the inequality at the end points. This leads to the inequalities

$$\beta[1 - (K_1/J)] > \gamma_3[1 - (K_1/K_3)] \text{ and } \beta[1 - (K_3/J] > 0.$$

The second of these is satisfied if and only if

$$J > K_3. \tag{3.5}$$

The first only requires that

$$\beta > \gamma_3[1 - (K_1/K_3)]/[1 - (K_1/J)]. \tag{3.6}$$

Thus we have shown how to choose the parameters in the functions (3.1) so that the Hypotheses 2.1 are satisfied.

In order to have a biologically realistic model, we should require the death rates to be increasing functions of ρ. This is equivalent to the requirement that

$$\beta/J < \min\{\gamma_1/K_1, \gamma_2/K_2, \gamma_3/K_3\}.$$

This inequality is compatible with (3.6) if and only if

$$J > K_1 + \gamma_3[1 - (K_1/K_3)]/[\min\{\gamma_1/K_1, \gamma_2/K_2, \gamma_3/K_3\}],$$

which is at least as strict as (3.5).

It is usually observed in nature that the dimensionless advantage $[D_1 - D_3]/[D_1 + D_3]$ of the fitter allele A is very small. The logistic model has this property when the parameters J and β are large.

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4 A speed limit.

Let $(\rho_1(\mathbf{x},t), \rho_2(\mathbf{x},t), \rho_3(\mathbf{x},t))$ be any solution of (2.3) whose initial values satisfy the inequalities (2.7). Theorem 2.1 implies that for any $\epsilon > 0$ and any $c < c_-$ there is a T_ϵ such that the set

$$\mathcal{N}_\epsilon(t) := \{\mathbf{x} : \rho_1(\mathbf{x},t) \le \epsilon, \rho_2(\mathbf{x},t) \le \epsilon, K_3 - \rho_3(\mathbf{x},t) \le \epsilon\}$$

contains the ball $\{|\mathbf{x}| \le ct\}$ when $t \ge T_\epsilon$. That is, the set $\mathcal{N}_\epsilon$ spreads in all directions at a speed which is greater than any number below c_-. In this section we present an upper bound c_+ on the speed with which the set $\mathcal{N}_\epsilon(t)$ can spread.

Theorem 4.1. *Assume that the conditions of Theorem 2.1 are satisfied. Suppose that the initial values of the density $q = 2\rho_3 + \rho_2$ of the A allele have the additional property that they are zero outside a bounded set.*

Define the number

$$c_+ := 2\sqrt{D_1(K_1) - D_3(K_1)}, \tag{4.1}$$

Then for any $c > c_+$

$$\liminf_{t\to\infty}[\inf_{|\mathbf{x}| \ge ct} \rho_1(\mathbf{x},t)] \ge K_1 \ \text{and} \ \lim_{t\to\infty}[\sup_{|\mathbf{x}| \ge ct} \rho_3(\mathbf{x},t)] = 0. \tag{4.2}$$

It follows that the first and third equation in (2.15), which, according to Theorem 2.1, are satisfied when $c < c_-$, are violated when $c > c_+$.

The proof of this theorem is at the end of the Appendix.

Remark. Hypothesis (2.12) shows that $D_1(\rho) - D_2(\rho) \le \frac{1}{2}[D_1(\rho) - D_3(\rho)]$. Setting $\rho = K_1$ then shows that $c_- \le c_+/\sqrt{2}$, so that Theorems 2.1 and 4.1 do not imply that the system (2.3) has an asymptotic spreading speed, or even that one component of one particular solution has an asymptotic spreading speed.

5 Discussion.

The conclusions of Theorem 2.1 do not require knowledge about the behavior of $B(\rho)$ and the $D_i(\rho)$ outside the set $K_1 \le \rho \le K_3$. For example, the fitnesses $B - D_i$ need not be decreasing outside this interval. In particular, the fitnesses may all be negative for sufficiently small ρ. In such a case, the extinction state (0,0,0) is a local attractor, so that the model (2.3) has a strong Allee effect.

As we pointed out at the end of Section 2, the lower bound c_- in Theorem 2.1 coincides with the speed of the linearization of the Fisher equation (1.3) with the death rates $D_i = D_i(K_1)$. Hence, c_- is also a lower bound for the spreading speed c^* of the equation (1.3) when the death rates are

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those of (2.3) at the unstable equilibrium $(K_1, 0, 0)$. An upper bound for c^* is obtained by observing that the heterozygote intermediate inequalities imply that $D_1 - D_2 \leq D_1 - D_3$ and $D_2 - D_3 \leq D_1 - D_3$. It then follows that $c^* \leq 2\sqrt{D_1 - D_3}$. This shows that for the equation (1.3) with $D_i = D_i(K_1)$ we have the bounds

$$c_- \leq c^* \leq c_+.$$

Thus, Theorems 2.1 and 4.1 are consistent with the conjecture that c^* is also the asymptotic spreading speed of the system (2.3). However, to prove this conjecture, one would have to show the very strong statement that for every suitable solution the three functions ρ_1, ρ_2, and $K_3 - \rho_3$ approach their limits 0 with the asymptotic speed c^*.

The strengthened form (2.12) of the heterozygote intermediate condition $D_1(\rho) \geq D_2(\rho) \geq D_3(\rho)$ was only used in the proof of Lemma 2.2, and the strengthened form (2.10) of the natural condition $K_1 < K_2 < K_3$ was only used in the proof of Lemma 2.4. Neither of these conditions seems to be biologically significant. It is quite possible that these extra conditions can be eliminated by using a different proof. It was, in fact, shown in [12] that one can prove the uniform convergence to $(0, 0, K_3)$ of a solution of (2.3) in a bounded domain with impenetrable boundaries without them. On the other hand, the assumption that the three genotypes have the same diffusivity is vital to our proofs.

The present paper is only a first look at the long-time behavior of solutions of the non-cooperative system (2.3). Much further work needs to be done on this problem.

6 Appendix: Proofs

Many of the proofs of the lemmas of Section 2 and the proof of Theorem 4.1 will be based upon a form of the maximum principle for parabolic operators discovered by A. Friedman in Part II of [4] and known as the Phragmén-Lindelöf principle. It has the advantage that it can be applied when, as here, the habitat is unbounded. The following proposition states and proves a result which is weaker than that of Friedman, but is more easily proved.

Proposition 6.1. *Let $\mathcal{D}$ be a domain in the half-space $\{(\mathbf{x}, t) : t > 0\}$.*

Let $v(\mathbf{x}, t)$ be a continuous function on the closure of $\mathcal{D}$ with the following properties.

1. *$v(\mathbf{x}, t)$ is smooth in $\mathcal{D}$, and*

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} v \leq 0 \text{ at all } (\mathbf{x}, t) \text{ in } \mathcal{D} \text{ at which } v > 0.$$

2. *$v(\mathbf{x}, t) \leq 0$ at the boundary points of $\mathcal{D}$.*

3. *For every $T > 0$, the function $v(\mathbf{x}, t)$ is uniformly bounded above for all $(\mathbf{x}, t)$ in $\mathcal{D}$ with $0 \leq t \leq T$.*

Then $v(\mathbf{x}, t) \le 0$ for all $(\mathbf{x}, t)$ in $\mathcal{D}$.

Proof. Define the function

$$w(\mathbf{x}, t) := v(\mathbf{x}, t)/[3nt + 1 + |\mathbf{x}|^2],$$

where n is the dimension of the $\mathbf{x}$-space. By replacing v by $[3nt + 1 + |\mathbf{x}|^2]w$ in the above Assumption 1, we find that

$$[3nt + 1 + |\mathbf{x}|^2]\frac{\partial w}{\partial t} - [3nt + 1 + |\mathbf{x}|^2]\nabla^2 w - 4\mathbf{x} \cdot \nabla w + nw \le 0 \text{ when } w > 0. \quad (6.1)$$

Suppose for the sake of contradiction that $v(\bar{\mathbf{x}}, \bar{t}) > 0$ for some $(\bar{\mathbf{x}}, \bar{t})$ in D. Then also $w(\bar{\mathbf{x}}, \bar{t}) > 0$. Define the set

$$\mathcal{S} := \{(\mathbf{x}, t) \text{ in } \mathcal{D} : 0 \le t \le \bar{t} \text{ and } w(\mathbf{x}, t) \ge w(\bar{\mathbf{x}}, \bar{t})\}.$$

By Assumption 3, there is a constant $L \le 0$ such that $v(\mathbf{x}, t) \le L$ for $(\mathbf{x}, t)$ in $\mathcal{D}$ and $0 \le t \le \bar{t}$. Therefore, $w(\bar{\mathbf{x}}, \bar{t}) \le w(\mathbf{x}, t) \le L/[1 + |\mathbf{x}|^2]$ on $\mathcal{S}$, so that $|\mathbf{x}|^2 \le L/w(\bar{\mathbf{x}}, \bar{t})$. That is, $\mathcal{S}$ is a nonempty closed bounded set. Because $w(\mathbf{x}, t) \le 0$ at boundary points of $\mathcal{D}$, $\mathcal{S}$ is disjoint from the boundary. Thus, t attains its minimum value $\hat{t} > 0$ on $\mathcal{S}$ at a point $(\hat{\mathbf{x}}, \hat{t})$ of $\mathcal{D}$. This point has the properties

$$w(\mathbf{x}, t) \le w(\bar{\mathbf{x}}, \bar{t}) = w(\hat{\mathbf{x}}, \hat{t}) \text{ for } (\mathbf{x}, t) \text{ in } \mathcal{D} \text{ and } 0 \le t \le \hat{t}.$$

Elementary calculus then shows that

$$\frac{\partial w(\hat{\mathbf{x}}, \hat{t})}{\partial t} \ge 0, \ \nabla w(\hat{\mathbf{x}}, \hat{t}) = 0, \text{ and } \nabla^2 w(\hat{\mathbf{x}}, \hat{t}) \le 0.$$

Because $w(\hat{\mathbf{x}}, \hat{t}) = w(\bar{\mathbf{x}}, \bar{t}) > 0$, these inequalities show that the left-hand side of (6.1) at the point $(\hat{\mathbf{x}}, \hat{t})$ is strictly positive, which contradicts (6.1). Thus the assumption that $v(\bar{\mathbf{x}}, \bar{t}) > 0$ for some point of $\mathcal{D}$ leads to a contradiction. We conclude that $v(\mathbf{x}, t) \le 0$ for all $(\mathbf{x}, t)$ in $\mathcal{D}$, which is the statement of Proposition 6.1. □

Proof of Proposition 2.1. We define the new functions $\tilde{B}(\rho)$ and $\tilde{D}_i(\rho)$ by

$$\tilde{B}(\rho) := \begin{cases} B(\rho) \text{ for } K_1 \le \rho \le K_3 \\ B(K_1) \text{ for } 0 \le \rho \le K_1 \\ B(K_3) \text{ for } \rho \ge K_3 \end{cases}$$

and

$$\tilde{D}_i(\rho) := \begin{cases} D_i(\rho) \text{ for } K_1 \le \rho \le K_3 \\ D_i(K_1) \text{ for } 0 \le \rho \le K_1 \\ D_i(K_3) \text{ for } \rho \ge K_3 \end{cases} \quad \text{for } i = 1, 2, 3.$$

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These functions are continuous and piecewise continuously differentiable, and their one-sided derivatives are uniformly bounded. Therefore, we can find the solution $(\tilde{\rho}_1(\mathbf{x}, t), \tilde{\rho}_1(\mathbf{x}, t), \tilde{\rho}_1(\mathbf{x}, t))$ of the system which is obtained from (2.3) by replacing B and the D_i by $\tilde{B}$ and the $\tilde{D}_i$ and ρ by $\tilde{\rho}$, where $\tilde{\rho}$ satisfies the initial conditions

$$\tilde{\rho}_i(\mathbf{x}, t) = \rho_i(x, t).$$

By adding the three equations of (2.3) with B, D_i, and ρ_i replaced by the tilde functions and using the inequalities (2.8), we obtain the inequality

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \tilde{\rho} = [\tilde{B}(\tilde{\rho}) - \tilde{D}_1(\tilde{\rho})]\tilde{\rho}_1 + [\tilde{B}\tilde{(\rho)} - \tilde{D}_2(\tilde{\rho})]\tilde{\rho}_2 + [\tilde{B}(\tilde{\rho}) - \tilde{D}_3(\tilde{\rho})]\tilde{\rho}_3]$$

$$\leq 0 \text{ when } \tilde{\rho} \geq K_3.$$
$$(6.2)$$

The conditions $B(K_3) - D_i(K_3) \leq 0$ show that

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} [\tilde{\rho} - K_3] \leq 0 \text{ when } \tilde{\rho}(\mathbf{x}, t) - K_3 \geq 0.$$

This is Assumption 1 of Proposition 6.1 with $v := \rho - K_3$. Assumption 2 follows from the fact that $\tilde{\rho}(\mathbf{x}, 0) = \rho(\mathbf{x}, 0) \leq K_3$, and Assumption 3 is valid because the usual construction of the solution of (2.3) by iterating the corresponding system of integral equations shows that $\sup_{\mathbf{x}} \tilde{\rho}(\mathbf{x}, t)$ grows at most exponentially in t. Proposition 6.1 now shows that $\tilde{\rho}(\mathbf{x}, t) - K_3 \leq 0$ for $t \geq 0$. That is, $\tilde{\rho}(\mathbf{x}, t) \leq K_3$ for $t \geq 0$.

The analogous argument shows that the right-hand side of the first line of (6.2) is non-negative for $\tilde{\rho} \leq K_1$. Then Proposition 6.1 applied to $v := K_1 - \tilde{\rho}$ shows that $\tilde{\rho} \geq K_1$ for $t \geq 0$. That is, $K_1 \leq \tilde{\rho} \leq K_3$.

Since $\tilde{B}$ and the $\tilde{D}_i$ agree with B and the D_i on the interval $[K_1, K_3]$, the function $\tilde{\rho}$ satisfies the original equation (2.3) and has the same initial values as ρ. Therefore, $\rho(\mathbf{x}, t) = \tilde{\rho}(\mathbf{x}, t)$. We have thus shown that $K_1 \leq \rho(\mathbf{x}, t) \leq K_3$ for $t \geq 0$, which is the statement of Proposition 2.1. $\qquad \square$

Remarks. 1. It is easily verified that the Hypotheses 2.1 imply the conditions of Proposition 2.1. Since Theorem 2.1 concerns solutions of (2.3) whose initial conditions satisfy the inequalities (2.7), we shall use the inequalities $K_1 \leq \rho(\mathbf{x}, t) \leq K_3$ in all the proofs which follow.

2. Proposition 2.1 shows that as long as $K_1 \leq \rho(\mathbf{x}, 0) \leq K_3$, the solution of (2.3) is independent of the values of B and the D_i outside the interval $[K_1, K_3]$.

3. Because the set $\{(\rho_1, \rho_2, \rho_3) : \rho_1 \geq 0, \rho_2 \geq 0, \rho_3 \geq 0, K_1 \leq \rho_1 + \rho_2 + \rho_3 \leq K_3\}$ is convex, Proposition 2.1 also follows from Theorem 1 of [11].

Proof of Lemma 2.1. By subtracting the third equation of (2.3) from the first, we find that

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} [\rho_1 - \rho_3] = [B(\rho) - D_1(\rho)]\rho_1 - [B(\rho) - D_3(\rho)]\rho_3.$$

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Since $B(\rho) - D_1(\rho)$ is non-increasing and vanishes at K_1, we see that $[B(\rho) - D_1(\rho)] \leq 0$ on the interval $[K_1, K_3]$. Similarly, we see that $B(\rho) - D_3(\rho) \geq 0$ on this interval. Therefore

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} [\rho_1 - \rho_3 - K_1] \leq 0.$$

Since $\rho_1(\mathbf{x}, 0) - \rho_3(\mathbf{x}, 0) \leq K_1$ by (2.7), the application of Proposition 6.1 to the function $v := \rho_1 - \rho_3 - K_1$ in the half-space $t > 0$ shows that $\rho_1(\mathbf{x}, t) - \rho_3(\mathbf{x}, t) \leq K_1$ for all $t \geq 0$. This is the statement (2.16) of Lemma 2.1. $\quad\square$

Proof of Lemma 2.2. An exercise in using the chain rule together with patient manipulation shows that if $(\rho_1(\mathbf{x}, t), \rho_2(\mathbf{x}, t), \rho_3(\mathbf{x}, t))$ is a solution of (2.3) and h is defined by (2.2), then

$$
\begin{aligned}
\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} h = & -(2/\rho^3) \left| [\tfrac{1}{2}\rho_2 + \rho_3] \nabla[\rho_1 + \tfrac{1}{2}\rho_2] - [\rho_1 + \tfrac{1}{2}\rho_2] \nabla[\rho_1 + \tfrac{1}{2}\rho_2] \right|^2 \\
& - \tfrac{1}{4} [2D_2(\rho) - D_1(\rho) - D_3(\rho)] \rho_2^2 \rho^{-1} \\
& - \{ D_1(\rho) + D_3(\rho) - \rho^{-1}[D_1(\rho)\rho_1 + D_2(\rho)\rho_2 + D_3(\rho)\rho_3] \} h.
\end{aligned}
$$
(6.3)

The first term on the right is the cross-differentiation term. The advantage of the function h is that this term is non-positive. The inequality (2.12) shows that the second term is also non-positive. Thus we obtain the differential inequality

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} h \leq -\{ D_1(\rho) + D_3(\rho) - \rho^{-1}[D_1(\rho)\rho_1 + D_2(\rho)\rho_2 + D_3(\rho)\rho_3] \} h.$$
(6.4)

Because the inequalities (2.12) imply the heterozygote intermediate inequalities $D_1(\rho) \geq D_2(\rho) \geq D_3(\rho)$, we see that $D_1\rho_1 + D_2\rho_2 + D_3\rho_3 \leq D_1\rho$. Therefore, the coefficient of h on the right of (6.4) has the property

$$-\{ D_1(\rho) + D_3(\rho) - \rho^{-1}[D_1(\rho)\rho_1 + D_2(\rho)\rho_2 + D_3(\rho)\rho_3] \} \leq -D_3(\rho) \leq -\delta,$$

where $\delta := \min_{K_1 \leq \rho \leq K_3} D_3(\rho) > 0$. Thus we see that

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} h \leq -\delta h \quad \text{when } h \geq 0.$$

It follows that

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} [h - \max\{\sup h(\mathbf{x}, 0), 0\} e^{-\delta t}] \leq -\delta[h - \max\{\sup h(\mathbf{x}, 0), 0\} e^{-\delta t}]$$

$$\leq 0 \quad \text{when } h(\mathbf{x}, t) - \max\{\sup h(\mathbf{x}, 0), 0\} e^{-\delta t} \geq 0.$$

This shows that the function

$$v(\mathbf{x}, t) := h(\mathbf{x}, t) - \max\{\sup h(\mathbf{x}, 0), 0\} e^{-\delta t}$$

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satisfies Assumption 1 of Proposition 6.1. Since $v(\mathbf{x}, 0) \leq 0$ and $v(\mathbf{x}, t) \leq K_3 e^{\delta t}/4$, Proposition 6.1 implies that $v(\mathbf{x}, t) \leq 0$ for $t \geq 0$, which is the statement of Lemme 2.2. □

Proof of Lemma 2.3. Adding the second equation of (2.3) to twice the third equation shows that

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} q = [B(\rho) - D_2(\rho)]\rho_2 + 2[B(\rho) - D_3(\rho)]\rho_3.$$

Because $D_3 \leq D_2$, the right-hand side is bounded below by $[B(\rho) - D_2(\rho)]q$.

It is easily verified that $\rho = \rho_1 - \rho_3 + q$. Therefore Lemma 2.1 shows that

$$\rho \leq K_1 + q.$$

Because (2.11) with $i = 2$ states that $B - D_2$ is positive and decreasing for $K_1 \leq \rho < K_2$, we conclude that

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} q \geq [B(K_1 + q) - D_2(K_1 + q)]q \text{ for } 0 \leq q \leq K_2 - K_1. \quad (6.5)$$

We now define $\hat{q}$ to be the solution of the initial value problem

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} \hat{q} = [B(K_1 + \hat{q}) - D_2(K_1 + \hat{q})]\hat{q}$$

$$\hat{q}(\mathbf{x}, 0) = \min\{q(\mathbf{x}, 0), \tfrac{1}{2}[K_2 - K_1]\}. \quad (6.6)$$

Because of of (2.11) with $i = 2$, this equation is of Fisher-KPP type. In particular, the function $B(K_1 + \hat{q}) - D_2(K_1 + \hat{q})]$ decreases from $B(K_1) - D_2(K_1)$ to 0 as ρ_2 increases from 0 to $K_2 - K_1$. It follows (see, e.g. [5, 1, 2, 10]) that (6.6) has the asymptotic spreading speed $2\sqrt{B(K_1) - D_2(K_2)}$. Because (2.11) with $i = 1$ shows that $B(K_1) = D_1(K_1)$, we can write this speed as $2\sqrt{D_1(K_1) - D_2(K_2)}$. In particular,

$$\lim_{t \to \infty} \left[\min_{|\mathbf{x}| \leq ct} \hat{q}(\mathbf{x}, t)\right] = K_2 - K_1 \text{ when } c < c_- := 2\sqrt{D_1(K_1) - D_2(K_1)]}. \quad (6.7)$$

By subtracting the two sides of the inequality (6.5) from those of the equation (6.6), we obtain the inequality

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} [\hat{q} - q] \leq [B(K_1 + \hat{q}) - D_2(K_1 + \hat{q})]\hat{q} - [B(K_1 + q) - D_2(K_1 + q)]q$$

(6.8)

Since $B' - D_2' < 0$ by (2.11), the derivative of the function $[B(K_1 + q) - D_2(K_1 + q)]q$ is bounded above by $B(\rho) - D(\rho) \leq B(K_1) - D_2(K_1) = D_1(K_1) - D_2(K_1)$ when $0 \leq q \leq K_2 - K_1$. The mean value theorem then shows that the right-hand side of (6.8) is bounded by $[D_1(K_1) - D_2(K_1)][\hat{q} - q] \leq 0$ when $\hat{q} - q \geq 0$. Thus,

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} [(\hat{q} - q)e^{-[D_1(K_1) - D_2(K_1)]t}] \leq 0 \text{ when } \hat{q} - q \geq 0.$$

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Since the initial condition in (6.6) shows that $\hat{q}(\mathbf{x}, 0) - q(\mathbf{x}, 0) \leq 0$, Proposition 6.1 with $v := [\hat{q} - q]e^{-[D_1(K_1) - D_2(K_1)]t}$ shows that

$$q(\mathbf{x}, t) \geq \hat{q}(\mathbf{x}, t) \text{ for } t \geq 0.$$

This and the above equation (6.7) immediately yield the statement (2.21) of Lemma 2.3. $\qquad\square$

Proof of Lemma 2.4. The proof will use upper bounds for the two terms on the right of the first equation of (2.3). Lemma 2.2 immediately shows that there is a positive constant m such that

$$B(\rho)h \leq me^{-\delta t}. \tag{6.9}$$

In order to bound the coefficient $B - D_1$ of ρ_1 in the first term of the right-hand side of the first equation of (2.3), we first choose any number $\tilde{c}$ with
$$0 < c < \tilde{c} < c_-.$$
Lemma 2.3 with c replaced by $\tilde{c}$ shows that for any η with $0 < \eta < K_2 - K_1$, there is a $t^{(\eta)}$ such that

$$q \geq K_2 - K_1 - \eta \text{ when } |\mathbf{x}| \leq \tilde{c}t \text{ and } t \geq t^{(\eta)}.$$

Because $\rho \geq \frac{1}{2}q$ and $B - D_1$ is decreasing, we see that

$$\begin{aligned} B(\rho) - D_1(\rho) \leq &B\left(\tfrac{1}{2}q\right) - D_1\left(\tfrac{1}{2}q\right) \leq B\left(\tfrac{1}{2}[K_2 - K_1 - \eta]\right) \\ &- D_1\left(\tfrac{1}{2}[K_2 - K_1 - \eta]\right) \text{ for } |\mathbf{x}| \leq \tilde{c}t \text{ and } t > t^{(\eta)}. \end{aligned} \tag{6.10}$$

The hypothesis (2.10) shows that $3K_1 > K_2$ so that $\frac{1}{2}[K_2 - K_1] > K_1$. We choose η so small that $\frac{1}{2}[K_2 - K_1 - \eta] > K_1$. Because $B - D_1$ is decreasing and $B(K_1) - D_1(K_1) = 0$, this shows that

$$\nu := -\{B(\tfrac{1}{2}[K_2 - K_1 - \eta]) - D_1(\tfrac{1}{2}[K_2 - K_1 - \eta])\} > 0. \tag{6.11}$$

This and the inequality (6.10) show that

$$B(\rho) - D_1(\rho) \leq -\nu.$$

We substitute this and the inequality (6.9) into the first equation of (2.3) to see that

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\}\rho_1 \leq -\nu\rho_1 + me^{-\delta t} \text{ for } |\mathbf{x}| \leq \tilde{c}t, \ t \geq t^{(\eta)}. \tag{6.12}$$

We note that $\tilde{c} > c$, and that the function $[\nu - \mu^2]/\mu$ decreases from $+\infty$ to $-\infty$ as μ goes from 0 to ∞. We choose a number $\mu > 0$ such that

$$c < [\nu - \mu^2]/\mu < \tilde{c}. \tag{6.13}$$

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It is easily verified that if x_1 is one of the Euclidean coordinates of the **x**-space, then for any positive γ the function

$$\hat{\rho}_1(x_1, t) := \gamma e^{[-\nu+\mu^2]t} \cosh(\mu x_1) + m[e^{-\delta t} - e^{-\nu t}]/[\nu - \delta] \qquad (6.14)$$

satisfies the equation

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} \hat{\rho}_1 = -\nu\{\hat{\rho}_1 - m[e^{-\delta t} - e^{-\nu t}]/[\nu - \delta]\} + me^{-\delta t}.$$

The second term in (6.14), interpreted as the limiting value $mte^{-\delta t}$ when $\nu = \delta$, is non-negative for $t \geq 0$. Thus,

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} \hat{\rho}_1 \geq -\nu\hat{\rho}_1 + me^{-\delta t} \qquad (6.15)$$

and

$$\hat{\rho}_1(x_1, t) \geq \gamma e^{[-\nu+\mu^2]t} \cosh(\mu x_1). \qquad (6.16)$$

We observe that when $|x_1| = \tilde{c}t$, the coefficient of γ on the right-hand side has the lower bound

$$e^{[-\nu+\mu^2]t} \cosh(\mu\tilde{c}t) \geq \tfrac{1}{2} e^{\{-([\nu-\mu^2]/\mu)+\tilde{c}\}\mu t}$$

Because of the right inequality in (6.13), the coefficient of t in the exponential is positive, so that the right-hand side approaches infinity with t. It follows that $e^{[-\nu+\mu^2]t} \cosh(\mu x_1)$ is uniformly positive on the set $\{(x_1, t) : |x_1| = \tilde{c}t, \ t \geq 0$. The same is true on the set

$$\{(x_1, t) : |x_1| \leq \tilde{c}t, \ 0 \leq t \leq t^{(\eta)}\}\}, \qquad (6.17)$$

which is bounded in the x_1-t space.

We now choose the parameter γ in (6.14) so large that the right-hand side of (6.16) is bounded below by K_3 on these sets. Then

$$\hat{\rho}_1(x_1, t) \geq K_3 \geq \rho_1(\mathbf{x}, t)$$

on the boundary of the domain

$$\mathcal{D} := \{(\mathbf{x}, t) : |x_1| < \tilde{c}t, \ t > t^{(\eta)}\},$$

as well as on the set (6.17).

By subtracting the equation (6.15) from (6.12), we see that

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\} [\rho_1 - \hat{\rho}_1] \leq -\nu[\rho_1 - \hat{\rho}_1].$$

Proposition 6.1 applied to the function $v := \rho_1 - \hat{\rho}_1$ in the domain $\mathcal{D}$ shows that the inequality

$$\rho_1(\mathbf{x}, t) \leq \hat{\rho}_1(x_1, t) = \gamma e^{[-\nu+D\mu^2]t} \cosh(\mu x_1) + m[e^{-\delta t} - e^{-\nu t}]$$
$$\text{for } |x_1| \leq \tilde{c}t$$

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is valid for $t \geq t^{(\eta)}$ as well as on the set (6.17). That is, it is true for all $t \geq 0$.

Because $\cosh(\mu x_1)$ is increasing in $|x_1|$ and is bounded above by $e^{\mu|x_1|}$, and because $|x_1| \leq |\mathbf{x}|$, this gives the bound

$$\max_{|\mathbf{x}| \leq ct} \rho_1(\mathbf{x}, t) \leq \gamma e^{-\{([\nu - D\mu^2]/\mu) - c\}\mu t} + m[e^{-\delta t} - e^{-\nu t}]/[\nu - \delta] \text{ for } |x_1| \leq ct, \ t \geq 0.$$

The left inequality of (6.13) shows that the first term is a multiple of a negative exponential. We conclude that if we define

$$\hat{\alpha} := \min\{\nu - D\mu^2 - c\mu, \delta\} > 0,$$

then there is an $M_1 > 0$ such that

$$\max_{|\mathbf{x}| \leq ct} \rho_1(|\mathbf{x}|, t)] \leq M_1 e^{-\hat{\alpha} t} \text{ for } t \geq 0.$$

This is the statement of Lemma 2.4. $\qquad\square$

Proof of Lemma 2.5. The definition (2.2) of h shows that

$$\rho_2^2 = 4[\rho h + \rho_3 \rho_1].$$

Because $0 \leq \rho_3 \leq \rho \leq K_3$ and $\hat{\alpha} \leq \delta$, Lemmas 2.2 and 2.4 immediately imply the statement of Lemma 2.5. $\qquad\square$

Proof of Lemma 2.6. Write the last equation of (2.3) in the form

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\}[K_3 - \rho_3] = -[B(\rho) - D_3(\rho)]\rho_3 - B(\rho)h. \tag{6.18}$$

Because $[B(\rho) - D_3(\rho)]' < 0$ on the closed interval $[K_1, K_3]$, there is a number

$$\tilde{\nu} := \max\{-[B(\rho) - D_3(\rho)]'\} > 0. \tag{6.19}$$

Because $B(K_3) - D_3(K_3) = 0$ and $\rho \leq K_3$, the mean value theorem shows that

$$-[B(\rho) - D_3(\rho)] \leq -\tilde{\nu}[K_3 - \rho] = -\tilde{\nu}[K_3 - \rho_3 - \rho_1 - \rho_2].$$

On the other hand, we see from the definition (2.2) of h that

$$-h \leq \rho_1\rho_3/\rho \leq \rho_1.$$

Since $B(\rho) \geq 0$, we can put the two preceding inequalities into the equation (6.18) to see that

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\}[K_3 - \rho_3] \leq -\tilde{\nu}[K_3 - \rho_3] + \tilde{\nu}[\rho_1 + \rho_2] + B(\rho)\rho_1. \tag{6.20}$$

$B(\rho)$ is, of course, uniformly bounded on $[K_1, K_3]$. We now choose a $\tilde{c}$ with $c < \tilde{c} < c_-$ and apply Lemmas 2.4 and 2.5 with c replaced by $\tilde{c}$ and Lemma 2.2 to find that there is a constant $\tilde{m}$ such that

$$\left\{\frac{\partial}{\partial t} - \nabla^2\right\}[K_3 - \rho_3] \leq -\tilde{\nu}[K_3 - \rho_3] + \tilde{m}e^{-\frac{1}{2}\hat{\alpha} t} \text{ for } |\mathbf{x}| \leq \tilde{c}t. \tag{6.21}$$

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This inequality is just the inequality (6.12) with ρ_1 replaced by $K_3 - \rho_3$, ν replaced by $\tilde{\nu}$, m replaced by $\tilde{m}$, δ replaced by $\frac{1}{2}\hat{\alpha}$, and $t^{(\eta)}$ replaced by 0. The part of the proof of Lemma 2.4 which follows the equation (6.12) immediately leads to the conclusion that there are a positive $\bar{\alpha} \leq \frac{1}{2}\hat{\alpha}$ and an M_3 such that the statement (2.24) of Lemma 2.6 is valid. $\qquad\square$

Proof of Theorem 2.1. Lemmas 2.4, 2.5, and 2.6 clearly imply the statements (2.15) of Theorem 2.1.

Proof of Theorem 4.1. We see from (2.3) that

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} q = [B(\rho) - D_2(\rho)]\rho_2 + 2[B(\rho) - D_3(\rho)]\rho_3,$$

Because $D_2 \geq D_3$, this implies that

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} q \leq [B(\rho) - D_3(\rho)]q.$$

Because (2.11) shows that $B(\rho) - D_3(\rho)$ is decreasing and $B(K_1) = D_1(K_1)$, we see that

$$B(\rho) - D_3(\rho) \leq B(K_1) - D_3(K_1) = D_1(K_1) - D_3(K_1).$$

Therefore,

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} q \leq [D_1(K_1] - D_3(K_1)]q. \tag{6.22}$$

Because $q(\mathbf{x}, 0)$ vanishes outside a bounded set, the constant

$$M_+ := \sup_{\mathbf{x}} \left[q(\mathbf{x}, 0) e^{\sqrt{D_1(K_1) - D_3(K_1)}|\mathbf{x}|} \right] \tag{6.23}$$

is finite. Let x_1 be one of the Euclidean coordinates of the $\mathbf{x}$-habitat. It is easily verified that the function

$$\bar{q} := M_+ e^{-\sqrt{[D_1(K_1) - D_3(K_1)]}x_1 + 2[D_1(K_1) - D_3(K_1)]t}$$

is a solution of the equation

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} \bar{q} = [D_1(K_1) - D_3(K_1)]\bar{q}.$$

Subtracting the two sides of this equation from those of the inequality (6.22) shows that the function

$$v := [q - \bar{q}]e^{-[D_1(K_1) - D_3(K_1)]t}$$

satisfies the inequality

$$\left\{ \frac{\partial}{\partial t} - \nabla^2 \right\} v \leq 0.$$

Because (6.23) shows that $v(\mathbf{x}, 0) \leq 0$, and because the function v is bounded above, Proposition 6.1 shows that $v \leq 0$. Therefore,

$$q(\mathbf{x}, t) \leq \bar{q}(\mathbf{x}, t) = M_+ e^{-\frac{1}{2}c_+[x_1 - c_+ t]}, \tag{6.24}$$

where $c_+ = 2\sqrt{D_1(K_1) - D_3(K_1)}$.

We now observe that for any prescribed point of the habitat we can rotate the Euclidean coordinate system in such a way that this point lies on the non-negative x_1 axis. In the new coordinates $x_1 = |\mathbf{x}|$, while any other coordinates are 0. Then the inequality (6.24) becomes

$$q(\mathbf{x}, t) \leq M_+ e^{-\frac{1}{2}c_+[|\mathbf{x}| - c_+ t]}.$$

Because the right-hand side is decreasing in $|\mathbf{x}|$, this shows that

$$\sup_{|\mathbf{x}| \geq ct} q(\mathbf{x}, t) \leq M_+ e^{-\frac{1}{2}c_+[c - c_+]t}.$$

When $c > c_+$, the right-hand side approaches zero as $t \to \infty$.

Because $\rho_1 \geq 0$ and $\rho_2 \geq 0$, this implies that the suprema of both ρ_1 and ρ_2 on the exterior of the ball $|\mathbf{x}| < ct$ approach zero uniformly. In particular, we find the second statement in (4.2). Because $\rho_1 + \rho_2 + \rho_3 \geq K_1$, we also obtain the first statement, which finishes the proof of Theorem 4.1. $\qquad\square$

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Erratum for The retreat of the less fit allele in a population-controlled model for population genetics by H. F. Weinberger

The proof of Lemma 2.4 is correct when the habitat is one-dimensional. However, the fact that the function $\hat{\rho}_1$ defined by formula (6.14) approaches zero on the part of the cone $|\mathbf{x}| = \tilde{c}t$ where $x_1 = 0$ invalidates the argument that $\rho_1 \leq \hat{\rho}_1$ for $|\mathbf{x}| \leq \tilde{c}t$ when the habitat is multidimensional. This gap is easily repaired by replacing the function $\cosh \mu x_1$ in (6.14) by a radially symmetric positive solution $\Psi(|\mathbf{x}|)$ of the equation $\nabla^2 \Psi = \mu^2 \Psi$. When the habitat has dimension 2, one can let $\Psi := I_0(\mu|\mathbf{x}|)$ where I_0 is the usual Bessel function with imaginary argument. In three dimensions, one can let $\Psi := [\sinh \mu|\mathbf{x}|]/[\mu|\mathbf{x}|]$.