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Segregation and mixing in degenerate diffusion in population dynamics

Thomas P. Witelski[*]

Department of Mathematics, 2-336 Massachusetts Institute of Technology,
77 Massachusetts Avenue, Cambridge, MA 02139-4307, USA

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Abstract. We study the qualitative properties of degenerate diffusion equations used to describe dispersal processes in population dynamics. For systems of interacting populations, the forms of the diffusion models used determine if the population will intermix or remain disjoint (segregated). The dynamics and stability of segregation boundaries between competing populations is analyzed. General population models with segregation and mixing interactions are derived and connections to behavior in fluid mechanical systems are addressed.

Key words: Population dynamics – Nonlinear diffusion – Porous media equation – Degenerate diffusion – Dispersal

1 Introduction

We study the qualitative properties of different models used to describe dispersal processes in population dynamics. Our focus is the use of models based on nonlinear degenerate parabolic partial differential equations, also called porous media equations. It will be shown that problems with systems of interacting populations can yield different types of behavior depending on the forms of the models used. Following a brief review of reaction-diffusion systems for population dynamics, we will study two important phenomena exhibited by such models – segregation and mixing. Examples of biological systems displaying these behaviors will be given. Strong parallels between population dynamics models and flows of thin films of viscous fluids will be examined. We conclude with a formulation of population dynamics systems that describe such forms of group interactions.

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1.1 Dynamics of a single population

The behavior of large populations, such as herds of animals or colonies of bacteria, can often be represented by solutions of reaction-diffusion equations. These equations model the evolution of the population with respect to dispersal in space and interactions among the individuals, such as birth, death, competition, and cooperation. Fisher's equation [9, 1],

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u), \quad 0 \leqq u(x,t) \leqq 1 \ , \tag{1}$$

where $u(x,t)$ is the population density, is the most fundamental model for the evolution of a single population with diffusion, birth, and death processes. Fisher's original work considered the spreading of a gene throughout a population, but (1) has also been applied to combustion problems [11] and chemical systems [9]. More detailed descriptions of the behavior of specific populations can be obtained by using specialized models for the diffusion and interaction processes. The general form of Fisher's equation is

$$\frac{\partial u}{\partial t} = -\nabla \cdot \boldsymbol{J} + F(u) \ , \tag{2}$$

where $\boldsymbol{J}$ is the population flux vector and $F(u)$ is the nonlinear interaction term. Gurney and Nisbet [5, 6] suggest that an important modeling consideration for population dynamics is the desire of individuals to avoid overcrowded areas. Neglecting random diffusive motion in the population, this behavior is characterized by the flux $\boldsymbol{J} = u\boldsymbol{v}$, where the dispersal velocity $\boldsymbol{v}$ is a vector opposite to the direction of maximal population density increase, $\boldsymbol{v} \propto -\nabla u$. In general, we should allow both local density and local gradients to contribute to anti-crowding dispersal, therefore the velocity can be written as

$$\boldsymbol{v} = -k(u)\nabla u \ , \tag{3}$$

where the dispersivity $k(u)$ is an increasing function of the population density, say $k(u) = u^{n-1}$, for $n \geqq 1$, then the flux may be written as

$$\boldsymbol{J} = -u^n \nabla u \ , \tag{4}$$

and for $n = 1$ we recover the "directed motion" model of Gurney and Nisbet. We note that this flux can also be written as

$$\boldsymbol{J} = -D(u)\nabla u \ , \tag{5}$$

where the diffusion coefficient is $D(u) = u^n$. Neglecting the interaction term in (2), this flux model yields a nonlinear diffusion equation called the porous media equation [2],

$$\frac{\partial u}{\partial t} = \nabla \cdot (u^n \nabla u) \ , \tag{6}$$

which has applications to many physical systems [1, 2, 17] including the fluid dynamics of thin films [12, 14–16]. Murray [9] describes how this model has been used to represent "population pressure" in biological systems. Equation (6) is called a degenerate parabolic differential equation because the diffusion coefficient $D(u) = u^n$ does not satisfy the condition for classical diffusion equations, $D(u) > 0$ [18]. Population distributions for equation (6) can have distinct boundaries, called interfaces, beyond which the population density is identically zero. This property is illustrated by the well-known exact solution of (6) in one dimension [19]

$$u(x,t) = \left(\frac{n}{2(n+2)\ t^{n/(n+2)}} \left[C - \frac{x^2}{t^{2/(n+2)}} \right]^+ \right)^{1/n}, \qquad (7)$$

where $C > 0$ is an arbitrary constant and $[w]^+ = \max(w, 0)$ (see Fig. 1). Also note that the interfaces of solutions to (6) move with finite speed for $t > 0$; for (7), the interfaces are given by $x_*(t) = \pm\sqrt{C}t^{1/(n+2)}$. This characteristic makes model (4) particularly attractive for problems in population dynamics; it explicitly enforces the idea that a population should spread with a finite speed if all of the individual members move with finite speeds. In contrast, solutions of models like (1), with linear, classical diffusion, do not have sharp interfaces and instantaneously spread to cover the entire domain. For the study of the spread of a disease, the existence of a well-defined, sharp interface is important for separating infected and un-infected populations. This characteristic will be fundamental to our later discussion of segregation. The choice of the exponent n in (4) and (6) can be determined from an underlying physical model or from empirical data. For the motion of thin viscous films, (6) with $n = 3$ can be derived from the Navier-Stokes equations [16]. Lacking a physical law to describe the complex behavior in a system, an appropriate

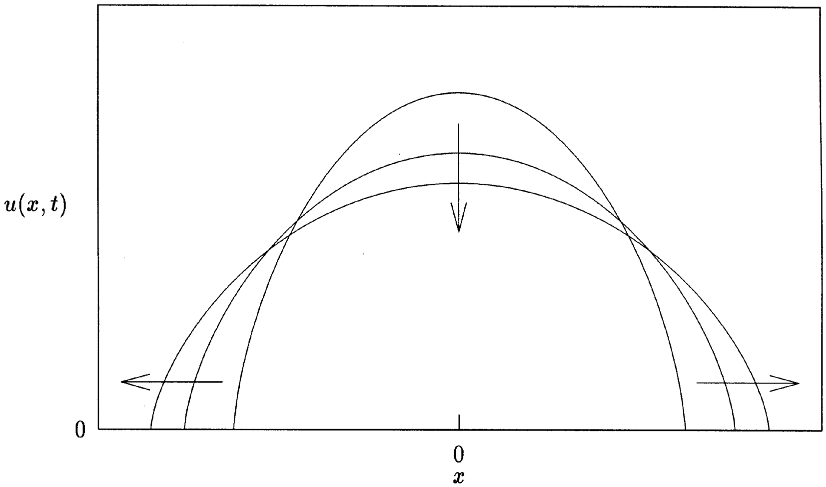

Fig. 1. The dynamics of a finite spreading population (7) for equation (6)

value for the parameter n can be determined by comparing known solutions, like (7), with empirical data. This approach is often used to study groundwater diffusion in porous media [12], and it could be used in population dynamics to improve qualitative and quantitative agreement of models. Effects of the exponent n include controlling the structure of the population distribution near the interface (see Fig. 2). Newman [1, 8, 10, 11] has found traveling wave solutions with sharp interfaces for Fisher's equation (2) with flux (4). We have studied merging behavior for two initially separated populations of the same species as they spread into the same region [13] (see Fig. 3). When the two

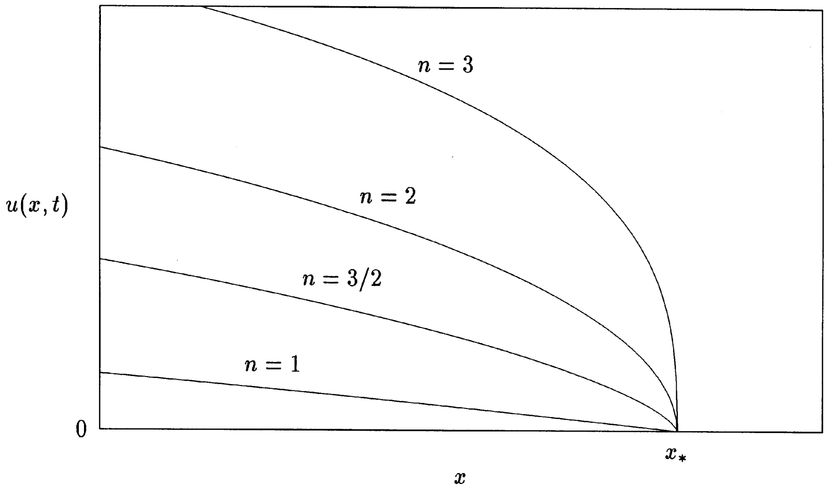

Fig. 2. The population density distribution near the interface for different values of n in solution (7)

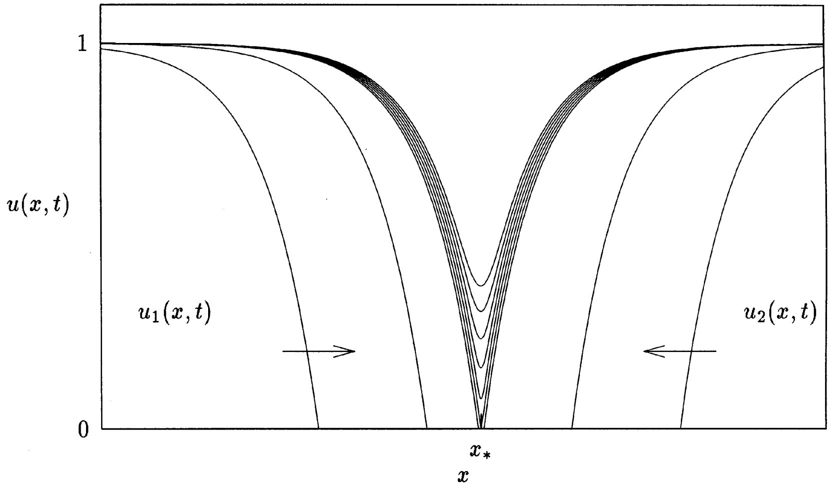

Fig. 3. Merging populations for a porous-Fisher's equation

populations of indistinguishable animals spread into the unpopulated area, the sharp interfaces at the leading edge of each herd disappear as the two groups merge into one larger population.

1.2 Dynamics of interacting populations

The study of the dynamics of several interacting populations generally involves the use of a system of reaction-diffusion equations and can yield a much broader variety of effects. Consider an environment containing N distinguishable populations, $u_i(\boldsymbol{x}, t)$, $i = 1 \ldots N$; the evolution of this system could be given by the model

$$\frac{\partial u_i}{\partial t} = -\nabla \cdot \boldsymbol{J}_i + F_i(u_j) , \tag{8}$$

where $\boldsymbol{J}_i$ is the flux of population u_i. This is a very general model that can encompass a broad range of possible behaviors and applications; we will specialize it to forms that describe various biological systems. The classical model of a reaction-diffusion system for a two-species problem is [21]

$$\frac{\partial u_1}{\partial t} = D_1 \nabla^2 u_1 + F_1(u_1, u_2), \qquad \frac{\partial u_2}{\partial t} = D_2 \nabla^2 u_2 + F_2(u_1, u_2) . \tag{9}$$

In this model, coupling between u_1 and u_2 occurs only through the interaction terms. Extensive studies of model (9) neglecting diffusive effects exist in the literature [9]. In this article, we will focus on the modeling of the diffusive terms, and will for the most part neglect the nonlinear reaction terms that represent birth and death processes. In the absence of the coupling through the F_i terms, the populations in (9) would diffuse independently of each other. A biological interpretation of this model suggests that it contains only weakly interacting populations; it could represent two species that live in the same region but do not compete for the same type of "ecological niche" or living space. An example is a region of the ocean inhabited by fish (in the water) and sea birds in the air above. In describing populations vying for space in the same habitat, Gurtin and Pipkin [7] state the principle that groups seeking to avoid crowds will move opposite to the gradient of the *total* population. In [7], it is also remarked that a weighted sum

$$U(\boldsymbol{x}, t) = \sum_{i=1}^{N} \rho_i u_i(\boldsymbol{x}, t) , \tag{10}$$

might be used as a measure of the total effective population density. This construction can be motivated by considering a set of species with different characteristics; small, quiet animals should be assigned a low relative weight, while larger, more aggressive species consume more resources, require more space per capita, and should have a large weighting in (10). We conclude that all of the populations u_i in (8) will have $\boldsymbol{J}_i \propto -\nabla U$. We will now consider how different choices for the functional forms of diffusion coefficients in the population fluxes can yield qualitatively different behaviors. We will begin with a discussion of a simple model that has been studied extensively in the literature.

2 A simple segregation model

Bertsch et al. [4, 3] have rigorously analyzed certain properties of the population dynamics model given in one dimension by the equations,

$$\frac{\partial u_1}{\partial t} = \frac{\partial}{\partial x}\left(u_1 \frac{\partial U}{\partial x}\right), \tag{11}$$

$$\frac{\partial u_2}{\partial t} = k\frac{\partial}{\partial x}\left(u_2 \frac{\partial U}{\partial x}\right), \tag{12}$$

where the total population is $U = u_1 + u_2$ and $k > 0$ is a dispersivity constant. If the populations are disjoint or separated, where population u_1 is nonzero, u_2 is identically zero, and vice versa, then the total population reduces to $U = u_1$ and $U = u_2$ respectively (see Fig. 4). While the populations are separated by unpopulated regions, each of (11, 12) reduces to a porous media equation (6) with $n = 1$, and the populations will diffuse independently for a finite time until their interfaces meet [12]. Bertsch et al. have proved that even when u_1 and u_2 share a common interface, the populations will remain disjoint or "segregated" for all times (see Fig. 5). It is easy to demonstrate this principle with an example. If $k = 1$, then (11, 12) can be added together to yield a porous media equation (6) with $n = 1$ for the total population density $U(x, t)$ [3, 4]. Solving for $U(x, t)$, we may then determine u_1 and u_2 independently; the equation for u_1 becomes

$$\frac{\partial u_1}{\partial t} - \frac{\partial U}{\partial x}\frac{\partial u_1}{\partial x} = u_1 \frac{\partial^2 U}{\partial x^2}\ . \tag{13}$$

This is a quasilinear equation for $u_1(x, t)$ in terms of the known total population $U(x, t)$ and can be expressed in characteristic form [20] as

$$\frac{du_1}{dt} = u_1 \frac{\partial^2 U}{\partial x^2} \quad \text{on} \quad \frac{dx}{dt} = -\frac{\partial U}{\partial x}\ . \tag{14}$$

If we denote the interface position by $x_*(t)$, we can parameterize the boundary between the two populations that are segregated at time t_0 in terms of the density u_1 as $x_*(u_1, t_0) = x_*(t_0)$ for all $0 \leqq u_1 \leqq U$ (see Fig. 5). For this initial condition at $t = t_0$, the segregation boundary is explicitly independent of the population density u_1. Since the differential equation for the characteristic curve $(14)_2$ is independent of the parameter u_1, the interface position will remain independent of u_1 for all times, segregation will be preserved. This

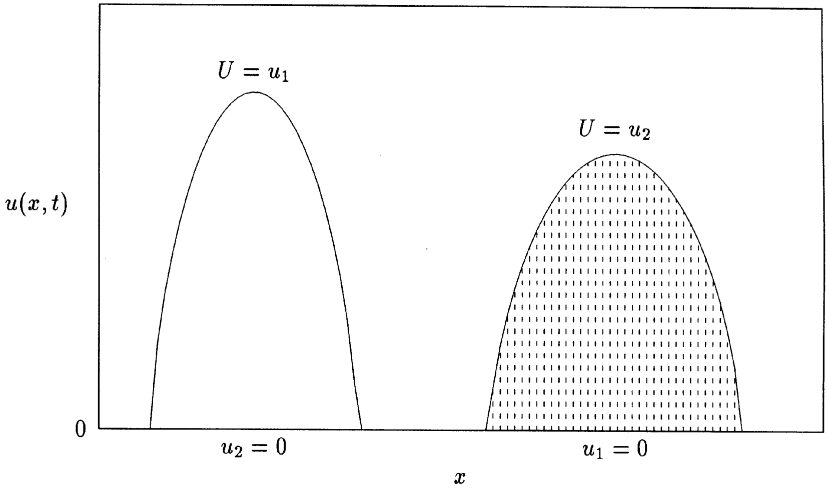

Fig. 4. Two initially separated populations, u_1 and u_2

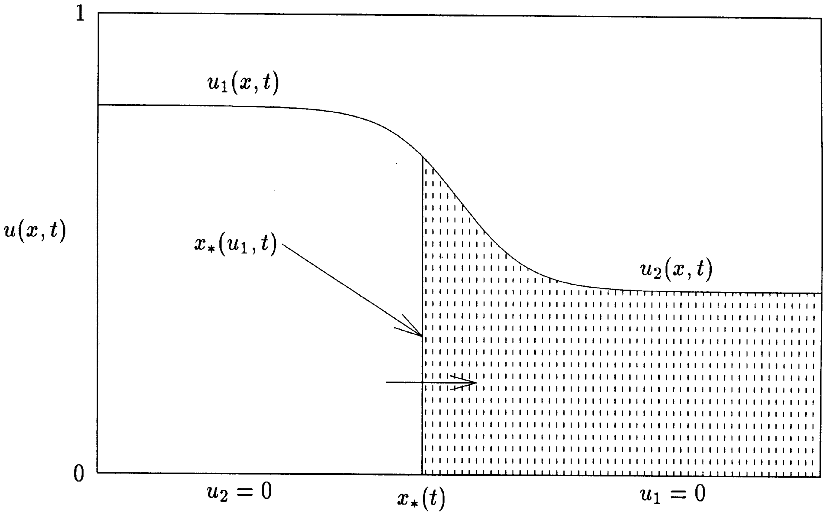

Fig. 5. Two segregated populations and the motion of the common interface, or segregation boundary

behavior can be interpreted as having the two populations pushing on the opposite sides of a movable but impenetrable rigid wall; the presence of the "wall" is a consequence of the functional forms of the population fluxes in (11, 12). This model could be used to describe two hostile populations involved in a battle over a territorial boundary. It is possible to analyze the motion and stability of this boundary to yield an understanding of some of the qualitative properties of the solutions of (11, 12).

2.1 Dynamics of the interface

As described above, the motion of the segregation boundary is given by

$$\frac{dx}{dt} = -\frac{\partial U}{\partial x}\,; \tag{15}$$

this is a simple gradient system. The motion of the interface is governed by the local gradient of the potential function U, which for our problem is the total population. For time-independent potentials, $U = U(x)$, equation (15) is a classical problem and the behavior of the solutions is understood in terms of dynamics in a one-dimensional phase space, $x_*(t)$ will move towards a local minimum of $U(x)$. For time-dependent potentials $U(x,t)$, solutions of (15) can have more complicated behaviors [22, 23]; here we will focus on one class of these solutions. It is clear that a fixed interface x_* can only exist at a fixed maximum or minimum of $U(x,t)$ – at a time-independent critical point, where $U_x(x_*, t) = 0$ for all $t > 0$. As in the study of autonomous systems, the next step in the analysis is to determine the stability of the fixed point.

In [3], Bertsch et al. prove that segregated solutions of (11, 12) remain segregated for all times, but they leave the problem of non-segregated initial data as an open question. Non-segregated or "mixed" populations contain a region of overlap where both populations are nonzero (see Figs. 6, 7). The overlap region contains populations of varied local composition, in the ratio u_1 to u_2. Analogous descriptions are used in the study of pure liquids mixing under favorable thermodynamic conditions to form a single locally homogeneous "mixed" phase. The stability of the segregation boundary determines if the overlap region of a slightly mixed population will increase or decrease. Mixing perturbations could be introduced into segregated solutions from external effects, such as nonlinear interaction terms, convective terms, or spatial inhomogeneitities that are not included in the basic model (11, 12). Consider a perturbed initial condition for the interface,

$$\tilde{x}_*(u_1, t = 0) = x_* + \varepsilon\tilde{x}(u_1)\,, \tag{16}$$

where $0 < \varepsilon \ll 1$ is a small parameter (see Figs. 6, 7, where a tanh-like function is used for the perturbation $\tilde{x}(u_1)$). From linear stability analysis, we can show that the asymptotic behavior of $\tilde{x}_*$ is determined by $U_{xx}(x_*)$. If $U_{xx} > 0$ then the interface is stable, $\tilde{x}_*(t \to \infty) \to x_*$ (see Fig. 6); if $U_{xx} < 0$, the interface is unstable (see Fig. 7). The local concavity of the total population, U_{xx}, can be related to the local gathering or dispersal and corresponding increase or decrease of the local population density, see $(14)_1$. We are able to conclude that dispersing populations tend to mix, while merging populations tend to segregate! This is a rather surprising result, but it is a fundamental consequence of the form of model (11, 12). The dynamics of the interface can be reasoned by relating the motion of population u_1 (13) to a population described by a nonlinear convection-diffusion model, like Burgers' equation. In the dispersing case, the interface is the trailing edge of the population and has a tendency to broaden (see Fig. 6). In the merging case, the interface is the

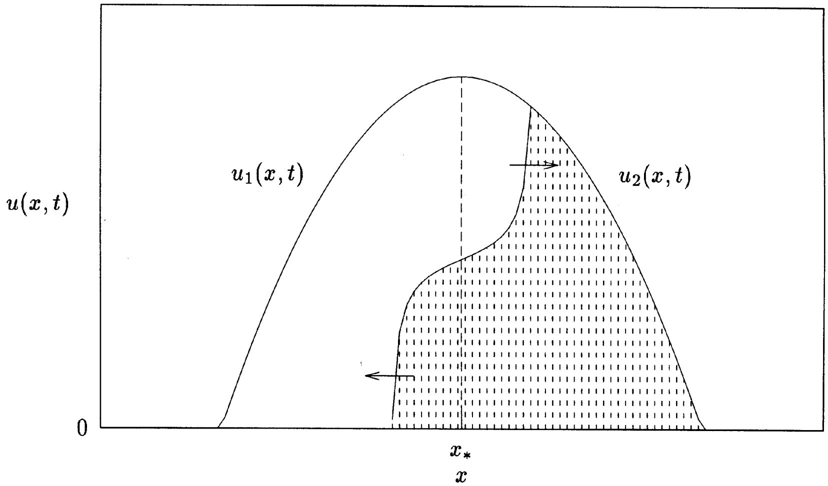

Fig. 6. Instability of a perturbed interface in a dispersing population with $U_{xx} < 0$

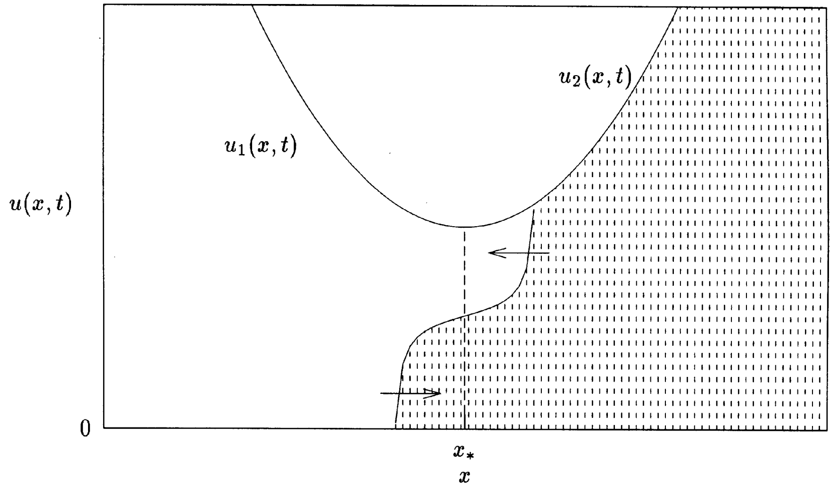

Fig. 7. Stability of a perturbed interface in a merging population with $U_{xx} > 0$

leading edge of the advancing population and tends to steepen (see Fig. 7). In the next section we will derive the general form of models that preserve segregation.

2.2 General segregation models

Before proceeding to the analysis of general nonlinear segregation systems, we consider the general case of system (11, 12) with $k \neq 1$. For $k \neq 1$, the equation for U can not be decoupled from $u_1(x,t)$,

$$\frac{\partial U}{\partial t} = \frac{\partial}{\partial x}\left((kU + (1-k)u_1)\frac{\partial U}{\partial x} \right), \tag{17}$$

As shown in [3], the solution of this equation is a weak solution; $U(x,t)$ is continuous but it is not smooth, $U(x,t) \in C^0(x)$. The total population is continuous at the segregation boundary, $U(x_*) = u_1(x_*^-) = u_2(x_*^+)$, but it has a discontinuity in the first derivative, $U_x(x_*^-) = kU_x(x_*^+)$. This fact makes (17) awkward to solve; it is advisable to solve system (11, 12) directly, as a moving boundary problem with the above continuity conditions at the interface. Solving for u_1 and u_2 and then constructing U from their sum, we can still write (11) in a characteristic form like (14), though more care is required since U is a weak solution. The resulting complications however do not change the fundamental fact that the equation for the characteristic curves (15) is independent of u_1; hence from the argument made in Sect. 2, it is clear that the condition for the preservation of segregation will still be satisfied. Both cases $k = 1$ and $k \neq 1$ are of interest in describing population dynamics problems. As mentioned above, the $k = 1$ problem can describe the interaction of two competing hostile groups of the same species. For $k \neq 1$, the two groups still belong to the same species, since their dispersivities have the same functional form, but they are different breeds, with one group being of a faster moving variety of animals, for $k > 1$.

To determine the general form of diffusion models that preserve segregation, consider the system

$$\frac{\partial u_1}{\partial t} = \frac{\partial}{\partial x}\left(D_1(u_1, U)\frac{\partial U}{\partial x}\right), \tag{18}$$

$$\frac{\partial u_2}{\partial t} = \frac{\partial}{\partial x}\left(D_2(u_2, U)\frac{\partial U}{\partial x}\right), \tag{19}$$

where D_1 and D_2 are diffusion coefficient functions. This generalized model is somewhat more broad than a form discussed in [7]; these equations will be considered in more detail in the following section. As in system (11, 12), summing (18, 19) yields a diffusion equation for the total population,

$$\frac{\partial U}{\partial t} = \frac{\partial}{\partial x}\left(D(u_1, U)\,\frac{\partial U}{\partial x}\right), \tag{20}$$

where $D(u_1, U) = D_1(u_1, U) + D_2(U - u_1, U)$. Assuming that we can obtain the solution $U(x,t)$, possibly as a weak solution, we can write (18) as a quasilinear equation for $u_1(x,t)$ in terms of $U(x,t)$,

$$\frac{\partial u_1}{\partial t} - \frac{\partial D_1}{\partial u_1}\frac{\partial U}{\partial x}\frac{\partial u_1}{\partial x} = D_1(u_1, U)\frac{\partial^2 U}{\partial x^2} + \frac{\partial D_1}{\partial U}\left(\frac{\partial U}{\partial x}\right)^2, \tag{21}$$

and in characteristic form as

$$\frac{du_1}{dt} = D_1(u_1, U)\frac{\partial^2 U}{\partial x^2} + \frac{\partial D_1}{\partial U}\left(\frac{\partial U}{\partial x}\right)^2 \quad \text{on} \quad \frac{dx}{dt} = -\frac{\partial D_1}{\partial u_1}\frac{\partial U}{\partial x}. \tag{22}$$

To insure preservation of segregation, we require that the differential equation for the characteristic curves $(22)_2$ be independent of u_1, and we find that D_1 must take the form

$$D_1(u_1, U) = A_1(U)\, u_1 + B_1(U)\,, \tag{23}$$

where $A_1(U)$ and $B_1(U)$ are arbitrary functions of the total population. To guarantee that (18) is a degenerate diffusion equation, we require that $D_1(u_1, u_1) = 0$ when $u_1 = 0$, so $B_1(0) = 0$ and $A_1(0)$ is finite. Applying the same analysis for the motion of the segregation boundary to the equation for population u_2, we similarly find that

$$D_2(u_2, U) = A_2(U)\, u_2 + B_2(U)\,, \tag{24}$$

where $A_2(U)$ and $B_2(U)$ are other arbitrary functions satisfying the above conditions. Since the segregation boundary $x_*(t)$ is common to both populations, its characteristic equation must satisfy

$$\frac{dx_*}{dt} = -\left.\frac{\partial D_1}{\partial u_1}\frac{\partial U}{\partial x}\right|_{x_*^-} = -\left.\frac{\partial D_2}{\partial u_2}\frac{\partial U}{\partial x}\right|_{x_*^+}, \tag{25}$$

or

$$A_1(U)\, U_x(x_*^-) = A_2(U)\, U_x(x_*^+)\,. \tag{26}$$

If we require that $U(x, t)$ is a smooth, classical solution of (20), then $U_x(x_*^-) = U_x(x_*^+)$ and $A_1(U) = A_2(U)$ for all U. Moreover, we find that the diffusion coefficient for equation (20) must be a function of only the total population,

$$D(U) = A(U)\, U + B(U)\,, \tag{27}$$

where $A(U) = A_1(U) = A_2(U)$ and $B(U) = B_1(U) + B_2(U)$. *If* $A_1(U) \neq A_2(U)$ then U will be a weak solution satisfying the condition (26) on its derivative at x_*. In this case, the diffusion coefficient for (20) can be written in the form

$$D(u_1, U) = \tilde{A}(U)\, u_1 + \tilde{B}(U)\,, \tag{28}$$

where $\tilde{A}(U) = A_1(U) - A_2(U)$ and $\tilde{B}(U) = B(U) + A_2(U)\, U$. These two cases are the natural generalizations of the $k = 1$ and $k \neq 1$ problems for system (11, 12). Note that equation (17) for system (11, 12) with $k \neq 1$ has a diffusion coefficient of the form (28). Here we have shown that if the total population is a smooth function, then its evolution is independent of the dynamics of the internal conflict between the segregated groups. These two groups need not be identical in nature; their diffusion coefficients can differ by a function of the total population, $B_2(U) - B_1(U)$. We now conclude with a discussion of more general models and the importance of mixing interactions.

3 Mixing in general population models

In modeling the dynamics of a single population we have described some of the important qualitative differences between linear and degenerate diffusion.

The influence on the population density profile of different choices for the diffusion coefficient was also addressed (recall Fig. 2). With these two considerations, a good model for the general dispersive behavior in a single population can be determined. For systems of interacting populations, developing a reaction-diffusion model that fully describes the possible range of behaviors requires more in-depth studies.

In systems of two or more populations there are more qualitative features that need to be incorporated into the model. In the previous sections we focused on the segregation property for a class of degenerate diffusion equations; examples of systems that might be accurately described by these models were mentioned. Yet, there are also many systems where such models would be inappropriate; often, naturalists will relocate a small population of an endangered species to another area near a larger population of the species. Hopefully, the new animals would be accepted by the main population and allowed to mix-in freely. However, if a segregation model described these populations, then the relocated group would not integrate with the main population, and thus would effectively remain isolated. Clearly, problems like this, the use of "tagged" animals to follow herds, and many other situations require models that allow mixing behavior.

We will now give a general framework for formulating population dynamics models that allows for mixing and other considerations. As described in Sect. 1.2, it is important to specialize general reaction-diffusion systems like (8) to describe the fundamental dynamics of interacting population, yet it would also be desirable to have a model that is sufficiently general to be applicable to a range of different related problems. Our generalized model for the flux of population u_i is

$$\boldsymbol{J}_i = \int_{u_i} \boldsymbol{v}_i \, du \tag{29}$$

where $\boldsymbol{v}_i$ is the dispersal velocity, and is given by

$$\boldsymbol{v}_i = -k_i(u, u_i, u_j, U) \nabla U , \tag{30}$$

where k_i is the dispersivity of population u_i. Observe that if k_i is a constant, then (29) yields $\boldsymbol{J}_i = -k_i u_i \nabla U$, the directed motion model of Gurney and Nisbet; therefore it becomes clear that (11, 12) is the simplest of a large array of possible models. Flux (29) can also be expressed as a generalization of (5),

$$\boldsymbol{J}_i = -D_i(u_i, u_j, U) \nabla U , \tag{31}$$

where the diffusion coefficient is given by

$$D_i(u_i, u_j, U) = \int_{u_i} k_i(u, u_i, u_j, U) \, du . \tag{32}$$

The dispersivity in (30) and (32) is given as a very general functional form in order to represent many possible influences on the rate of dispersal, such as:

a) the overall level of crowding (the U dependence),

b) the local density of other friendly or hostile species (the u_j dependence),
c) the local density of competitors within the group (the u_i dependence).

There are also a number of constraints on the model:

a) the dispersivities of different populations of the same species should have the same functional form,

$$k_1(u, u_1, U) = k_2(u, u_2, U)$$

a) to be degenerate, the diffusion coefficients should satisfy the condition

$$D_i(0, 0, 0) = 0$$

c) in isolation, different populations of the same species should have the same diffusion coefficient,

$$D_1(u_1, 0, u_1) = D_2(u_2, 0, u_2)$$

d) the diffusion coefficient for a total population entirely composed of groups of the same species must be the same as the diffusion coefficient for the isolated species,

$$D(U) = \sum_i D_i(u_i, u_j, U), \qquad U = \sum_i u_i \ ,$$

$$D(u) = D_i(u, 0, u) \quad \text{for all } i$$

The last constraint is the most restrictive condition, as it suggests a nonlinear superposition principle. It represents the assumption that a single homogeneous population can be arbitrarily subdivided into smaller subgroups without changing the dynamics of the population. In situations where this assumption is not valid, condition (d) can be relaxed.

Other significant features of this model are the use of integrals over populations, and ordering of the populations. The flux (29) is given by an integral of the dispersal velocity over the population; this can be used to allow for density-dependent distributions of the dispersal velocity in the group; this is the source of the u dependence in k_i. Similar approaches might be used to incorporate age-structuring of populations [7, 6]. In an attempt to better classify the types of interactions that can occur within the total population, we also allow for a representation of a social hierarchy or "pecking order" among the groups. The groups can be ordered in terms of some measure of their territorial dominance or influence, from most important to least important, $u_1, u_2, \ldots, u_N$. This type of behavior occurs in many populations and has obvious implications for dispersal in the system. Consider two groups of the same species occupying the same region; a dominant, established population, u_1, and a newly introduced group, u_2. We might imagine a case where the dominant group's dispersal is unaffected by the presence of u_2, while the new group is forced to "move around" u_1. A simple model for this system with $k = k(u)$ yields the fluxes

$$\boldsymbol{J}_1 = -\nabla U \int_0^{u_1} k(u)\, du = -D(u_1)\nabla U \ , \tag{33}$$

$$J_2 = -\nabla U \int_{u_1}^{u_1+u_2} k(u)\,du = -(D(U) - D(u_1))\nabla U\ , \tag{34}$$

and the diffusion system

$$\frac{\partial u_1}{\partial t} = \nabla \cdot (D(u_1)\nabla U)\ , \tag{35}$$

$$\frac{\partial u_2}{\partial t} = \nabla \cdot ((D(U) - D(u_1))\nabla U)\ , \tag{36}$$

Clearly, (35, 36) satisfies the superposition constraint (d). Observe that system (11, 12) with $k = 1$ is a special case of (35, 36) with $D(u) = u$. This linear form of the diffusion coefficient is responsible for segregation in (11, 12). From $(22)_2$, we see that other functional forms of $D(u)$ will introduce u_1 dependence in the equation for the characteristic curves and hence segregation interfaces will generally deform to generate mixing, even without initial perturbations. In the following example we will demonstrate this type of behavior and examine the parallels between population dynamics and fluid mechanics of lubrication flows.

Diffusive spreading of thin layers of liquids [14, 15] under the influence of gravity is a phenomena similar to population dispersal in a number of ways. As described earlier, like the population models that we have been studying, the dynamics of liquid films is given by a porous media equation [16]. For lubrication problems, the analogue of local population density is the thickness of the liquid layer, u. We are currently studying lubrication flows of layers of immiscible liquids [24]; these are problems concerned with the nature of mixing processes, much like our present study of population dynamics. Like populations that avoid crowding, fluid layers have fluxes of the form $J_i \propto -\nabla U$, where U is the total "effective" thickness (10). This quantity is in fact proportional to the local hydrodynamic pressure, which reinforces the term "population pressure" used earlier. The dynamics of most common fluids can be given in terms of two physical properties – the density and the viscosity. If two liquids have the same density and viscosity then they are effectively the same fluid. The situation in population dynamics is not so clear. It is likely that more parameters are needed to describe the characteristics of groups. Indeed, species with different "social structures" might obey radically different dynamics; within our model (29), these dynamics are given by specifying the form of the dispersivity. Consider a system with two groups of the same species, having the common dispersivity

$$k(u, U) = \tfrac{3}{2}u^2 - 3uU\,. \tag{37}$$

This functional form was derived from a lubrication problem for a flow of two distinguishable layers of the same liquid, say one layer is marked with a visible dye [15, 24]. For population dynamics, this problem can represent the study of the relocation and integration of a tagged group of animals into a larger population of the same species. We note that for problems involving flows of genuinely different liquids, the general form $k = k(u, u_i, u_j, U)$ is needed. From (37) we derive the fluxes for the two groups u_1 and u_2

$$\boldsymbol{J}_1 = -\nabla U \int_0^{u_1} k(u, U)\,du = -(u_1^3 + \tfrac{3}{2}u_1^2 u_2)\nabla U \,, \tag{38}$$

$$\boldsymbol{J}_2 = -\nabla U \int_{u_1}^{u_1+u_2} k(u, U)\,du = -(u_2^3 + \tfrac{3}{2}u_1^2 u_2 + 3u_1 u_2^2)\nabla U \,, \tag{39}$$

and the degenerate diffusion equations in one dimension,

$$\frac{\partial u_1}{\partial t} = \frac{\partial}{\partial x}\left((u_1^3 + \tfrac{3}{2}u_1^2 u_2)\frac{\partial U}{\partial x}\right), \tag{40}$$

$$\frac{\partial u_2}{\partial t} = \frac{\partial}{\partial x}\left((u_2^3 + \tfrac{3}{2}u_1^2 u_2 + 3u_1 u_2^2)\frac{\partial U}{\partial x}\right). \tag{41}$$

We note that summing (40, 41) yields the equation for the total population

$$\frac{\partial U}{\partial t} = \frac{\partial}{\partial x}\left(U^3 \frac{\partial U}{\partial x}\right), \tag{42}$$

and the system obeys the constraints on the diffusion coefficients with $D(u) = D_1(u, 0, u) = D_2(u, 0, u) = u^3$. Observe that if we had used a different form of dispersivity, say $\tilde{k}(u) = 3u^2$, then we would still obtain (42), but with a different system (40, 41). This illustrates the point that it is not sufficient to know the diffusive behavior of the total population, the nature of the interactions between groups must also be understood.

Writing (40) in characteristic form, we obtain

$$\frac{du_1}{dt} = \tfrac{1}{2}u_1^2(3U - u_1)\frac{\partial^2 U}{\partial x^2} + \tfrac{3}{2}u_1^2\left(\frac{\partial U}{\partial x}\right)^2 \quad \text{on}$$

$$\frac{dx}{dt} = -\tfrac{3}{2}u_1(2U - u_1)\frac{\partial U}{\partial x}\,. \tag{43}$$

We will solve a simple example for (42) and (43) with an initially segregated population, and the total population given by (7) with $n = 3$ (see Figs. 8, 9). Observe that after a short time, the tagged population becomes completely engulfed by the main group and mixes in as the population continues to disperse.

We conclude with a brief example of how the ideas given above can be used to formulate reaction-diffusion systems. Suppose that in the absence of birth and death the dispersive dynamics of the population is given by (40, 41). Additionally, assume that the full dynamics, including birth and death processes, is given by Fisher's equation for the total population

$$\frac{\partial U}{\partial t} = \frac{\partial}{\partial x}\left(U^3 \frac{\partial U}{\partial x}\right) + U(1 - U)\,. \tag{44}$$

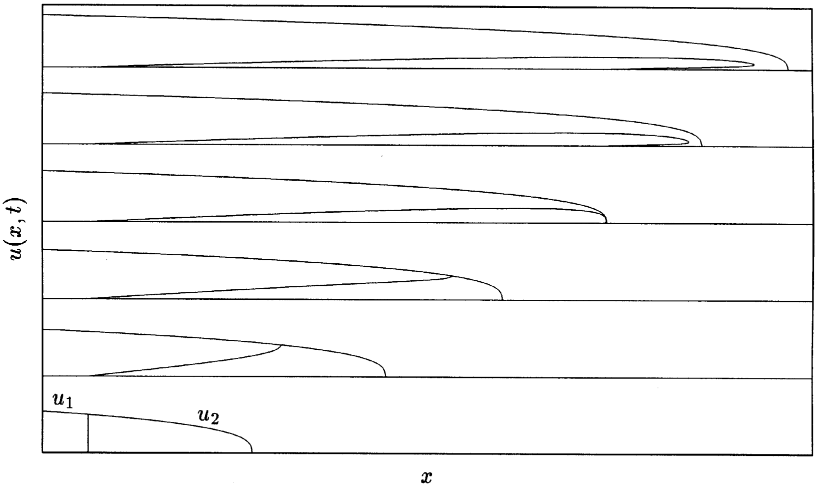

Fig. 8. Mixing of initially segregated populations in system (40, 41)

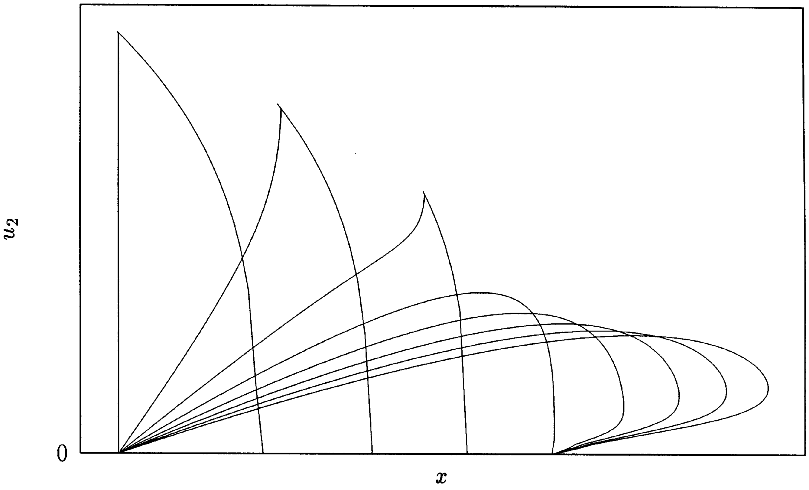

Fig. 9. Detail of the behavior of the distribution of population u_2 during mixing for system (40, 41)

To determine the dynamics of each group u_1 and u_2, we must determine an appropriate splitting of the reaction term $F(U) = U(1 - U)$. For the tagged population u_1, it is clear that F_1 should not contain any growth terms; while the individuals in the group may reproduce, the "tags" that we are following certainly will not. Hence, one plausible choice for the reaction terms is $F_1 = -u_1^2 - u_1 u_2$, $F_2 = u_1 + u_2 - u_2^2 - u_1 u_2$, yielding the system

$$\frac{\partial u_1}{\partial t} = \frac{\partial}{\partial x}\left((u_1^3 + \tfrac{3}{2}u_1^2 u_2)\frac{\partial U}{\partial x}\right) - u_1 U \ , \tag{45}$$

$$\frac{\partial u_2}{\partial t} = \frac{\partial}{\partial x}\left((u_2^3 + \tfrac{3}{2}u_1^2 u_2 + 3u_1 u_2^2)\frac{\partial U}{\partial x}\right) + U - u_2 U \, . \tag{46}$$

We are currently studying models like (45, 46) for lubrication flows of reactive liquids [24].

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