# A NOTE ON INTERACTING POPULATIONS THAT DISPERSE TO AVOID CROWDING*

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**Abstract.** In this note we derive partial differential equations for populations that disperse to avoid crowding, paying particular attention to situations in which the ease of dispersal is not uniform among individuals. We develop equations for the dispersal of a finite number of interacting biological groups and for a single age-structured group, and we give conditions under which the latter equations reduce to the former. In all cases the equations generalize the classical porous flow equation—a degenerate parabolic equation that exhibits a myriad of interesting effects. For the special case of two groups we deduce a simple solution in which the species remain segregated for all time.

**1. Basic equations.** We consider the dispersal[1] of $N$ biological groups in $\mathbf{R}^M$. The groups may correspond, for example, to different biological species or to different age classes of the same species. We assume that the dispersal of each group is described by three functions:

$$\begin{aligned} &u_n(t, \mathbf{x}), && \text{the } \textit{population density}, \\ &\mathbf{v}_n(t, \mathbf{x}) && \text{the } \textit{dispersal velocity}, \\ &\sigma_n(t, \mathbf{x}), && \text{the } \textit{population supply}. \end{aligned}$$

The field $u_n(t, \mathbf{x})$ gives the number of individuals of group $n$, per unit "volume", at position $\mathbf{x}$ at time $t$; its integral over any region $R$ gives the population of that group in $R$. The flow of population from point to point is described by the dispersal velocity $\mathbf{v}_n(t, \mathbf{x})$, which represents the average velocity of individuals of group $n$. The field $\sigma_n(t, \mathbf{x})$ gives the rate at which individuals are supplied at $\mathbf{x}$, for example, by births and deaths. These fields are assumed to be consistent with the *balance law*[2],

$$\partial u_n/\partial t = -\operatorname{div}(u_n \mathbf{v}_n) + \sigma_n.$$

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[1]General discussions of dispersal are contained in the review articles of Levin [1976] and McMurtrie [1978] and in the books of Okubo [1980] and Nisbet and Gurney [1982].

[2]Cf., e.g., [1977, Eq. (2.3)]. We use standard notation: lightface letters are scalars, boldface letters are vectors in $\mathbf{R}^M$; $\nabla$, div, and $\Delta$, respectivelu, denote the gradient, divergence, and laplacian in $\mathbf{R}^M$.

We limit our attention to groups which disperse to avoid crowding.[3] With this in mind, we suppose that

$$\mathbf{v}_n = -k_n \nabla U, \tag{1.1}$$

with $k_n$ a constant called the *dispersivity* and

$$U = \sum_n u_n \tag{1.2}$$

the total population, so that *each group disperses* (*locally*) *toward lower values of total population*.[4] Thus assuming

$$\sigma_n = \sigma_n(u), \qquad u = (u_1, u_2, \dots, u_N),$$

the underlying partial differential equation takes the form

$$\partial u_n/\partial t = k_n \operatorname{div}(u_n \nabla U) + \sigma_n(u). \tag{1.3}$$

Since we are concerned with dispersal in *all* of $\mathbf{R}^M$, we need only adjoin to (1.3) initial conditions of the form

$$u_n(0, \mathbf{x}) = \mathring{u}_n(\mathbf{x}),$$

with $\mathring{u}_n$ prescribed.

Note that for $k_n = k$ the same for all $n$ and $\Sigma\sigma_n(u)$ a function $\sigma(U)$ of $U$ alone, (1.3) yields

$$\frac{\partial U}{\partial t} = \frac{k}{2}\Delta(U^2) + \sigma(U), \tag{1.4}$$

the porous flow equation with kinetics.[5] The most interesting and unusual behavior occurs, however, when the dispersivity $k_n$ varies from group to group, for then the groups disperse with different speeds.

REMARK 1. In the relations (1.1), (1.2) all groups are assigned equal weight. This assumption is not crucial. Indeed, in place of (1.2) we could take

$$U = \sum_n \beta_n u_n,$$

with each $\beta_n$ a strictly-positive constant. Then, defining

$$w_n = \beta_n u_n,$$

we once again recover the basic equations (1.2) and (1.3), but with $u_n$ replaced by $w_n$.

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[3] The effects of population on dispersal are demonstrated in the field studies and experiments of Morisita [1950, 1954] (water striders and ant lions), Ito [1952] (aphids), Kono [1952] (rice weevils). These studies are discussed by Okubo [1980, §6] and Shigesada [1980]. See also the remarks of Carl [1971] concerning the dispersal of arctic ground squirrels.

[4] Cf. the discussion of Gurtin and MacCamy [1977, §6]. See also Busenberg and Travis [1983], who utilize an assumption of the form (1.1) with $k_n$ independent of $n$. We saw this paper after completing our study.

[5] Theories of population dynamics based on (1.4) have been given by Gurney and Nisbet [1975, 1982] and Gurtin and MacCamy [1977] (see also Shigesada [1980]). For general studies concerning the porous flow equation see, for example, Oleinik [1965], Aronson [1969], Peletier [1981].

REMARK 2. In some instances it might be appropriate to allow the dispersivities $k_n$ to be functions of $u_n$ and $U$. In this instance (1.3) is replaced by

$$\frac{\partial u_n}{\partial t} = \operatorname{div}[u_n k_n(u_n, U)\nabla U] + \sigma_n(u).$$

REMARK 3. Theories of the type presented here are often based on the balance law

$$\frac{\partial u_n}{\partial t} = -\operatorname{div}\mathbf{J}_n$$

with $\mathbf{J}_n$, the mass-flux of species $n$, given by a constitutive equation of the form

$$\mathbf{J}_n = \mathbf{J}_n(u, \nabla u), \qquad u = (u_1, u_2, \dots, u_N).$$

It seems to us, however, that in modelling phenomena such as dispersal induced by population pressure, our intuitive predjudices are most easily expressed in terms of constitutive relations for the dispersal velocity

$$\mathbf{v}_n = \frac{1}{u_n}\mathbf{J}_n,$$

since $\mathbf{v}_n$ measures, among other things, the desire of individuals to migrate.

An example of a model formulated in terms of the mass flux is that proposed by Shigesada, Kawasaki, and Teramoto [1979] in which

$$\mathbf{J}_n = -\nabla\left[u_n\left(\alpha_n + \sum_k \beta_{nk}u_k\right)\right].$$

Unfortunately, the corresponding dispersal velocity has an unpleasant feature. Indeed, let $N = 2$ (for convenience); then $\mathbf{v}_1$, say, satisfies

$$\mathbf{v}_1 = -\left(\frac{\alpha_1}{u_1} + 2\beta_{11} + \beta_{12}\frac{u_2}{u_1}\right)\nabla u_1 - \beta_{12}\nabla u_2,$$

and,for $u_2$, $\nabla u_1$, $\nabla u_2$ fixed, $|\mathbf{v}_1|$ generally increases with decreasing $u_1$, a result which appears to contradict their supposition of dispersal to avoid crowding (cf. the discussion of [1977]).

**2. Relation to the theory of age-structured populations.** We consider the theory of age-structured dispersal as formulated by Gurtin and MacCamy [1977], in which individuals disperse to avoid crowding. We assume that the process of dispersal is sufficiently fast that births and deaths are negligible. Then, writing $\rho(a, t, \mathbf{x})$ for the number of individuals —per unit age and volume—of age $a$ at $(t, \mathbf{x})$, the underlying partial differential equation takes the form

$$\frac{\partial\rho(a,t)}{\partial a} + \frac{\partial\rho(a,t)}{\partial t} = k(a)\operatorname{div}[\rho(a,t)\nabla P(t)], \tag{2.1}$$

where

$$P(t,\mathbf{x}) = \int_0^\infty \rho(a,t,\mathbf{x})\,da \tag{2.2}$$

is the spatial density, while $k(a)$ represents the *dispersivity* of individuals of age $a$. (For convenience, we have suppressed the variable $\mathbf{x}$ in (2.1).)

To (2.1) and (2.2) we add two requirements: the first, which follows from our neglect of births, asserts that

$$\rho(a,t,\mathbf{x}) = 0 \quad \text{when } a = 0; \tag{2.3}$$

the second is the initial condition

$$\rho(a,t,\mathbf{x}) = \mathring{\rho}(a,\mathbf{x}) \quad \text{when } t = 0, \tag{2.4}$$

with $\mathring{\rho}$ prescribed.

It follows from (2.3) that

$$\rho(a,t,\mathbf{x}) = 0 \quad \text{for } t \geqslant a. \tag{2.5}$$

To see this let $\tau = t - a$ and write

$$\hat{\rho}(a,\tau) = \rho(a,\tau + a).$$

Then

$$\partial\hat{\rho}(a,\tau)/\partial a = k(a)\,\mathrm{div}\left[\hat{\rho}(a,\tau)\nabla P(\tau + a)\right] \tag{2.6}$$

with initial condition (cf. (2.3))

$$\hat{\rho}(0,\tau) = 0 \quad \text{for } \tau \geqslant 0. \tag{2.7}$$

For each fixed value of $\tau$, (2.6) and (2.7) are satisfied by $\hat{\rho}(a,\tau) = 0$, and this solution is unique if $P$ is sufficiently regular. This implies (2.5).

The Eq. (2.1) can be greatly simplified when $k$ has the form

$$k(a) = \kappa e^{\gamma a}$$

with $\kappa > 0$ and $\gamma$ constants. Indeed, let $\alpha = a - t$ and

$$f(\alpha,t,\mathbf{x}) = \rho(t + \alpha,t,\mathbf{x}).$$

Then (2.1) takes the form

$$\frac{\partial f(\alpha,t)}{\partial t} = \kappa e^{\gamma\alpha}e^{\gamma t}\,\mathrm{div}\left[f(\alpha,t)\nabla P(t)\right],$$

and the change in time-scale

$$\tau = \kappa(e^{\gamma t} - 1)/\gamma$$

yields

$$\frac{\partial g(\alpha,\tau)}{\partial\tau} = e^{\gamma\alpha}\,\mathrm{div}\left[g(\alpha,\tau)\nabla G(\tau)\right] \tag{2.8}$$

with

$$g(\alpha,\tau,\mathbf{x}) = f(\alpha,t(\tau),\mathbf{x}) \qquad G(\tau,\mathbf{x}) = P(t(\tau),\mathbf{x}).$$

Further, by (2.5), (2.2) takes the form

$$G(\tau,\mathbf{x}) = \int_0^\infty g(\alpha,\tau,\mathbf{x})\,d\alpha, \tag{2.9}$$

and the end conditions (2.3) (actually (2.5)) and (2.4) now become

$$\begin{aligned} g(\alpha,\tau,\mathbf{x}) &= 0 && \text{when } \alpha = 0, \\ g(\alpha,\tau,\mathbf{x}) &= \rho_o(\alpha,\mathbf{x}) && \text{when } \tau = 0. \end{aligned} \tag{2.10}$$

The Eq. (2.8), (2.9), and (2.10) make sense even when $\alpha \in \{1, 2, \ldots, N\}$ is a discrete variable, provided (2.9) is replaced by the sum

$$G(\tau, \mathbf{x}) = \sum_{\alpha=1}^{N} g(\alpha, \tau, \mathbf{x}). \tag{2.11}$$

In fact, (2.8), (2.7) have exactly the form (1.2), (1.3) with $\sigma \equiv 0$. Our remaining discussion will be concerned with this discrete system.

**3. A simple solution.** We consider the system (1.3) with $\sigma \equiv 0$, $M = 1$, and $N = 2$, and without loss in generality take

$$k_1 = 1, \qquad k_2 = \frac{1}{\kappa}.$$

Then, writing

$$u_1 = \alpha, \qquad u_2 = \beta,$$

(1.3) becomes

$$\begin{aligned} \frac{\partial \alpha}{\partial t} &= \frac{\partial}{\partial x}\left(\alpha \frac{\partial U}{\partial x}\right), \\ \kappa \frac{\partial \beta}{\partial t} &= \frac{\partial}{\partial x}\left(\beta \frac{\partial U}{\partial x}\right), \\ U &= \alpha + \beta. \end{aligned} \tag{3.1}$$

Guided by the solution by Barenblatt [1952] and Pattle [1959]—for the porous flow equation (1.4) with initial data a delta distribution—we let

$$\begin{aligned} \alpha(t, x) &= t^{-1/3} A(\xi), \\ \beta(t, x) &= t^{-1/3} B(\xi), \\ U(t, x) &= t^{-1/3} Q(\xi), \\ \xi &= t^{-1/3} x. \end{aligned} \tag{3.2}$$

Substituting (3.2) into (3.1) yields the relations

$$-(\xi A)'/3 = (Q'A)', \qquad -\kappa(\xi B)'/3 = (Q'B)',$$

with $' = d/d\xi$. Assuming that the solutions are compactly supported in $x$ (and hence $\xi$),

$$(Q' + \xi/3)A = 0, \qquad (Q' + \kappa\xi/3)B = 0; \tag{3.3}$$

hence $A(\xi)$ and $B(\xi)$ cannot be simultaneously nonzero at a point $\xi$.

We look for a solution which has $A$ supported in an interval $(\xi_\alpha, \eta)$, $B$ in an interval $(\eta, \xi_\beta)$; that is, we look for a solution with

$$\begin{aligned} A \neq 0, \quad B = 0 \quad \text{on } (\xi_\alpha, \eta), \\ A = 0, \quad B \neq 0 \quad \text{on } (\eta, \xi_\beta), \end{aligned} \tag{3.4}$$

Further, we require that $Q$ be continuous, but we allow $A$ and $B$ to suffer jump discontinuities; thus, as $Q = A + B$,

$$\begin{aligned} Q(\xi_\alpha) &= A(\xi_\alpha) = 0, \\ Q(\xi_\beta) &= B(\xi_\beta) = 0, \\ A(\eta^-) &= B(\eta^+). \end{aligned} \tag{3.5}$$

By (3.3) and (3.4),

$$\begin{aligned} Q'(\xi) &= -\xi/3 \quad \text{on } (\xi_\alpha, \eta), \\ Q'(\xi) &= -\kappa\xi/3 \quad \text{on } (\eta, \xi_\beta), \end{aligned}$$

and the solution of these equations subject to (3.5) is

$$\begin{aligned} Q(\xi) &= A(\xi) = (\xi_\alpha^2 - \xi^2)/6 \quad \text{on } (\xi_\alpha, \eta), \\ Q(\xi) &= B(\xi) = \kappa(\xi_\beta^2 - \xi^2)/6 \quad \text{on } (\eta, \xi_\beta), \end{aligned}$$

with the added restriction that

$$\eta^2(\kappa - 1) = \kappa\xi_\beta^2 - \xi_\alpha^2.$$

Leaving aside the trivial case $\kappa = 1$, we take $\kappa > 1$ for definiteness. Then

$$\eta^2 = \frac{\kappa\xi_\beta^2 - \xi_\alpha^2}{\kappa - 1} \tag{3.6}$$

and $\eta^2 > \xi_\beta^2$ if $\xi_\beta^2 > \xi_\alpha^2$, $\eta^2 < \xi_\beta^2$ if $\xi_\beta^2 < \xi_\alpha^2$, so that

$$\eta^2 > \xi_\beta^2 > \xi_\alpha^2 \quad \text{or} \quad \eta^2 < \xi_\beta^2 < \xi_\alpha^2. \tag{3.7}$$

It is tacit that

$$\xi_\alpha < \eta < \xi_\beta,$$

an inequality incompatible with the first of (3.7). Also, from (3.6) we see that $\kappa\xi_\beta^2 > \xi_\alpha^2$. Thus the restrictions on $\xi_\alpha$ and $\xi_\beta$ are

$$\xi_\alpha < 0, \quad \xi_\beta > 0, \quad \xi_\beta < |\xi_\alpha| < \sqrt{\kappa}\,\xi_\beta. \tag{3.8}$$

When $\xi_\alpha$ and $\xi_\beta$ are chosen subject to these restrictions, then $|\eta|$ is given by (3.6); either sign can be chosen for $\eta$.

In view of $(3.2)_4$, the point $\xi = \xi_\beta$ corresponds to the curve $x = \xi_\beta t^{1/3}$. This curve represents the wave front marking the advance of species $\beta$ into the unpopulated portion of the habitat. Since $\xi_\beta > 0$, this front moves to the right. Similarly, since $\xi_\alpha < 0$, the front $x = \xi_\alpha t^{1/3}$ governing the spread of species $\alpha$ moves to the left. The speeds of these two fronts are

$$v_\alpha(t) = \tfrac{1}{3}|\xi_\alpha| t^{-1/3}, \qquad v_\beta(t) = \tfrac{1}{3}\xi_\beta t^{-1/3},$$

and the last of (3.8) tells us that

$$v_\beta < v_\alpha < \sqrt{\kappa}\, v_\beta,$$

so that the $\alpha$-front moves faster than the $\beta$-front. (Since $\kappa > 1$, the dispersivity of species $\alpha$ is larger than that of species $\beta$.)

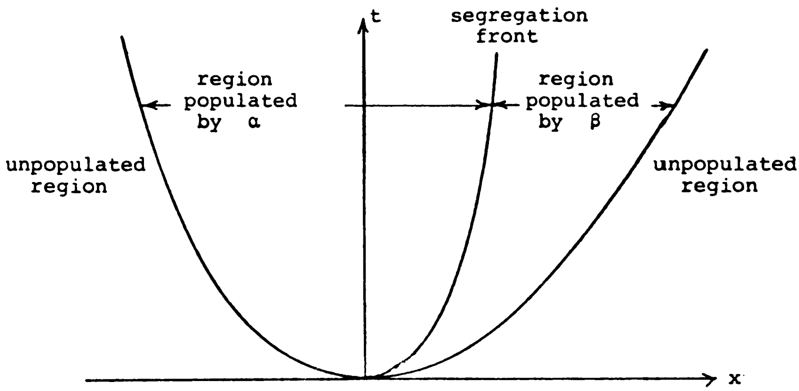


FIG. 1. The three fronts.

The front defined by $x = \eta t^{1/3}$ divides the region populated by species $\alpha$ from that populated by $\beta$, and is marked by jump discontinuities in both $\alpha$ and $\beta$. This front can move either to the right or to the left, and it moves slower than the $\alpha$ and $\beta$ fronts just discussed.

It is not difficult to verify that all three fronts move with a velocity equal to the dispersal velocity of individuals situated at the front. Of course, consistent with this conclusion is the fact that the dispersal velocities of the two species coincide at the *segregation front* $x = \eta t^{1/3}$. This result (with $(3.5)_3$) corresponds to the usual jump relation satisfied at a shock and is exactly the condition that renders the foregoing a weak solution of the system (3.1).

In closing we emphasize the following interesting property of the solution above: even though the dispersivities of the two species are unequal, the species do not disperse through one and other, but rather *remain segregated for all time*.

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