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Addendum to "Random population dispersal in a linear hostile environment"

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We extend the previous results, describing the population dispersal that occurs in some insects and small animal populations when this process is not strictly random, by including both the downgradient diffusion and the full Pearl-Verhulst logistic growth term in the equation of evolution. Motivated by the increasing fragmentation of natural habitats that is the result of human activities, we consider a finite habitat surrounded by a hostile environment. Previous work [Phys Rev. E **62**, 4032 (2000)] considered only the case of an unbounded habitat, obviating issues concerned with the critical habitat size and the adoption of strategies best suited to achieve lower densities by dispersal through downgradient diffusion.

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I. INTRODUCTION

Dispersal of insects and small animals occurs due to a combination of factors whose interplay is still not well understood [1]. A number of laboratory and field studies of different insect species [2] and small animals [3] indicated the need for a reassessment of the then existing mathematical descriptive paradigm. The latter was based on the Fisher equation [4] and successfully used in the seminal work of Skelam [5] describing the dispersal of muskrats and also oak trees. In that descriptive framework dispersal is treated as a purely random process, described by simple diffusion, and the population density $n(x,t)$ is assumed to evolve according to

$$\frac{\partial}{\partial t}n=D_0\frac{\partial^2}{\partial x^2}n+\beta(1-n/N), \tag{1}$$

i.e., through a superposition of diffusion and a logistic, Pearl-Verhulst (PV), growth term. Here D_0 is the diffusion coefficient, β is the growth rate, and N is the habitat carrying capacity; in what follows we scale n to N.

A conclusion that followed from the studies cited above was that in some species dispersion is not solely due to random movement, but that it is at least partly due to a desire to lower the local density. This confers some advantages relative to increased survival, e.g., it results in equilibrium densities below the carrying capacity providing a buffer in the event resources, which for some reason are diminished and, also, it reduces competition for resources in single species habitats.

A number of approaches to modifying Eq. (1) have been taken to describe a more nuanced view of the dispersal process. A common feature of these approaches is the replacement of the flux $j=-D_0(\partial/\partial x)n$ with a density-dependent diffusion coefficient $D(n)_{-}$ that increases with n so that diffusion is enhanced, where the density is high-favoring downgradient diffusion. This introduces a second nonlinearity into Eq. (1), which itself remains unsolved except for the steady state case in a finite habitat [5], and the pertubative [6] and the special [7] traveling wave solutions for an infinite habitat. Here we will consider $D=D_0+D_1n$. This diffusion model follows from an analysis of lion-ant dispersal in a laboratory setting [8,9] and has also been postulated on purely theoretical grounds as describing biased random motion [10]. Previous work [9–12] which has only considered the case of an unbounded habitat, has with a single exception [13] taken $D_0=0$. When the PV growth term is replaced with a linear Malthusian growth term [9–11] this allows the resulting generalization of Eq. (1) to be transformed into an equation previously studied and solved in connection with the flow in a porous medium [14]. Neglecting D_0 was justified in the case of lion-ant dispersal [9] for which this term was shown to be small except near the dispersal front in the infinite space being considered. Traveling wave solutions for the case where $D=D_\alpha n^\alpha$ together with the generalized PV growth term $\beta n^{\upsilon}(1-n)$ have also been studied [12].

As humans expand the range of their activities the fragmentation of natural habitats has become all too common. This provides the motivation here for considering dispersal in a finite habitat surrounded by a hostile environment. We retain both the full PV growth term and take $D=D_0+D_1n$, since near the boundaries at $x=0$, L where the density becomes vanishingly small, the D_0 term can become dominant and cannot be neglected *a priori*. Since the equation we will need to consider is analytically more complex than Eq. (1), it is unlikely that an exact solution can be found. However, we are able to obtain an approximate solution through the use of a technique applied earlier to Eq. (1) [15]. The solution found here does shows the expected qualitative behavior, particularly in the case of the equilibrium solution which is reduced from that for the case of purely random dispersal. In the following section we first describe, then apply the method of solution. A discussion of the solution found then follows in Sec. III.

II. FORMULATION AND SOLUTION

As discussed above, we consider

$$\frac{\partial}{\partial t}n=D_0\frac{\partial^2}{\partial x^2}n_{xx}+D_1[(n_x)^2+nn_{xx}]+\beta n(1-n), \tag{2}$$

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where n has been normalized to N and D_1 here and in what follows has a factor N^{-1} incorporated into it. The habitat size is L and the boundary conditions are $n(0,t)=n(L,t)=0$, where for reasons of simplicity we consider dispersal in only one dimension. The method of solution that we employ here is similar to that used in obtaining normal solutions to the Boltzmann equation [16] and has been described in detail previously [15]. Briefly, we ignore the fact that Fourier analysis is intended to apply to linear equations [17] and look for solutions of the form

$$n(x,t)=\sum A_n(t)\sin(n\pi x/L), \tag{3}$$

where $A_n(t)=A_n(A_1(t))$, $n=2,3,\ldots$. As in the case of the Boltzmann equation, we do not necessarily expect such special solutions to be accurate at very short times; this depends on the nature of the initial condition. In the context of the Boltzmann equation, this is known as initial slip [18,19].

Substitution of Eq. (3) into Eq. (2), followed by multiplication by $\sin(n\pi x/L)$, and then integration over x lead to equations for the A_n; for $n=1$, we find

$$\begin{aligned}\frac{d}{dt}A_1&=A_1[\beta-D_0(\pi/L)^2]-A_1^2[(4\pi D_1/3L^2)+(8\beta/3\pi)]\\&\quad+O(A_1A_2,A_1A_3,\ldots,A_2^2,A_2A_3,\ldots)\\&\equiv A_1K_{11}+A_1^2K_{12}+\cdots.\end{aligned}\tag{4}$$

Assuming for simplicity that the initial condition is symmetric about $x=L/2$, so that $A_{2n}=0$, the equation for the remaining A_n is

$$\begin{aligned}\frac{d}{dt}A_n&=A_n[\beta-D_0(\pi n/L)^2]+\frac{A_1^2}{n(n-2)(n+2)}[8\beta/\pi\\&\quad+(4\pi D_1/L^2)(n^2-2)+(8\pi D_1/L^2)]\\&\quad+(\text{higher-order terms})\\&\equiv A_nK_{n1}+A_1^2K_{n2}+(\text{higher-order terms}),\end{aligned}\tag{5}$$

where here and below "higher-order terms" denotes terms that are of the same form (with differing numerical coefficients) as those shown explicitly in Eq. (4).

In order to close these equations, we make use of the assumed functional dependence of the A_n for $n>1$ to rewrite Eq. (5) using the substitutions

$$\frac{d}{dt}A_n=\frac{\delta}{\delta A_1}A_n\frac{d}{dt}A_1 \tag{6}$$

and

$$A_n=a_{n1}A_1+a_{n2}A_1^2+\cdots, \tag{7}$$

so that

$$\begin{aligned}\frac{d}{dt}A_n&=(a_{n1}A_1+2a_{n2}A_1^2+\cdots)(A_1K_{11}+A_1^2K_{12}+\cdots)\\&=(a_{n1}A_1+a_{n2}A_1^2+\cdots)K_{n11}^{\;\;2}+A_1^2K_{n2}+\cdots.\end{aligned}\tag{8}$$

It follows that $A_n=O(A_1^2)$, so that to $O(A_1^2)$ we have

$$A_1(t)=\frac{K_{11}A_1(0)}{[K_{11}+K_{12}A_1(0)]e^{-K_{11}t}-K_{12}A_1(0)}. \tag{9}$$

For $n>1$ the A_n can be found to any desired order in A_1 from Eqs. (4–8) and, as noted above, it is immediately apparent from comparison of the $O(A_1)$ terms on either side of Eq. (5) that $a_{n1}=0$, so that all of the terms indicated as "higher order" are at least of $O(A_1^3)$, and for small values of A_1 can be neglected on intermediate and long time scales for which dependence on initial data is weak. Further, we can determine the higher approximations to any desired order in A_1 through the simple algorithm that follows directly from Eq. (8), e.g., equating terms of $O(A_1^2)$, we find

$$a_{n2}=\frac{K_{n2}}{2K_{11}-K_{n1}},\quad n=3,5,\ldots. \tag{10}$$

This indicates that the coefficients of the presumed small A_1^2 terms become smaller with increasing n as n^{-1}; it can also be verified that a_{n3}, a_{n4},... also decrease with increasing n so that Eq. (9) provides a good qualitative description subject to the restrictions noted earlier (A_1 small, times for which dependence on the initial data is weak).

III. DISCUSSION

There are two qualitative features of the solution that follow "by inspection" from Eq. (9). First, if D_0 is identically zero there is no critical habitat size below which an initial population becomes extinct. This is intuitive; as the popula-

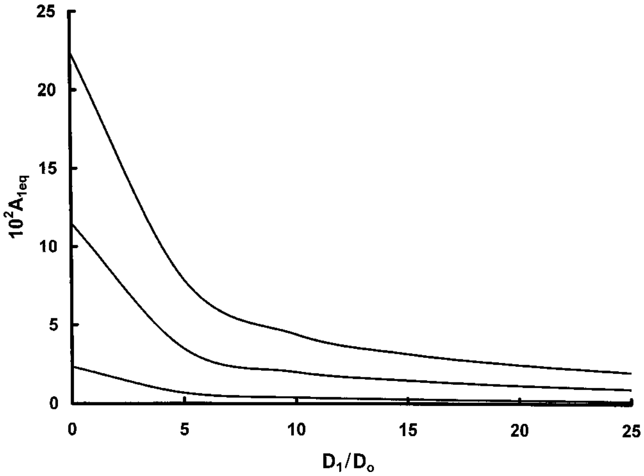

FIG. 1. 10^2A_{1eq} versus the purposeful dispersal. D_1/D_0 for $L_c/L=0.99$ (top curve), $L_c/L=0.95$ (middle curve), and $L_c/L=0.90$ (bottom curve).

tion falls diffusion to the boundary decreases allowing the interior population to recover sufficiently to avoid extinction, and a stable [20] equilibrium with $A_1(\infty)=|K_{11}/K_{12}|$ is established [21]. When $D_0 \neq 0$ the population can become extinct if D_0 is too large regardless of the value of D_1; the critical length is $L_c = \pi(D_0/\beta)^{1/2}$, unchanged from that when dispersal is solely due to random movement. It also follows from Eq. (9) that when a surviving equilibrium population is established, increasing nonrandom dispersal, i.e., increasing D_1, will decrease population densities throughout the habitat thereby reducing vulnerability to the possibility of resource shortages.

In Fig. 1, we illustrate the interplay between D_0 and D_1 (the latter normalized by N) for several values of L_c/L. If the ratio D_1/D_0 is considered as a measure of purposeful dispersal, we see from Fig. 1 that the degree to which this occurs must increase as the habitat size becomes larger relative to the critical length in order to achieve the same preferred density limit. The most effective strategy to follow in doing this would be to decrease random dispersal, which not only increases purposeful dispersal but also decreases L_c as well. This is more effective than the other available alternative, decreasing the birth rate, which is also likely to be more strongly influenced by factors unrelated to dispersal.

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