

A Diffusion-Based Theory of Organism Dispersal in Heterogeneous Populations

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ABSTRACT: We develop a general theory of organism movement in heterogeneous populations that can explain the leptokurtic movement distributions commonly measured in nature. We describe population heterogeneity in a state-structured framework, employing advection-diffusion as the fundamental movement process of individuals occupying different movement states. Our general analysis shows that population heterogeneity in movement behavior can be defined as the existence of different movement states and among-individual variability in the time individuals spend in these states. A presentation of moment-based metrics of movement illustrates the role of these attributes in general dispersal processes. We also present a special case of the general theory: a model population composed of individuals occupying one of two movement states with linear transitions, or exchange, between the two states. This two-state “exchange model” can be viewed as a correlated random walk and provides a generalization of the telegraph equation. By exploiting the main result of our general analysis, we characterize the exchange model by deriving moment-based metrics of its movement process and identifying an analytical representation of the model’s time-dependent solution. Our results provide general and specific theoretical explanations for empirical patterns in organism movement; the results also provide conceptual and analytical bases for extending diffusion-based dispersal theory in several directions, thereby facilitating mechanistic links between individual behavior and spatial population dynamics.

Keywords: diffusion, heterogeneity, variability, model, movement, dispersal.

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Population biologists have become increasingly interested in the spatial dimension of populations, and organism movement is embraced among the fundamental processes underlying population dynamics (e.g., Taylor 1991; Turchin 1998; Cain et al. 2000; Nathan and Muller-Landau 2000). Accordingly, an understanding of organism movement can be important for the management of pests (Turchin and Thoeny 1993), conserved species (Ruckelhaus 1997; Schultz 1998), fisheries (Sibert et al. 1999; Zabel 2002), and species invasions (Shigesada et al. 1995; Kot et al. 1996; Neubert et al. 2000; Clark et al. 2001). One implication of these findings is that biologists require a theoretical framework for conceptualizing, understanding, and predicting the movements of organisms.

Classical diffusion-based models are foundational in theories of dispersal. They have proven useful because they can be derived as continuum approximations to random walks (Turchin 1998; Okubo and Levin 2002), and they have explained some of the movement patterns of populations (e.g., Dobzhansky and Wright 1943; Skellam 1951; Turchin and Thoeny 1993; Turchin 1998; Okubo and Levin 2002; Zabel 2002). However, one potential empirical deficiency of diffusion-based models is the classic prediction of Gaussian movement distributions. Indeed, distributions of distances moved that are Gaussian (normal), with the mean position linear in the advection rate and the variance linear in the diffusion rate, are fundamental to advection-diffusion processes, but they are qualitatively different from the leptokurtic movement distributions that are usually indicated in empirical analyses of organism movement. Leptokurtic movement distributions have positive kurtosis attributable to more probability mass over the mean and extreme values than a corresponding Gaussian distribution (i.e., a Gaussian distribution with the same mean and variance), which has a kurtosis of 0 (when adjusting by 3; Stuart and Ord 1987; D’Agostino et al. 1990; Okubo and Levin 2002). Leptokurtic movement distributions are commonly observed in nature (Turchin 1998; Okubo and Levin 2002), arising in dispersal studies of plants (Kot et al. 1996; Clark et al. 1999; Cain et al. 2000; Nathan and Muller-Landau 2000), insects (Dobzhansky and Wright 1943;

Plant and Cunningham 1991; Gomez and Zamora 1999), fishes (Skalski and Gilliam 2000; Gilliam and Fraser 2001; Rodríguez 2002), birds (Paradis et al. 1998; Forero et al. 1999), and mammals (Sandell et al. 1991; Price et al. 1994).

Accordingly, studies in dispersal ecology have worked to develop models that can predict leptokurtic movement distributions. Several of these studies, which frequently focus on the population-level consequences of movement, have de-emphasized diffusion-based approaches by suggesting a variety of phenomenological (in the sense described by Turchin [1998]) dispersal kernels (Kot et al. 1996; Turchin 1998; Clark et al. 1999, 2001; Higgins and Richardson 1999; Neubert and Caswell 2000; Neubert et al. 2000; Rodríguez 2002). However, the classic advection-diffusion equation can be adapted to account for leptokurtic movement distributions. Several biologists (Dobzhansky and Wright 1943; Plant and Cunningham 1991; Turchin 1998; Cronin et al. 2000; Skalski and Gilliam 2000; Okubo and Levin 2002) have recognized that a population composed of individuals occupying two or more different movement states (where an organism in each state exhibits rates of movement that are unique to that state) can generate leptokurtic movement distributions in a diffusion-based model because sums or integrals of Gaussian movement distributions can produce leptokurtic movement distributions. We and others (Cronin et al. 2000; Skalski and Gilliam 2000) have referred to this idea as the population heterogeneity hypothesis/model. In this article, we extend the population heterogeneity hypothesis embodied in earlier work by developing and analyzing a general theory of organism movement in populations consisting of individuals occupying one of n movement states, and we develop a narrower yet biologically meaningful subset of the general theory (two movement states with transitions between states) and analyze its features in more detail. Our intent is to provide insight into the manner in which the varying behavior of individuals maps into population-level patterns of movement and to provide a new diffusion-based model with population heterogeneity that can be statistically fit to data; we also seek to stimulate empirical research that identifies and quantifies the set of biological mechanisms that underlie population-level patterns of movement, including sources of population heterogeneity.

A General Framework for Movement

Our theory is based on two main premises. First, we specify the biased random walk to be the fundamental movement process of individuals in our model, and we approximate the random walk by using its continuum counterpart, the classic advection-diffusion equation (Turchin 1998; Okubo and Levin 2002). Second, we suppose that at each point

in time every individual occupies one of n movement states.

The conditions under which we develop the theory are the same as those that have been traditionally emphasized in the field of organism movement (Turchin 1998; Okubo and Levin 2002); that is, we track movements of a population of individuals released from points in an infinite spatial domain. We use these conditions because they are relevant to the kinds of movement data that are often collected (Dobzhansky and Wright 1943; Skellam 1951; Plant and Cunningham 1991; Turchin and Thoeny 1993; Cronin et al. 2000; Skalski and Gilliam 2000; Gilliam and Fraser 2001; Zabel 2002) and are relatively simple mathematically (Strauss 1992; Turchin 1998; Okubo and Levin 2002). We illustrate our theory in one-dimensional space by considering movement along a line. Extensions to two and three spatial axes, as well as to other types of initial and boundary conditions, are usually straightforward, using standard methods for studying differential equations (e.g., Strauss 1992). However, the ideas are not so easily transferable to finite spatial domains. Therefore, our results are most appropriately applied to empirical settings where the landscape (or habitat) for organism movement and its subsequent measurement is large relative to the dispersal rate of the organism of interest.

With these basic assumptions in mind, the development of the general theory is facilitated by imagining the movement of a focal individual exhibiting a biased random walk along an infinite line. Position in space, x , is position on the real line, so $x \in (-\infty, +\infty)$, and x denotes magnitude and direction, so that distance moved can be positive (movement to the right) or negative (movement to the left). Accordingly, the individual's movement while in the i th state can be described in probabilistic terms by the classic advection-diffusion equation (Turchin 1998; Okubo and Levin 2002) so that

$$\frac{\partial P_i(x, t)}{\partial t} = D_i \frac{\partial^2 P_i(x, t)}{\partial x^2} - \beta_i \frac{\partial P_i(x, t)}{\partial x}, \quad (1)$$

where $P_i(x, t)$ is the spatial probability density of the individual's position while occupying the i th state (i.e., the probability that the individual is near position x at time t when occupying the i th state), and D_i and β_i are the rates of diffusion (a measure of an organism's total movement rate, or tendency to move in any direction) and advection (a measure of an organism's net movement rate, or tendency to move in a particular direction), respectively, of the individual while occupying the i th state. An important assumption is that the state-dependent movement rates do not depend on the individual's current position in space (e.g., habitat type): D_i and β_i are constants and do not depend on x . Spatial dependence in movement rates com-

plicates the analysis considerably, but this problem has been approached in advection-diffusion settings (e.g., Grünbaum 2000), and our results can potentially aid in this area (see “Discussion”). Even without explicit spatial dependence of movement rates, an individual’s state, in biological terms, could be described by one or more of the many different features of the organism’s phenotype that may correlate with movement behavior, including wing morphology (Zera and Denno 1997), body size (Paradis et al. 1998; Skalski and Gilliam 2000; Zabel 2002), age (Forero et al. 1999), sex (Price et al. 1994), growth rate (Skalski and Gilliam 2000; Fraser et al. 2001; Gilliam and Fraser 2001), energetic reserves (O’Riain et al. 1996), reproductive activity (O’Riain et al. 1996; Langellotto and Denno 2001), predation risk (Gilliam and Fraser 2001), and boldness (Fraser et al. 2001). A handful of empirical studies have documented organisms that appear to occupy different movement states per se. Among-individual variability in movement behavior has been observed in salmonids (McLaughlin et al. 1992; Bradford and Taylor 1997; Brännäs and Eriksson 1999) and a killifish (Fraser et al. 2001), and alternating resting and moving behavior has been described in beetles (Firle et al. 1998). Further, a foraging locus, with “rover” and “sitter” alleles, has been associated with fast and slow movement phenotypes in the fruit fly (e.g., Sokolowski et al. 1997), and there is evidence that a dispersal polymorphism in a marine polychaete has a heritable component (Toonen and Pawlik 2001).

Equation (1) implies that an individual with initial density $P(x_0, t_0)$ that enters state i at time t_0 and remains in state i for time s_i will disperse according to a Gaussian redistribution kernel (i.e., the Gaussian probability density is the “fundamental solution” of the advection-diffusion process; Strauss 1992), such that

$$\begin{aligned} P_i(x_i, t_0 + s_i) &= \int_{-\infty}^{+\infty} G_i(x_i - x_0, s_i) P(x_0, t_0) dx_0 \\ &= \int_{-\infty}^{+\infty} \frac{\exp\left[\frac{-(x_i - x_0 - \beta_i s_i)^2}{4D_i s_i}\right]}{\sqrt{4\pi D_i s_i}} P(x_0, t_0) dx_0 \end{aligned} \quad (2)$$

describes the spatial density for the new position of the individual at time $t_0 + s_i$. Equation (2) models, in a probabilistic sense, the transitions from position x_0 at time t_0 to position x_i at time $t_0 + s_i$ via the Gaussian kernel, $G_i(x_i - x_0, s_i)$.

The description of movement given by equations (1) and (2) can be extended to apply to an individual occupying any set of the n possible states during a time interval $[0, t]$. In this setting, an individual can enter any of the n states any number of times during time t . Accordingly, let

m be the number of ordered states occupied by the individual in sequence during the time interval $[0, t]$, and let $s = (s_1, s_2, \dots, s_m)'$ be a column vector (y' denotes the transpose of a vector y) describing the amounts of time spent in each of these m states (not necessarily unique with respect to the movement parameters; note that $\sum_{i=1}^m s_i = t$). Note that if an individual changes state k times during time t , then $m = k + 1$. Given s , equation (2) can be applied m times to any arbitrary initial density, $P(x_0, t_0)$. Thus, the individual’s spatial density after occupying m movement states during time $t = \sum_{i=1}^m s_i$ can be computed as

$$\begin{aligned} P\left(x_m, t_0 + \sum_{i=1}^m s_i\right) &= \\ &\int_{-\infty}^{+\infty} G_m(x_m - x_{m-1}, s_m) \int_{-\infty}^{+\infty} G_2(x_2 - x_1, s_2) \dots \\ &\dots \int_{-\infty}^{+\infty} G_1(x_1 - x_0, s_1) P(x_0, t_0) dx_0 dx_1 \dots dx_{m-1} \\ &= \int_{-\infty}^{+\infty} \frac{\exp\left[\frac{-(x_m - x_0 - \beta_1 s_1 - \beta_2 s_2 - \dots - \beta_m s_m)^2}{4(D_1 s_1 + D_2 s_2 + \dots + D_m s_m)}\right]}{\sqrt{4\pi(D_1 s_1 + D_2 s_2 + \dots + D_m s_m)}} P(x_0, t_0) dx_0, \end{aligned} \quad (3)$$

where the integrals are convolutions (Strauss 1992) of Gaussian kernels with Gaussian densities that result in Gaussian densities so that the final $m - 1$ integrals can be evaluated without specifying the initial density, $P(x_0, t_0)$. Under the simplifying assumption that $P(x_0, t_0) = \delta(x_0)$ (the initial condition is a δ function corresponding to an initial point release), the integral over x_0 in equation (3) has a Gaussian form,

$$P\left(x_m, t_0 + \sum_{i=1}^m s_i\right) = \frac{\exp\left[\frac{-(x_m - \beta_1 s_1 - \beta_2 s_2 - \dots - \beta_m s_m)^2}{4(D_1 s_1 + D_2 s_2 + \dots + D_m s_m)}\right]}{\sqrt{4\pi(D_1 s_1 + D_2 s_2 + \dots + D_m s_m)}}. \quad (4)$$

The analytical construction of the expression in equation (4) is important because it shows that an individual that spends time in different states with different diffusion and advection rates nonetheless has a Gaussian movement distribution (this idea is identical to the concept of advection-diffusion with temporally varying rates; Turchin 1998; Okubo and Levin 2002). It also shows that knowledge of the detailed sequence of transitions among

various states, denoted with the vector s , is not required. Instead, because the s_i 's enter into the Gaussian kernel in equation (4) in a linear fashion, it is sufficient to specify only the total amount of time spent in each of the n (unique with respect to the movement parameters) states during the time interval $[0, t]$. This result applies because the total amount of time spent in the i th state, τ_i , is related to s by $\tau_i = \sum_{\Psi_i} s_j$ where $\Psi_i = \{s_j | s_j \text{ is time spent in state } i\}$. Accordingly, the column vector $\tau = (\tau_1, \tau_2, \dots, \tau_n)'$ can be substituted for s in equation (4) to obtain

$$G(x, \tau) = \frac{\exp\left[\frac{-(x - \beta_1\tau_1 - \beta_2\tau_2 - \dots - \beta_n\tau_n)^2}{4(D_1\tau_1 + D_2\tau_2 + \dots + D_n\tau_n)}\right]}{\sqrt{4\pi(D_1\tau_1 + D_2\tau_2 + \dots + D_n\tau_n)}}, \quad (5)$$

where the function $G(x, \tau)$ describes a diffusion-based redistribution kernel for an individual occupying n movement states (with corresponding state-specific movement rates) during time $t = \sum_{i=1}^n s_i = \sum_{i=1}^n \tau_i$.

Equation (5) applies to an individual having a particular value for τ , but it can be extended to apply to a population of individuals. Any value of τ for an individual drawn at random from the population can be treated as the value taken on by a random vector of the same dimension, $T(t) = [T_1(t), T_2(t), \dots, T_n(t)]'$, where $\tau \in \Gamma = \{(\tau_1, \tau_2, \dots, \tau_n) | \tau_1 + \tau_2 + \dots + \tau_n = t\}$. Treating $T(t)$ as a random vector (i.e., a random/stochastic process; Gardiner 1985; Ricciardi 1986; Grimmett and Stirzaker 2001) allows for heterogeneous rates of movement in the population. Thus, if $R(\tau, t)$ is a probability density for $T(t)$, then the equation

$$P(x, t) = \int_{\Gamma} G(x, \tau) R(\tau, t) d\tau \quad (6)$$

describes, via a mixture of Gaussian movement distributions, the spatial density for a population of individuals with heterogeneous movement behaviors.

The population's spatial density, as represented in equation (6), is useful for several reasons. First, the construction of equation (6) elucidates a framework for relating the movement behaviors of individuals to the spatial spread of a population because the spatial densities of individuals moving by different rates of diffusion and advection are integrated (or summed) to give the aggregate spatial density of the population: $P(x, t)$. The prediction of leptokurtic movement distributions can arise directly from this integration because, as noted earlier, sums (or integrals) of Gaussian movement distributions can produce leptokurtic movement distributions similar to those observed in na-

ture. Earlier models of the population heterogeneity hypothesis are special cases of equation (6) (Plant and Cunningham 1991; Cronin et al. 2000; Skalski and Gilliam 2000; Okubo and Levin 2002).

Further, equation (6) motivates a definition of the population heterogeneity hypothesis. Population heterogeneity enters into the model via two interacting pathways: the set of movement rates, $\{\beta_i, D_i\}_{i=1}^n$, and the probability density function for time spent in each movement state, $R(\tau, t)$. Indeed, equation (6) can be used to define the population heterogeneity hypothesis by requiring that different movement states, represented by $\{\beta_i, D_i\}_{i=1}^n$, must exist in a population and also by requiring that nonzero among-individual variability in the amount of time spent in at least one of these movement states must exist, where this variability is captured in the random vector $T(t)$, with probability density $R(\tau, t)$. If either the first or the second condition does not hold, then the population is homogeneous in terms of movement. These ideas support the utility of an empirical research program that works not only to measure state-dependent movement rates per se (information that can be used to predict spatial population dynamics) but also to identify the genetic, physiological, behavioral, ecological, and evolutionary factors that determine state-dependent movement rates (information that provides understanding of the mechanisms that determine organism movement).

The spatial density given by equation (6) is also useful because it can be used to generate metrics of the movement process. For any given time t , the spatial density can be interpreted as a probability density function for a random variable $X(t)$, where $X(t) \in (-\infty, +\infty)$ is the distance moved by an individual after time t (i.e., $X(t)$ is a stochastic process). Thus equation (6) can be used to compute useful descriptions of $X(t)$, such as the mean, variance, skewness, and kurtosis (app. A). These metrics illustrate the role of population heterogeneity in determining organism movement by decomposing measures of the movement process into the interacting effects of the two underlying sources of population heterogeneity: a set of different movement states, $\{\beta_i, D_i\}_{i=1}^n$, and among-individual variability in the time spent in at least one of the movement states, represented via $T(t)$.

Using equation (6), the mean distance moved by an individual is

$$E[X(t)] = \beta_1 E[T_1(t)] + \beta_2 E[T_2(t)] + \dots + \beta_n E[T_n(t)], \quad (7)$$

a sum of the advection rates weighted by the mean amounts of time spent in each state, where E denotes expectation. The mean distance moved only depends on the advection rates as in the classic advection-diffusion

model. However, in contrast to the classic model, the variance of the distance moved can depend on both the rates of diffusion and advection (the variance in the classic model only depends on the diffusion rate). The variance of the distance moved is

$$\begin{aligned} \text{Var}[X(t)] = & 2\{D_1E[T_1(t)] + D_2E[T_2(t)] + \cdots + D_nE[T_n(t)]\} \\ & + \text{Var}[\beta_1T_1(t) + \beta_2T_2(t) + \cdots + \beta_nT_n(t)], \end{aligned} \quad (8)$$

a sum of diffusion rates weighted by the mean amounts of time spent in each state plus the variance of the total distance moved via advection. The dependence of equation (8) on rates of advection, even in a very simple model, can lead to nonlinear and accelerating variances of $X(t)$ as time progresses (Skalski and Gilliam 2000). If the population is homogeneous because either all of the β_i 's are equal or because all individuals have the same $T(t)$ (giving $\text{Var}[T_i(t)] = 0$, $i = 1, \dots, n$), then the latter term vanishes and the variance of $X(t)$ only depends on diffusion rates. In this case, the variance in $X(t)$ is always bounded by a term linear in t because $E[T_i(t)] \leq t$ for all i and t .

Metrics involving higher moments can also be analyzed, but the expressions become cumbersome. To simplify the notation, let $\beta = (\beta_1, \beta_2, \dots, \beta_n)'$ and $D = (D_1, D_2, \dots, D_n)'$. The skewness of $X(t)$, a measure of the asymmetry of a movement distribution about its mean (Stuart and Ord 1987; D'Agostino et al. 1990), can be expressed as

$$\begin{aligned} \text{skewness}[X(t)] &= \frac{E(\{X(t) - E[X(t)]\}^3)}{\{\text{Var}[X(t)]\}^{3/2}} \\ &= \frac{S_{\text{num}}}{S_{\text{den}}}, \end{aligned} \quad (9)$$

where

$$\begin{aligned} S_{\text{num}} &= E(\{\beta'T(t) - \beta'E[T(t)]\}^3) \\ &\quad + 3 \text{Cov}[\beta'T(t), 2D'T(t)], \\ S_{\text{den}} &= \{2D'E[T(t)] + \text{Var}[\beta'T(t)]\}^{3/2}, \end{aligned}$$

and Cov denotes covariance. The skewness of $X(t)$ depends on the skewness of $\beta'T(t)$, and the presence of the covariance term indicates that the effect of population heterogeneity on skewness is increased if total advection rate covaries positively with total diffusion rate. The skewness is a useful measure of population heterogeneity in rates of advection. If the population is homogeneous in terms of advection rates, because either all of the β_i 's are equal or all individuals have the same $T(t)$, then both terms in the

numerator of equation (9) are 0 and the skewness of $X(t)$ is 0.

The kurtosis of $X(t)$ (Stuart and Ord 1987; D'Agostino et al. 1990) can be expressed as

$$\begin{aligned} \text{kurtosis}[X(t)] &= \frac{E(\{X(t) - E[X(t)]\}^4)}{\{\text{Var}[X(t)]\}^2} - 3 \\ &= \frac{K_{\text{num}}}{K_{\text{den}}}, \end{aligned} \quad (10)$$

where

$$\begin{aligned} K_{\text{num}} &= E(\{\beta'T(t) - \beta'E[T(t)]\}^4) \\ &\quad - 3\{\text{Var}[\beta'T(t)]\}^2 + 3 \text{Var}[2D'T(t)] \\ &\quad + 6 \text{Cov}(2D'T(t), \{\beta'T(t) - \beta'E[T(t)]\}^2), \\ K_{\text{den}} &= \{2D'E[T(t)] + \text{Var}[\beta'T(t)]\}^2. \end{aligned}$$

Analogous to the skewness, the kurtosis of $X(t)$ depends on the kurtosis of $\beta'T(t)$, and the covariance term indicates an interaction between total rates of diffusion and variability in total advection rates that, if positive, can act to increase the effect of population heterogeneity on the kurtosis. Moreover, the kurtosis provides another kind of metric of population heterogeneity because it is a measure of population heterogeneity in rates of diffusion and advection. If the population is homogeneous in terms of diffusion and advection rates, either because all of the D_i 's are equal and all of the β_i 's are equal or because all individuals have the same $T(t)$, then all four terms in the numerator of equation (10) are 0 and the kurtosis of $X(t)$ is 0. Accordingly, the skewness and kurtosis are useful measures of population heterogeneity in movement rates because they are both equal to 0 if the population is homogeneous.

We have developed a general theory of organism movement in heterogeneous populations with the intent that the general model will provide insight into the manner in which the movement behavior of individuals translates into spatial dynamics in heterogeneous populations, thereby guiding the development and analysis of more specific models that incorporate the population heterogeneity hypothesis. The general theory also will stimulate empirical research that works to uncover the mechanisms that determine individual-level movement, including the estimation of functions and parameters of state-dependent movement processes that can be used to predict spatial population dynamics. In the next section, we develop and study a special case of the general theory.

A Two-State Model of Organism Movement

A more concrete version of the population heterogeneity hypothesis can be constructed by envisioning a population composed of individuals that occupy one of two movement states, slow or fast, and that make transitions between these two states (i.e., there is exchange of individuals between states). We call this the “exchange model.” Slow and fast individuals disperse by diffusion and advection with rates unique to the state: D_s and β_s , and D_f and β_f , are the rates of diffusion and advection for slow and fast individuals, respectively. A continuum approximation to a discrete random walk (Turchin 1998; Okubo and Levin 2002) based on these assumptions leads to a system of partial differential equations that describes the dynamical spatial densities of slow and fast individuals, giving

$$\begin{aligned} \frac{\partial S}{\partial t} &= D_s \frac{\partial^2 S}{\partial x^2} - \beta_s \frac{\partial S}{\partial x} - aS + bF \\ \frac{\partial F}{\partial t} &= D_f \frac{\partial^2 F}{\partial x^2} - \beta_f \frac{\partial F}{\partial x} + aS - bF \end{aligned} \quad (11)$$

where $S(x, t)$ and $F(x, t)$ are the spatial densities of slow and fast individuals, respectively, and parameters a and b are the rates at which individuals switch between slow and fast states. A critical feature of the exchange model is that it can be viewed as a continuum approximation to a generalized correlated random walk. When $D_s = D_f = 0$, $\beta_s = -\beta_f$, and $a = b$, equations (11) reduce to the telegraph model (Goldstein 1951; Turchin 1998; Okubo and Levin 2002), with speed parameter $\beta_s = -\beta_f$ and characteristic time of persistence $1/a = 1/b$. Correlated random walks have played a role in the study of organism movement in a variety of contexts (Othmer et al. 1988; McCullough and Cain 1989; Goldwasser et al. 1994; Holmes et al. 1994; Schultz 1998; Turchin 1998; Okubo and Levin 2002).

The exchange model is a special case of the general theory given by equation (6) and can be interpreted within that framework. For the present analysis of the exchange model, we consider an initial point release of individuals on an infinite line. That is, we assume the auxiliary conditions

$$\begin{aligned} P(x, 0) &= S(x, 0) + F(x, 0) \\ &= \frac{b}{a+b} \delta(x) + \frac{a}{a+b} \delta(x) = \delta(x), \quad (12) \\ P(\pm\infty, t) &= S(\pm\infty, t) + F(\pm\infty, t) = 0, \end{aligned}$$

where $b/(a + b)$ and $a/(a + b)$ are the steady state solutions to equations (11) when $D_s = D_f = \beta_s = \beta_f = 0$ and

$\delta(x)$ is a δ function (Strauss 1992). That is, $b/(a + b)$ and $a/(a + b)$ are the expected proportions of individuals in the slow and fast states. Our presentation of the general theory leaves the details of $T(t)$ unspecified, and the relevance of $T(t)$ to the exchange model is not immediately indicated by equations (11). In the framework of equation (6), the exchange model has $T(t) = [T_s(t), T_f(t)]'$ and $\tau \in \Gamma = \{(\tau_s, \tau_f) | \tau_s + \tau_f = t\}$, where $T_s(t)$ and $T_f(t)$ describe the cumulative amounts of time spent in the slow and fast states, respectively, by an individual during a time interval $[0, t]$. The spatial population density for the exchange model, $P(x, t)$, can now be expressed using equation (6) so that

$$\begin{aligned} P(x, t) &= S(x, t) + F(x, t) \\ &= \int_{\Gamma} G(x, \tau) R(\tau, t) d\tau \\ &= \int_0^t \int_0^{t-\tau_s} G(x, \tau_s, \tau_f) R(\tau_s, \tau_f, t) d\tau_s d\tau_f \quad (13) \\ &= \int_0^t G(x, \tau_s, t - \tau_s) R(\tau_s, t - \tau_s, t) d\tau_s \\ &= \int_0^t \frac{\exp\left\{-\frac{[x - \beta_s \tau_s - \beta_f(t - \tau_s)]^2}{4[D_s \tau_s + D_f(t - \tau_s)]}\right\}}{\sqrt{4\pi[D_s \tau_s + D_f(t - \tau_s)]}} \rho(\tau_s, t) d\tau_s, \end{aligned}$$

where $\rho(\tau_s, t) = R(\tau_s, t - \tau_s, t) = R(\tau_s, \tau_f, t)$ is the probability density function for $T_s(t)$. The double integral reduces to a single integral in equation (13) because it is computed only over the line defined by $\tau_s + \tau_f = t$ so that it is possible to write τ_f in terms of τ_s using $\tau_f = t - \tau_s$ and to therefore express the bivariate density $R(\tau_s, \tau_f, t)$ as the univariate density $\rho(\tau_s, t)$.

Equation (13) describes a mixture of Gaussians and indicates that specifying the marginal density for $T_s(t)$, $\rho(\tau_s, t)$, will lead to an explicit solution to the exchange model and permit a complete analysis of its behavior. By definition, the cumulative amount of time in the slow state, $T_s(t)$, increases identically to time for individuals in the slow state and does not change for individuals in the fast state. That is, $dT_s = dt$ for slow individuals, $dT_s = 0$ for fast individuals, and individuals switch between the two states with rates a and b . The equations $dT_s = dt$ and $dT_s = 0$, with switching behavior by analogy to stochastic differential equations, have an associated set of partial differential equations, the Fokker-Planck equations (Gardiner 1985; Ricciardi 1986),

$$\begin{aligned}\frac{\partial \rho_s}{\partial t} &= -\frac{\partial \rho_s}{\partial \tau_s} - a\rho_s + b\rho_f, \\ \frac{\partial \rho_f}{\partial t} &= a\rho_s - b\rho_f.\end{aligned}\quad (14)$$

Equations (14) determine the density of interest, $\rho(\tau_s, t)$, via the relation $\rho(\tau_s, t) = \rho_s(\tau_s, t) + \rho_f(\tau_s, t)$. The densities $\rho_s(\tau_s, t)$ and $\rho_f(\tau_s, t)$ are probability densities for $T_s(t)$ for individuals that are in the slow and fast states, respectively. Thus, summing $\rho_s(\tau_s, t)$ and $\rho_f(\tau_s, t)$ gives the density for $T_s(t)$ for any individual in the population. The appropriate initial conditions associated with equations (14) are then

$$\begin{aligned}\rho_s(\tau_s, 0) &= \frac{b}{a+b}\delta(\tau_s), \quad \rho_f(\tau_s, 0) = \frac{a}{a+b}\delta(\tau_s), \\ \frac{\partial \rho_s}{\partial t}(\tau_s, 0) &= -\frac{b}{a+b}\frac{\partial \delta(\tau_s)}{\partial \tau_s}, \quad \frac{\partial \rho_f}{\partial t}(\tau_s, 0) = 0.\end{aligned}\quad (15)$$

With $\rho(\tau_s, t)$ identified via equations (14) and (15), it is straightforward to show that the solution to the exchange model can be represented with the integral equation in equation (13). That is, by direct substitution, the following statement can be shown to be true: if $P(x, t) = S(x, t) + F(x, t)$ is specified with equation (13) and $\rho(\tau_s, t) = \rho_s(\tau_s, t) + \rho_f(\tau_s, t)$ satisfies equations (14) with the initial conditions in equations (15), then $P(x, t) = S(x, t) + F(x, t)$ satisfies the exchange model given by equations (11) with the auxiliary conditions in equations (12) (app. B).

The integral representation of the solution to the exchange model, a kind of summation over movement states, facilitates two important analyses of the exchange model: first, the determination of moment-based metrics of $X(t)$ in terms of the movement parameters (i.e., the advection and diffusion rates) and among-individual variability in time spent in each state (via metrics of $T_s(t)$) and second, the analytical determination of the time-dependent solution to the exchange model. Both analyses provide insight into the role of population heterogeneity in the movement process and provide a basis for quantitative assessment of heterogeneous movement in empirical settings.

The moments of $X(t)$ and $T(t)$ can be found using equations (11) and (14) and standard methods for analyzing stochastic processes (Gardiner 1985). The mean distance moved of individuals in a population following the exchange model is

$$\begin{aligned}E[X(t)] &= \beta_s E[T_s(t)] + \beta_f E[T_f(t)] \\ &= \beta_s E[T_s(t)] + \beta_f E[t - T_s(t)] \\ &= \beta_s \frac{b}{a+b}t + \beta_f \frac{a}{a+b}t,\end{aligned}\quad (16)$$

a weighted sum of the advection rates with the weights given by the mean amounts of time spent in each state. The variance of the distance moved is

$$\begin{aligned}\text{Var}[X(t)] &= 2\{D_s E[T_s(t)] + D_f E[T_f(t)]\} \\ &\quad + \text{Var}[\beta_s T_s(t) + \beta_f T_f(t)] \\ &= 2\{D_s E[T_s(t)] + D_f E[t - T_s(t)]\} \\ &\quad + (\beta_s - \beta_f)^2 \text{Var}[T_s(t)] \\ &= 2\left(D_s \frac{b}{a+b} + D_f \frac{a}{a+b}\right)t + (\beta_s - \beta_f)^2 \\ &\quad \times 2\left(\frac{ab}{(a+b)^3}t + \frac{ab}{(a+b)^4}\{\exp[-(a+b)t] - 1\}\right).\end{aligned}\quad (17)$$

The variance depends on a weighted sum of diffusion rates, but it also can depend on the advection rates. If the advection rates are not equal (i.e., $\beta_s \neq \beta_f$), then the variance depends on both diffusion and advection (as in the general model), and it is linear in the variance in cumulative amount of time spent in the slow state, $\text{Var}[T_s(t)]$, with the squared difference in advection rates acting as a linear coefficient. In this case, the variance initially increases at an accelerating rate with time, and, as time increases, becomes linear in time with an effective, or long-term, diffusion rate of

$$D_E = D_s \frac{b}{a+b} + D_f \frac{a}{a+b} + (\beta_s - \beta_f)^2 \frac{ab}{(a+b)^3}.\quad (18)$$

Interestingly, the effective diffusion rate depends on the rates of advection in the slow and fast states, as well as the rates of diffusion and exchange between the two states. The advection rates contribute more to the effective diffusion rate when the exchange rates are small and when the difference between the rates of advection in the two states is large. In contrast, if the advection rates are equal, then the variance is linear in time with a diffusion rate that depends only on the weighted sum of the diffusion rates of the slow and fast states.

Metrics involving higher moments such as skewness and kurtosis can also be determined, but as in the general model, the full expressions are lengthy and cumbersome. Accordingly, we do not give the expressions involving the moments of $T_s(t)$ in full detail. The skewness of $X(t)$ in the exchange model is

$$\text{skewness}[X(t)] = \frac{S_{\text{num}}}{S_{\text{den}}},\quad (19)$$

where

$$S_{\text{num}} = (\beta_s - \beta_f)^3 E\{[T_s(t) - E\{T_s(t)\}]^3\} + 3(\beta_s - \beta_f)2(D_s - D_f) \text{Var}[T_s(t)],$$

$$S_{\text{den}} = \{\text{Var}[X(t)]\}^{3/2}.$$

Equation (19) makes clear the role of heterogeneous advection rates in affecting skewness via the term $(\beta_s - \beta_f)$, which interacts with the skewness in $T_s(t)$ and the heterogeneity in diffusion rates to determine the skewness of $X(t)$. The kurtosis of $X(t)$ in the exchange model, for the simpler case when $\beta_s = \beta_f$, is

$$\text{kurtosis}[X(t)] = \frac{3[2(D_s - D_f)]^2 \text{Var}[T_s(t)]}{\{\text{Var}[X(t)]\}^2}. \tag{20}$$

Equation (20) makes clear the role of heterogeneous diffusion rates in affecting kurtosis via the term $(D_s - D_f)$, which acts directly on variability in $T_s(t)$ to determine the kurtosis of $X(t)$.

The mean, variance, skewness, and kurtosis, being summary descriptions of the movement process, provide a partial view of movement behavior in the exchange model. In particular, the skewness and kurtosis, which are measures of population heterogeneity in advection and diffusion rates, decline to 0 over time, suggesting that population heterogeneity declines to 0 over time. Population heterogeneity does, in fact, vanish over time via the exchange of individuals between states. Given enough time, this exchange homogenizes the population because, eventually, all individuals have spent about the same amounts of time in each state. Indeed, $T_s(t)$ becomes a random variable with coefficient of variation, $\text{CV}[T_s(t)] = \sqrt{\text{Var}[T_s(t)]}/E[T_s(t)]$, approaching 0 as time progresses. Since the population becomes homogeneous in terms of $T_s(t)$, our prediction is that the spatial population density $P(x, t)$ approaches a Gaussian density as time progresses. Asymptotic Gaussian densities are consistent with the asymptotic behavior of the variance of $X(t)$, which comes to increase linearly in time.

Moment-based metrics are summary statistics and do not provide a complete description of the exchange model. A full description can be obtained by identifying an analytical solution to the partial differential equations that specify the exchange model in equations (11). Application of the integral representation of $P(x, t)$ in equation (13) reveals an approach to solving equations (11). Equation (13) indicates that the specification of the marginal density for $T_s(t)$, $\rho(\tau_s, t)$, is all that is required to solve equations (11). The marginal density $\rho(\tau_s, t)$ can be identified by solving equations (14) using standard methods for linear

partial differential equations (app. C). Accordingly, the marginal density has solution

$$\rho(\tau_s, t) = \begin{cases} \frac{b}{a+b} \exp(-at)\delta(t - \tau_s) + \frac{a}{a+b} \exp(-bt)\delta(\tau_s) & \tau_s = 0, t \\ \exp[-bt + (b-a)\tau_s] \left\{ \left(\frac{2ab}{a+b} \right) I_0[2\sqrt{ab}\tau_s(t - \tau_s)] \right. & \tau_s \in (0, t) \\ \left. + \left(\frac{\sqrt{ab}[at + (b-a)\tau_s]}{a+b} \right) \left(\frac{I_1[2\sqrt{ab}\tau_s(t - \tau_s)]}{\sqrt{\tau_s(t - \tau_s)}} \right) \right\}, & \end{cases} \tag{21}$$

where I_0 and I_1 are modified Bessel functions of the first kind of order 0 and 1, respectively (Jeffrey 1995). Insertion of $\rho(\tau_s, t)$ from equation (21) into the integral in equation (13) provides an analytical solution to the exchange model. In this form, $P(x, t)$ can be studied directly and computed using standard methods for numerical integration (Kincaid and Cheney 1996).

We graph three solutions to the exchange model: for the case when $a > b > 0$ (exchange between states exists, and individuals, on average, spend more time in the fast state); when $\beta_f > \beta_s > 0$ (fast and slow individuals tend to move to the right by advection, with fast individuals having greater advective movement); and when $D_f > D_s > 0$ (diffusive movement exists in both states, with fast individuals exhibiting faster diffusive movement). This set of parameters illustrates heterogeneity in the movement rates and produces the kind leptokurtic movement distributions that have been observed in nature. Initially, when t is small, most individuals spend all of their time in either the slow or fast states so that $\rho(\tau_s, t)$ is approximately the weighted sum of two δ functions (fig. 1A). In this case, the integral solution simplifies to

$$P(x, t) \approx \frac{b}{a+b} \frac{\exp\left[-\frac{(x-\beta_s t)^2}{4D_s t}\right]}{\sqrt{4\pi D_s t}} + \frac{a}{a+b} \frac{\exp\left[-\frac{(x-\beta_f t)^2}{4D_f t}\right]}{\sqrt{4\pi D_f t}}, \tag{22}$$

a weighted sum of two Gaussian densities (one corresponding to each movement state) that can generate leptokurtic movement distributions (fig. 2A). Equation (22) is also the exact solution to the exchange model with zero exchange between slow and fast states, where individuals spend all of their time in one of the two states, so that $T_s(t) = t$ or $T_s(t) = 0$. Variants of this zero-exchange form

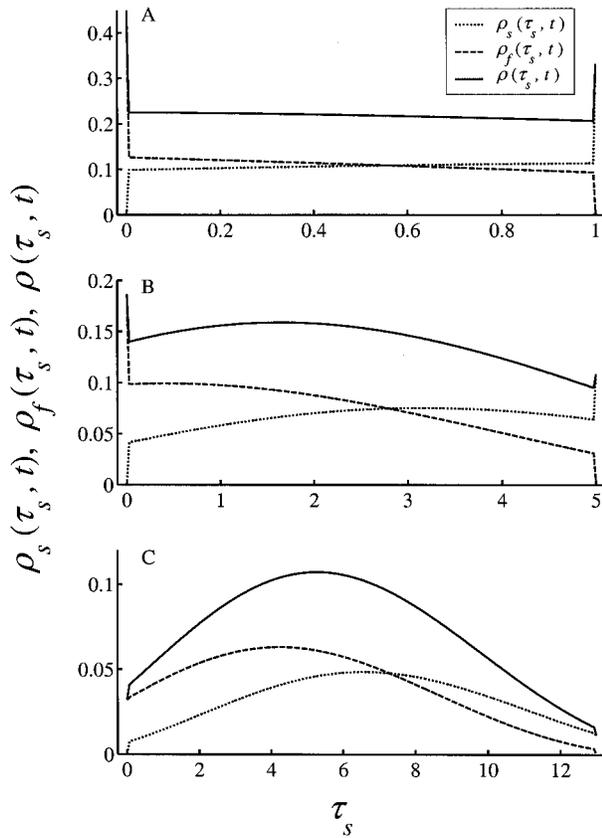


Figure 1: Probability density functions $\rho_s(\tau_s, t)$, $\rho_f(\tau_s, t)$, and $\rho(\tau_s, t)$ for the cumulative amount of time spent in the slow movement state $T_s(t)$ for individuals currently in the slow state, the fast state, or either state, respectively. During the dispersal process, individuals switch repeatedly between slow and fast movement states, spending exponentially distributed amounts of time in each state. Graphs of the marginal densities for $T_s(t)$, $\rho_s(\tau_s, t)$, $\rho_f(\tau_s, t)$, and $\rho(\tau_s, t)$ are shown plotted against τ_s for the times (A) $t = 1$, (B) $t = 5$, and (C) $t = 13$. The exchange rates $a = 0.28$ and $b = 0.22$ parameterize the switching process. The densities can have finite mass at the points $\tau_s = t$ and $\tau_s = 0$, and we plot the values of these masses at those two points since they are normally represented as δ functions when τ_s is a value taken on by a continuous random variable.

have been previously studied as models of persistent population heterogeneity (Skalski and Gilliam 2000; Okubo and Levin 2002), with $b/(a + b)$ and $a/(a + b)$ representing the proportions of individuals in the slow and fast states, respectively. Using the integral interpretation from equation (13), the proportions $b/(a + b)$ and $a/(a + b)$ are the probabilities that an individual drawn at random from the population has spent all of its time in the slow or fast states, respectively. Accordingly, the approximate solution of the exchange model for small t is an important special case of the population heterogeneity hypothesis that gener-

ates leptokurtic movement distributions and has formed the basis for previous diffusion-based models.

As time progresses, individuals come to spend time in both the slow and fast states (fig. 1B) so that the population becomes increasingly homogeneous at a rate that depends on the magnitude of exchange rates a and b . Thus the resulting spatial density, $P(x, t)$ (fig. 2B), reflects a state of population heterogeneity that is intermediate between the level reflected in equation (22) and complete homogeneity. Characterization of this intermediate stage is critical because it bridges the gap between initial (t near 0) and long-term movement behavior (large t), two scenarios that are typically more amenable to analytical treatment. Depending on parameter values, the spatial density at this inter-

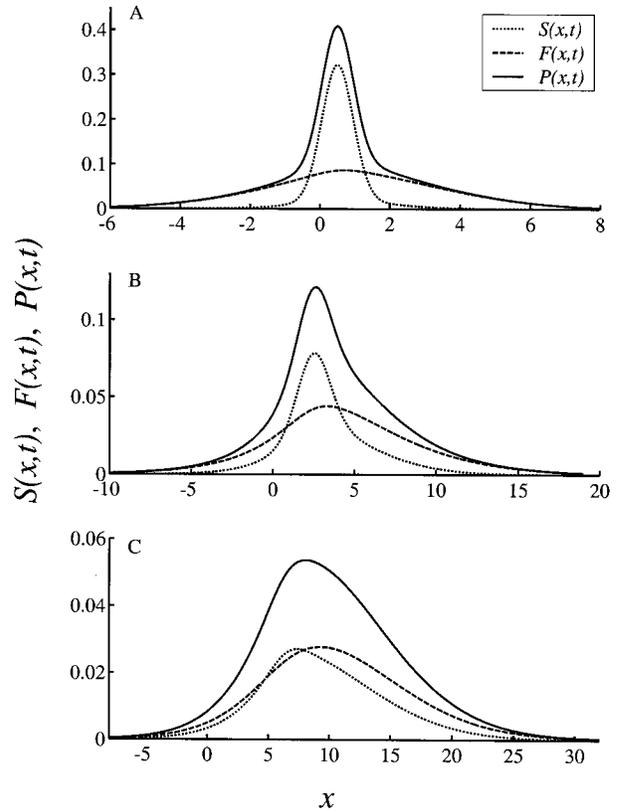


Figure 2: Probability density functions $S(x, t)$, $F(x, t)$, and $P(x, t)$ for the spatial position $X(t)$ for individuals currently in the slow movement state, the fast movement state, or either movement state, respectively. Movement rates, given by advection and diffusion parameters, determine the dispersal process for individuals that switch repeatedly between slow and fast movement states. Graphs of the spatial densities for $X(t)$, $S(x, t)$, $F(x, t)$, and $P(x, t)$ are shown plotted against x for (A) $t = 1$, (B) $t = 5$, and (C) $t = 13$. The times for which graphs are shown and the exchange rate parameters ($a = 0.28$ and $b = 0.22$) are identical to those used to generate figure 1. Movement is parameterized by rates of advection, $\beta_s = 0.5$ and $\beta_f = 1$, and diffusion, $D_s = 0.1$ and $D_f = 4$.

mediate stage has the potential to take on a variety of forms. Given sufficient time, the marginal density $\rho(\tau_s, t)$ and the spatial density $P(x, t)$ become Gaussian (figs. 1C, 2C), and the population becomes increasingly homogeneous in the sense that $CV[T_s(t)]$ approaches 0. Specifically, the spatial density becomes

$$P(x, t) \approx \frac{1}{\sqrt{2\pi \text{Var}[X(t)]}} \exp\left(-\frac{\{x - E[X(t)]\}^2}{2 \text{Var}[X(t)]}\right) \quad (23)$$

when t is large—the same form as the solution to the classic advection-diffusion equation. Thus, as time progresses, the exchange model predicts that the population undergoes a transition from complete heterogeneity to complete homogeneity with the consequence that the spatial population density undergoes a simultaneous transition from a simple weighted sum of two Gaussian densities (eq. [22]) to a single Gaussian density (eq. [23]). The rate at which the transition from heterogeneity to homogeneity progresses depends critically on the magnitude of the exchange rates, a and b .

Discussion

The results of a growing number of studies measuring the movement distributions of organisms have demonstrated that leptokurtic movement distributions are very common, if not ubiquitous, among a diverse group of taxa. One explanation is that the populations are heterogeneous in terms of movement behaviors: the integration of movement distributions of individuals moving at different rates can generate leptokurtic movement distributions.

The general theory presented in this article assumes that the movement of individuals, at some spatial-temporal scale, can be described by the classic advection-diffusion equation, a model whose fundamental description of the movement process is Gaussian (Strauss 1992; Turchin 1998; Okubo and Levin 2002), with kurtosis equal to 0. With this premise in mind, our general theory can generate leptokurtic movement distributions (i.e., positive kurtosis) because it creates movement distributions by integrating (or summing) Gaussian movement distributions of individuals whose movement rates are heterogeneous. The integration is implemented by identifying different movement states (in terms of diffusion and advection parameters) and characterizing the amounts of time individuals in the population spend in these movement states. The theory identifies a way to define population heterogeneity in movement and illustrates the manner in which population heterogeneity influences population-level patterns of movement. The results show that some basic metrics of the movement process, such as the mean,

variance, skewness, and kurtosis, depend critically on the nature of population heterogeneity in movement behavior and should therefore be estimated in studies of organism movement. In particular, the skewness is a measure of population heterogeneity in advection rates, and the kurtosis is a measure of population heterogeneity in both advection and diffusion rates. Thus, the analysis of the general theory makes clear the manner in which among-individual variability in movement behaviors maps to population-level patterns in dispersal under the population heterogeneity hypothesis.

A special case of the general theory, the exchange model, can produce a variety of movement patterns, including a set that transitions from leptokurtic (fig. 2A) to Gaussian spatial densities (fig. 2C). Because special cases of the exchange model can produce leptokurtic (as a two-state population heterogeneity model with zero exchange) or Gaussian (as the classic advection-diffusion equation) spatial densities, the exchange model is a valuable tool for hypothesis testing. For example, our work with stream fish suggests that leptokurtic movement distributions are quite common over our time scales of measurement (several months) and that the population heterogeneity hypothesis might apply in these systems (Skalski and Gilliam 2000; Fraser et al. 2001; Gilliam and Fraser 2001). Currently we are faced with the question as to what form the population heterogeneity may take. Specifically, if the source of population heterogeneity is of a transient nature (e.g., movement behavior is driven by a fish's temporary state of hunger or fear induced by a predator), then the leptokurtic patterns that we have observed may be transient (implying that the exchange model with $0 < a, b$ is a reasonable model). Conversely, if the source of population heterogeneity is permanent within each individual (e.g., movement behavior is permanently determined by a genetic effect or environmental conditions early in development), then the leptokurtic patterns that we have observed may be persistent (implying that the exchange model with $a = b = 0$, the population heterogeneity model with no exchange, is a reasonable model). Indeed, recent assays of behavior in a Trinidadian killifish suggest that a polymorphism in exploration propensity exists and is related to short-term movement behavior in field settings (Fraser et al. 2001). Results from other studies with salmonids are consistent with the existence of nontransient among-individual variability in movement behavior (McLaughlin et al. 1992; Bradford and Taylor 1997; Brännäs and Eriksson 1999). Accordingly, the exchange model proposed here, when statistically fit to the types of data sets analyzed in Skalski and Gilliam (2000) and Gilliam and Fraser (2001), provides a quantitative method for distinguishing among models specifying transient versus permanent population heterogeneity.

A benefit of having an explicit representation of the solution to the exchange model is that the expression can be used for statistical model fitting. The likelihood can be computed for a data set by numerically integrating the integral solution that is provided by insertion of equation (21) into equation (13). Several important models are special cases of the exchange model, including the cases just mentioned above, as well as some types of correlated random walks. Accordingly, likelihood ratio statistics can be used to test among these nested alternatives. A practical issue that must be confronted when fitting the exchange model and similar state-structured models to data involves the estimation of the initial proportions of the population in each movement state. The exchange model describes the dynamic flow of individuals between two movement states and requires as an initial condition the initial proportions of the population in each movement state. One approach is to assume that the initial proportions are the steady state proportions, $b/(a + b)$ and $a/(a + b)$, for slow and fast individuals, respectively (see eqq. [12] and [15]). The solutions we provide (figs. 1 and 2) adopt this strategy. A second approach is to relax our steady state assumption and treat the initial proportions as two additional parameters to be estimated during the model fitting. In this case, one may alter the initial conditions in equations (12) and (15) and use the methodology we have developed to solve the exchange model in this more general setting. Indeed, using these ideas, one could treat the steady state assumption as a hypothesis to be tested using available data. This type of model fitting to population-level observations coupled with individual-based observations of movement behavior over smaller scales provides a powerful methodology for understanding the mechanisms that underlie organism movements.

A variety of studies have made conceptual contributions to understanding and predicting dispersal. Recent theoretical work has emphasized the population-level implications of heterogeneous movement and/or leptokurtic movement distributions (Shigesada et al. 1995; Kot et al. 1996; Clark et al. 1999, 2001; Higgins and Richardson 1999; Neubert and Caswell 2000; Neubert et al. 2000). Some of these studies associate Gaussian movement distributions with diffusion-based models of movement and use this association as a motivation for adopting alternative (non-diffusion-based) approaches to modeling dispersal (Kot et al. 1996; Higgins and Richardson 1999; Neubert and Caswell 2000; Neubert et al. 2000; Clark et al. 2001). In contrast, our present work shows that a diffusion-based framework is sufficiently flexible to generate leptokurtic movement distributions by employing a state-structured framework. Furthermore, recent studies rely on models that are mixtures of component dispersal kernels and use marginal densities without a stated mechanistic basis

(Clark et al. 1999, 2001; Higgins and Richardson 1999; Rodríguez 2002). Our present framework shows how to mechanistically generate and interpret a mixture of Gaussian distributions in a state-structured framework using a marginal density, $R(\tau, t)$, that can be interpreted as a probability density function for the amount of time that individuals spend in each movement state.

Other theoretical studies have focused on the genesis of movement distributions, including leptokurtic forms (Plant and Cunningham 1991; Turchin and Thoeny 1993; Firle et al. 1998; Cronin et al. 2000; Skalski and Gilliam 2000; Morales 2002; Okubo and Levin 2002; Zabel 2002). Most of these studies have utilized diffusion-based models of movement that are conceptually related to the exchange model either as special cases (Skalski and Gilliam 2000; Okubo and Levin 2002) or as special cases supplemented by the addition of a linear mortality/disappearance term (Plant and Cunningham 1991; Turchin and Thoeny 1993; Cronin et al. 2000; the exchange model with density-independent mortality/disappearance can be written as $e^{-\mu}P(x, t)$, where μ is the instantaneous mortality/disappearance rate). In a modeling and empirical study of movement in beetles, Firle et al. (1998) recognized two movement states, active and resting, and built a model that is conceptually similar to the exchange model. A central conclusion of Firle et al. (1998) was that an intermediate scale of analysis was most appropriate for their investigation of beetle movement. While small and large scale movement behaviors were adequately described by random walks with homogeneous movement behaviors, these models did not capture intermediate scale movement behaviors in their study. The intermediate scale in their study corresponds, conceptually, to our figures 1B and 2B, where the population is exhibiting an intermediate level of population heterogeneity. Firle et al. (1998) used individual-based simulations coupled with detailed empirical observations to draw their conclusions, and our analytical results with the exchange model complement and corroborate their findings.

A major value of the general theory and the exchange model is that they provide a broad foundation for further work. The general theory shows that the description (either empirically or theoretically) of the marginal density for time spent in different movement states, $R(\tau, t)$, provides a path to understanding movement in heterogeneous populations. The exchange model specifies a particular form for the marginal density using $R(\tau, t) = \rho(\tau_s, t)$. Future work, both empirical and theoretical, can draw on this idea to identify forms for the marginal density that are appropriate for particular biological scenarios. Examples are motivated by our research on stream fish movement and foraging behavior. One reasonable working hypothesis is to suppose that individuals occupy two states: foraging

within a patch or moving among foraging patches. In this case, we might specify movement rates appropriate for each state and express the exchange rates between states as functions based on a habitat selection model. A second extension of the exchange model allows another type of population heterogeneity: among-individual variation in the exchange rates (i.e., individuals differ in their likelihood of switching between movement states). For example, equations (11) can be supplemented with a second set of similar equations representing an additional group of individuals with different exchange rates (\tilde{a} and \tilde{b}) but identical movement states, slow (with parameters D_s and β_s) and fast (with parameters D_f and β_f). The spatial population density then may be computed by using a weighted sum of solutions to the exchange model, one solution having exchange rates a and b and the second having exchange rates \tilde{a} and \tilde{b} . The weights would be given by the proportions of individuals in each class. In this scenario, the set of movement states achieved by all individuals is identical (all individuals can switch between fast and slow behaviors), as in the exchange model, but unlike the exchange model, the population heterogeneity is permanent because there are two groups of individuals with different tendencies to switch between the two states. A further extension, motivated by the Fraser et al. (2001) view of fish personality (“boldness”) as a continuous trait related to the propensity to switch from a “mover” to a “stayer” state, would treat a and b as having continuous variation within a population.

A variety of other extensions are potentially possible with the exchange model. Generalizations to two and three spatial dimensions involve only making the appropriate

adjustment to the Gaussian kernel. The incorporation of alternative initial conditions is also feasible because the integral solution is also a distribution kernel that can be applied to any arbitrary initial spatial density (i.e., assuming a point release is not necessary). The concept of the integral solution also provides a path to analytically approach the problem of modeling spatial dependence in movement rates. Different points in space can be considered to be different movement states (e.g., fast and slow habitats in Morales 2002). If probability densities for the amounts of time spent in these “spatial” states can be constructed, or approximated, based on knowledge of spatially dependent movement rates, then some analytical solutions may be constructed. Because the concept of the integral solution holds for a general set of exchange rates, including cases without conservation of probability mass, the exchange model provides a skeleton for writing more complex models. A variety of future studies are feasible and may encompass species invasions and interactions, the evolution of dispersal, and population genetic phenomena, including models having movement phenotypes with a Mendelian genetic basis.

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APPENDIX A

General Spatial Moments

Metrics of $X(t)$, such as the mean, variance, skewness and kurtosis, involve the moments of $X(t)$. The moments can be computed by using equation (6) to compute the moment-generating function for $X(t)$ (Grimmett and Stirzaker 2001). The moment-generating function for $X(t)$, using equation (6), is defined as

$$\begin{aligned} M(w, t) &= E\{\exp [wX(t)]\} \\ &= \int_{-\infty}^{+\infty} \exp (wx)P(x, t)dx \\ &= \int_{-\infty}^{+\infty} \exp (wx) \int_{\Gamma} G(x, \tau)R(\tau, t)d\tau dx. \end{aligned} \tag{A1}$$

Reversing the order of integration by computing the integral over x first, using the fact that $G(x, \tau)$ is a Gaussian kernel (see eq. [4]) and using the expression for a moment-generating function for a Gaussian distribution, gives

$$\begin{aligned}
 M(w, t) &= \int_{-\infty}^{+\infty} \exp(wx) \int_{\Gamma} G(x, \tau) R(\tau, t) d\tau dx \\
 &= \int_{\Gamma} \int_{-\infty}^{+\infty} \exp(wx) G(x, \tau) dx R(\tau, t) d\tau \\
 &= \int_{\Gamma} \exp(\beta'\tau w + D'\tau w^2) R(\tau, t) d\tau.
 \end{aligned} \tag{A2}$$

The k th derivative of $M(w, t)$, with respect to w evaluated at $w = 0$, is $E[X^k(t)]$, the k th moment of $X(t)$. The k th derivative is computed by taking the derivative inside the integral, evaluating the expression at $w = 0$, and integrating over Γ .

APPENDIX B

Integral Solution of the Exchange Model

The solution to the exchange model can be represented using the integral form in equation (13). That is, if $P(x, t) = S(x, t) + F(x, t)$ is specified with equation (13) and $\rho(\tau_s, t) = \rho_s(\tau_s, t) + \rho_f(\tau_s, t)$ satisfies equations (14) with the auxiliary conditions in equations (15), then $P(x, t) = S(x, t) + F(x, t)$ satisfies the exchange model given by equations (11) with the auxiliary conditions in equations (12). Using equation (13) we can represent $P(x, t)$ as

$$\begin{aligned}
 P(x, t) &= \int_0^t G(x, \tau_s, t - \tau_s) \rho(\tau_s, t) d\tau_s \\
 &= \int_0^t G(x, \tau_s, t - \tau_s) [\rho_s(\tau_s, t) + \rho_f(\tau_s, t)] d\tau_s \\
 &= S(x, t) + F(x, t)
 \end{aligned} \tag{B1}$$

so that

$$\begin{aligned}
 S(x, t) &= \int_0^t G(x, \tau_s, t - \tau_s) \rho_s(\tau_s, t) d\tau_s, \\
 F(x, t) &= \int_0^t G(x, \tau_s, t - \tau_s) \rho_f(\tau_s, t) d\tau_s,
 \end{aligned} \tag{B2}$$

where

$$G(x, \tau_s, t - \tau_s) = \frac{\exp\left\{\frac{-[x - \beta_s \tau_s - \beta_f(t - \tau_s)]^2}{4[D_s \tau_s + D_f(t - \tau_s)]}\right\}}{\sqrt{4\pi[D_s \tau_s + D_f(t - \tau_s)]}}.$$

Proceeding with $S(x, t)$ and $F(x, t)$ from equations (B2), we show that they satisfy the first differential equation in equations (11) (for brevity, we suppress the arguments of some functions). Switching the order of integration and differentiation when necessary, the left-hand side of the differential equation for slow individuals is

$$\text{LHS} = \frac{\partial S}{\partial t} = [G(x, \tau_s, t - \tau_s) \rho_s(\tau_s, t)]_{\tau_s=t} + \int_0^t G \frac{\partial \rho_s}{\partial t} + \frac{\partial G}{\partial t} \rho_s d\tau_s.$$

Substituting for $\partial\rho_s/\partial t$ using equations (14) gives

$$\text{LHS} = [G(x, \tau_s, t - \tau_s)\rho_s(\tau_s, t)]_{\tau_s=t} + \int_0^t \left[-\frac{\partial\rho_s}{\partial\tau_s} - a\rho_s + b\rho_f \right] G + \frac{\partial G}{\partial t} \rho_s d\tau_s.$$

Integrating the term $\partial\rho_s/\partial\tau_s \times G$ by parts gives

$$\begin{aligned} \text{LHS} &= [G(x, \tau_s, t - \tau_s)\rho_s(\tau_s, t)]_{\tau_s=t} - [G(x, \tau_s, t - \tau_s)\rho_s(\tau_s, t)]_{\tau_s=0} \\ &\quad + \int_0^t \frac{\partial G}{\partial\tau_s} \rho_s - aG\rho_s + bG\rho_f + \frac{\partial G}{\partial t} \rho_s d\tau_s \\ &= \int_0^t \left[\frac{\partial G}{\partial t} + \frac{\partial G}{\partial\tau_s} \right] \rho_s - aG\rho_s + bG\rho_f d\tau_s. \end{aligned} \tag{B3}$$

The right-hand side of the differential equation for slow individuals in equations (11) is

$$\begin{aligned} \text{RHS} &= D_s \frac{\partial^2 S}{\partial x^2} - \beta_s \frac{\partial S}{\partial x} - aS + bF \\ &= \int_0^t D_s \frac{\partial^2 G}{\partial x^2} \rho_s - \beta_s \frac{\partial G}{\partial x} \rho_s - aG\rho_s + bG\rho_f d\tau_s. \end{aligned}$$

Equating LHS with RHS and noticing that $-aG\rho_s + bG\rho_f$ occurs in both LHS and RHS reduces the problem to establishing the relation

$$\begin{aligned} \text{LHS} &= \text{RHS}, \\ \int_0^t \left(\frac{\partial G}{\partial t} + \frac{\partial G}{\partial\tau_s} \right) \rho_s d\tau_s &= \int_0^t \left(D_s \frac{\partial^2 G}{\partial x^2} - \beta_s \frac{\partial G}{\partial x} \right) \rho_s d\tau_s. \end{aligned} \tag{B4}$$

Proceeding in a similar fashion with the differential equation for fast individuals in equations (11) yields

$$\begin{aligned} \text{LHS} &= \text{RHS}, \\ \int_0^t \frac{\partial G}{\partial t} \rho_s d\tau_s &= \int_0^t \left(D_f \frac{\partial^2 G}{\partial x^2} - \beta_f \frac{\partial G}{\partial x} \right) \rho_f d\tau_s. \end{aligned} \tag{B5}$$

It is straightforward to show that the Gaussian kernel, $G(x, \tau_s, t - \tau_s)$, satisfies

$$\begin{aligned} \frac{\partial G}{\partial t} + \frac{\partial G}{\partial\tau_s} &= D_s \frac{\partial^2 G}{\partial x^2} - \beta_s \frac{\partial G}{\partial x}, \\ \frac{\partial G}{\partial t} &= D_f \frac{\partial^2 G}{\partial x^2} - \beta_f \frac{\partial G}{\partial x}, \end{aligned}$$

and therefore equations (B4) and (B5) are satisfied. Thus, the integral form of the solution in equation (13) solves the exchange model specified by equations (11) and (12).

APPENDIX C

 Analytical Determination of $\rho(\tau_s, t)$

The marginal density for $T_s(t)$, $\rho(\tau_s, t)$, can be computed by solving the system given in equations (14) with the initial conditions given in equations (15) using standard methods for solving linear partial differential equations (Strauss 1992). The solution can be represented as the sum of two component solutions based on a partitioning of the interval $[0, t]$, remembering that $\tau_s \in [0, t]$. One component solution is obtained on the boundary of $[0, t]$ at the points $\tau_s = 0$ and $\tau_s = t$, and the other component solution is obtained in the interior of $[0, t]$. The solution at the boundary points represents the probability mass of individuals that have spent all of their time in the slow and fast states, given by $\rho_s(\tau_s = t, t)$ and $\rho_f(\tau_s = 0, t)$, respectively (note that $\rho_s(\tau_s = 0, t) = \rho_f(\tau_s = t, t) = 0$ because individuals currently in one state could not have spent all of their time in the other state). The differential equations at these points are

$$\begin{aligned}\frac{\partial \rho_s(\tau_s = t, t)}{\partial t} &= -a\rho_s(\tau_s = t, t), \\ \frac{\partial \rho_f(\tau_s = 0, t)}{\partial t} &= -b\rho_f(\tau_s = 0, t),\end{aligned}\tag{C1}$$

with initial conditions

$$\begin{aligned}\rho_s(\tau_s = t, 0) &= \frac{b}{a+b} \delta(t - \tau_s) \Big|_{\tau_s=t}, \\ \rho_f(\tau_s = 0, 0) &= \frac{a}{a+b} \delta(\tau_s) \Big|_{\tau_s=0}.\end{aligned}\tag{C2}$$

We employ the δ function because there is finite probability mass at these boundary points. Equations (C1) and (C2) are readily solved as exponential decays to give the boundary point solutions

$$\begin{aligned}\rho_s(\tau_s = t, t) &= \frac{b}{a+b} \exp(-at) \delta(t - \tau_s) \Big|_{\tau_s=t}, \\ \rho_f(\tau_s = 0, t) &= \frac{a}{a+b} \exp(-bt) \delta(\tau_s) \Big|_{\tau_s=0}.\end{aligned}\tag{C3}$$

The other component solution is obtained over the open interval $(0, t)$ and requires more attention. The approach we employ is to transform the system in equations (14) to an equation whose solution is known (the Klein-Gordon equation from quantum physics; Strauss 1992). Introducing a new independent variable, $y = \tau_s - t/2$, and using the change of variables $\rho_s(\tau_s, t) = \tilde{\rho}_s(y, t)$ and $\rho_f(\tau_s, t) = \tilde{\rho}_f(y, t)$ transforms the problem to solving the more symmetric equations

$$\begin{aligned}\frac{\partial \tilde{\rho}_s}{\partial t} &= -\frac{1}{2} \frac{\partial \tilde{\rho}_s}{\partial y} - a\tilde{\rho}_s + b\tilde{\rho}_f, \\ \frac{\partial \tilde{\rho}_f}{\partial t} &= \frac{1}{2} \frac{\partial \tilde{\rho}_f}{\partial y} + a\tilde{\rho}_s - b\tilde{\rho}_f,\end{aligned}\tag{C4}$$

with initial conditions

$$\begin{aligned} \tilde{\rho}_s(y, 0) &= \frac{b}{a+b} \delta(y), & \tilde{\rho}_r(y, 0) &= \frac{a}{a+b} \delta(y), \\ \frac{\partial \tilde{\rho}_s}{\partial t}(y, 0) &= -\frac{1}{2} \frac{b}{a+b} \frac{\partial \delta(y)}{\partial y}, & \frac{\partial \tilde{\rho}_r}{\partial t}(y, 0) &= \frac{1}{2} \frac{a}{a+b} \frac{\partial \delta(y)}{\partial y}. \end{aligned} \tag{C5}$$

Equations (C4) can be combined to give an equation involving $\tilde{\rho}_s(y, t)$ alone or $\tilde{\rho}_r(y, t)$ alone. Applying this idea shows that $\tilde{\rho}_s(y, t)$ and $\tilde{\rho}_r(y, t)$ satisfy the same equation so that

$$\begin{aligned} \frac{\partial^2 \tilde{\rho}_s}{\partial t^2} - \frac{1}{4} \frac{\partial^2 \tilde{\rho}_s}{\partial y^2} + (b+a) \frac{\partial \tilde{\rho}_s}{\partial t} + \frac{b-a}{2} \frac{\partial \tilde{\rho}_s}{\partial y} &= 0, \\ \frac{\partial^2 \tilde{\rho}_r}{\partial t^2} - \frac{1}{4} \frac{\partial^2 \tilde{\rho}_r}{\partial y^2} + (b+a) \frac{\partial \tilde{\rho}_r}{\partial t} + \frac{b-a}{2} \frac{\partial \tilde{\rho}_r}{\partial y} &= 0. \end{aligned} \tag{C6}$$

Thus, solving for $\tilde{\rho}_s(y, t)$ is equivalent to solving for $\tilde{\rho}_r(y, t)$, and the solutions will differ only because the initial conditions differ. Accordingly, we illustrate the remainder of our solution by solving for $\tilde{\rho}_s(y, t)$. The next step is to execute a second change of variables using $\tilde{\rho}_s(y, t) = \exp\{-(a+b)/2t + (b-a)y\}w(y, t)$, producing the result that $w(y, t)$ satisfies the Klein-Gordon equation

$$\frac{\partial^2 w}{\partial t^2} - \frac{1}{4} \frac{\partial^2 w}{\partial y^2} - abw = 0, \tag{C7}$$

with initial conditions

$$\begin{aligned} w(y, 0) &= \frac{b}{a+b} \exp[(a-b)y] \delta(y), \\ \frac{\partial w}{\partial y}(y, 0) &= \frac{1}{2} \frac{b}{a+b} \exp[(a-b)y] \left[(a+b) \delta(y) - \frac{\partial \delta(y)}{\partial y} \right]. \end{aligned} \tag{C8}$$

Equation (C7) with initial conditions (C8) can be solved explicitly by Fourier transform using the convolution theorem and the identities

$$\begin{aligned} \mathcal{F}^{-1} \left\{ \frac{\sin [t\sqrt{c^2\omega^2 + (mi)^2}]}{\sqrt{c^2\omega^2 + (mi)^2}} \right\} &= \frac{I_0 \left(m\sqrt{t^2 - \frac{y^2}{c^2}} \right)}{2c}, \\ \mathcal{F}^{-1} \left\{ \frac{\cos [t\sqrt{c^2\omega^2 + (mi)^2}]}{\sqrt{c^2\omega^2 + (mi)^2}} \right\} &= \frac{mtI_1 \left(m\sqrt{t^2 - \frac{y^2}{c^2}} \right)}{2c\sqrt{t^2 - \frac{y^2}{c^2}}}, \end{aligned} \tag{C9}$$

where I_0 and I_1 denote modified Bessel functions of the first kind order 0 and 1, $i = \sqrt{-1}$ (the imaginary unit), m and c are parameters, and \mathcal{F}^{-1} denotes the inverse Fourier transform operation using wave number ω (Jeffrey 1995). Once $w(y, t)$ is computed, transforming back to the original coordinates using $\tilde{\rho}_s(y, t) = \exp\{-(a+b)/2t + (b-a)y\}w(y, t)$ and $y = \tau_s - t/2$ identifies the second component solution. Adding the two component solutions gives

$$\rho_s(\tau_s, t) = \begin{cases} \frac{b}{a+b} \exp(-at)\delta(t-\tau_s) & \tau_s = 0, t \\ \exp[-bt + (b-a)\tau_s] \left\{ \left(\frac{ab}{a+b} \right) I_0[2\sqrt{ab}\tau_s(t-\tau_s)] + \left(\frac{b}{a+b} \right) \frac{\sqrt{ab}\tau_s I_1[2\sqrt{ab}\tau_s(t-\tau_s)]}{\sqrt{\tau_s(t-\tau_s)}} \right\} & \tau_s \in (0, t) \end{cases} \quad (C10)$$

and

$$\rho_t(\tau_s, t) = \begin{cases} \frac{a}{a+b} \exp(-bt)\delta(\tau_s) & \tau_s = 0, t \\ \exp[-bt + (b-a)\tau_s] \left\{ \left(\frac{ab}{a+b} \right) I_0[2\sqrt{ab}\tau_s(t-\tau_s)] + \left(\frac{a}{a+b} \right) \frac{\sqrt{ab}(t-\tau_s) I_1[2\sqrt{ab}\tau_s(t-\tau_s)]}{\sqrt{\tau_s(t-\tau_s)}} \right\} & \tau_s \in (0, t) \end{cases} \quad (C11)$$

as the solutions to equations (14).

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