

Dispersal in a Statistically Structured Population: Fat Tails Revisited

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Submitted April 24, 2008; Accepted August 5, 2008; Electronically published December 31, 2008

Online enhancements: appendixes.

ABSTRACT: Dispersal has long been recognized as a crucial factor affecting population dynamics. Several studies on long-distance dispersal revealed a peculiarity now widely known as a problem of “fat tail”: instead of the rate of decay in the population density over large distances being described by a normal distribution, which is apparently predicted by the standard diffusion approach, field data often show much lower rates such as exponential or power law. The question as to what are the processes and mechanisms resulting in the fat tail is still largely open. In this note, by introducing the concept of a statistically structured population, we show that a fat-tailed long-distance dispersal is a consequence of the fundamental observation that individuals of the same species are not identical. Fat-tailed dispersal thus appears to be an inherent property of any real population. We show that our theoretical predictions are in good agreement with available data.

Keywords: dispersal, random walk, diffusion, structured population, dispersal curve, fat tail.

Introduction

Dispersal is a background for many phenomena in ecology (Clobert et al. 2001; Bullock et al. 2002). It is dispersal that makes ecological interactions essentially spatial, and it has been widely recognized that the properties of population dynamics in space and time can be very much different from their nonspatial counterparts.

One peculiarity of dispersal is that, although a large part of the dispersing population would normally remain close by, changing its position in space rather slowly, at the same time some individuals can travel over large distances. Remarkably, although the portion of the individuals involved in the long-distance dispersal is usually small (e.g., a few percent of the whole population), it has been proved that they play a crucial role in population dynamics, for in-

stance, by means of becoming the drivers of a high-rate invasion (Kot et al. 1996; Clark et al. 1998, 2001) or by inducing synchronization between different habitats (Jansen 1995; Blasius and Stone 2000).

A convenient way to quantify dispersal is the dispersal curve that shows the population density distribution as a function of the distance from a point source release. The long-distance dispersal then corresponds to the tail of the curve. Thus, identification of the mechanisms and processes affecting the tail, that is, the rate of population density decay at large distance, is crucial for the understanding of dispersal.

Note that a common definition of dispersal used in population biology is the movement of organisms from the natal site to the site of first reproduction. However, this definition actually mixes together two processes of different origin. In this note, we use a somewhat refined definition of dispersal that only addresses the movement and is not concerned with reproduction; that is, “dispersal is the movement of organisms away from their parent source” (Nathan 2001, p. 481).

The basic concepts and the whole theoretical framework have evolved considerably over the last 2 decades. Earlier studies on population dispersal were almost entirely done in terms of random walks or diffusion (Fisher 1937; Skellam 1951; Okubo 1980), which was shown to be in good agreement with field observations (Okubo and Chiang 1974; Kareiva 1983; Turchin 1998; Jopp 2006). Although it has long been recognized that diffusion may sometimes provide an oversimplified description of individual motion (see Holmes 1993), a diffusion-based approach has been used successfully in many studies in spatial ecology (Holmes et al. 1994; Shigesada and Kawasaki 1997; Okubo and Levin 2001; Cantrell and Cosner 2003; Petrovskii and Li 2006; Malchow et al. 2008).

There have also been growing concerns. One source of criticism of the standard diffusion/random walk approach has been that it predicts a normal distribution of the population density in the case of dispersal from a point source release. Although it is in agreement with some biological

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data (see Root and Kareiva 1984), there is also a growing body of evidence showing that the actual distribution can have a fatter tail, with a much lower rate of decay in population density at large distances (Kot et al. 1996; Shigesada and Kawasaki 2002; Jopp and Reuter 2005). Correspondingly, recent theoretical studies tend to denounce the random walk framework as inappropriate.

A full and consistent understanding of dispersal scenarios is still lacking, though. More complicated mechanisms, such as the Lévy flights, may provide a proper fitting for some field data (Viswanathan et al. 1996; Marell et al. 2002; Bartumeus et al. 2003; Ramos-Fernandez et al. 2004; Shlesinger 2006; but see also Edwards et al. 2007); however, it remains somewhat puzzling that the standard diffusion is seemingly inappropriate in spite of having been used successfully for so many spatial ecology problems. In this note, we show that it may not be the random walk itself that should be blamed but, instead, an oversimplified description of the dispersing population. The standard diffusion approach to population dispersal implies that all individuals are identical in terms of their dispersive ability. As soon as we take into account the inherent statistical variations of the individual parameters, the random walk approach results in a fat-tailed dispersal curve.

Note that the problem of the dispersal curve's tail has yet another aspect. Over recent years, many modeling studies have been done on the basis of integral difference equations. To the best of our knowledge, this approach was introduced to ecology by Kot and Schaffer (1986), and it has been growing increasingly popular ever since (Neubert et al. 1995; Kot et al. 1996; Neubert and Caswell 2000; Etienne et al. 2002; Schofield 2002; Fagan et al. 2005), in spite of some hidden potential pitfalls. (Recently, Lutscher and Petrovskii [2008] showed that the form of the integral difference equation is stage specific and may lead to wrong predictions about the population dynamics unless it is made consistent with the type of data collectible in the field.) According to that approach, dispersal is described by a kernel-based equation:

$$\tilde{n}(\mathbf{R}) = \int_{\Omega} k(|\mathbf{R} - \mathbf{R}'|)n(\mathbf{R}')d\mathbf{R}', \quad (1)$$

where $n(\mathbf{R})$ and $\tilde{n}(\mathbf{R})$ are the initial and the resulting population densities, respectively; $k(|\mathbf{R} - \mathbf{R}'|)$ is the dispersal kernel giving the probability density of finding at position \mathbf{R}' an offspring released at position \mathbf{R} ; and integration is taken over the whole available space. Obviously, here $k(|\mathbf{R} - \mathbf{R}'|)$ has the meaning of a dispersal curve from a point source release, and thus an appropriate choice can account for the fat tail of the emerging spatial distribution $\tilde{n}(\mathbf{R})$.

One problem with this approach is that the idea of an appropriate choice is often empirical when the kernel is simply fitted to relevant data. By now, little attention has been paid to the processes "behind the kernel," that is, what processes may lead to the formation of a kernel with given properties (but see Skarpaas and Shea 2007; for a review of this issue, see also Jongejans et al. 2008). Our findings reveal one possible mechanism showing that a fat-tailed kernel can appear as a result of a random walk diffusion modulated by inherent statistical variations in the dispersing population.

The note is organized as follows. In "Model," we quantify the statistical variations of the individual parameters in a given population by introducing a diffusivity distribution function ϕ . Having then analyzed a few cases of ϕ with different properties, we show that a fat-tailed spatial distribution is a common result. In "Mechanisms of Diffusivity Distribution," we make an insight into the "microscopic" properties of individual motion that may lead to different shapes of ϕ . In "Comparison with Field Data," we make a tentative comparison with some available field data. "Discussion and Concluding Remarks" provides a discussion.

Model

The analysis below is done for a general case of population dispersal; however, for convenience of interpretation only, we will talk about dispersal of insects. Let us consider an insect population described by its density $n(\mathbf{R}, t)$, where \mathbf{R} is position and t is time. We assume that motion of the individuals can be adequately described by random walks. Evolution of the population density is then given by the diffusion equation, and species diffusivity is quantified by the diffusion coefficient D . It should be mentioned here that, in the case of individual diffusive motion, D gives the rate of the mean square displacement, $\langle r^2 \rangle = 4Dt$; therefore, D provides a certain link between the individual-level and the population-level description of dispersal.

In order to exclude the impact of specific initial conditions, we consider the case of a single-point release when N_0 individuals of the given species are set free at the moment $t = 0$ at the position $\mathbf{R} = 0$. We consider dispersal in a two-dimensional space, for example, in a grassland of a field. For the sake of simplicity, we assume that the system is isotropic so that all motion directions are equivalent; that is, dispersal is not affected by wind or an environmental gradient. Using the polar coordinates $\mathbf{R} = (r, \theta)$, where the origin coincides with the release point, we find that the random walk approximation then results in the following Gaussian distribution of the population density over space:

$$n(\mathbf{R}, t) = \frac{N_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right) \quad (2)$$

(e.g., see Okubo 1980, 1986; Okubo and Levin 2001).

Equation (2) is obviously based on the assumption that all the individuals of a given population possess equal ability for self-motion so that population dispersal can be described by a single parameter D . In reality, however, it is not so. Most populations are structured with respect to a certain property (see Lomnicki 1988), and that may affect dispersive ability as well. The idea that the deviation of the insect dispersal curve from a normal distribution may appear as a result of a population structure was first explored by Dobzhansky and Wright (1943), who considered dispersal of a population consisting of two ranks, with their dispersal being described by diffusion coefficients $D_1 \neq D_2$. The emerging population distribution indeed differs from the normal distribution significantly at small and intermediate distances but has essentially Gaussian large-distance asymptotics. Furthermore, it is straightforward to see that the distribution will have the Gaussian tail for any finite number J of constituting ranks with different diffusivity D_1, \dots, D_J .

There exists, however, a different type of population structure that arises simply as a result of immanent statistical variation of individual parameters. Indeed, it is common knowledge that, even within the same cohort, individuals are not identical and the parameters affecting dispersive abilities—such as body weight, length of wings (if any), and so on—can vary significantly. In this case, diffusivity varies continuously, which can be taken into account by introducing a diffusivity distribution function $\phi(D)$ so that $\phi(D)dD$ gives the fraction of the population which diffusivity lies between D and $D + dD$. Let us denote the corresponding population density as $dn_D(r, t)$; then, instead of equation (2) we now have

$$dn_D(r, t) = \frac{N_0\phi(D)dD}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right), \quad (3)$$

where $\int_0^\infty \phi(D)dD = 1$.

What is measurable in dispersal experiments is the total population density n , which arises from contributions of all possible ranks:

$$n(\mathbf{R}, t) = \int dn_D(r, t) = \frac{N_0}{4\pi t} \int_0^\infty \frac{1}{D} \exp\left(-\frac{r^2}{4Dt}\right) \phi(D)dD. \quad (4)$$

Apparently, the resultant total population distribution over space given by $n(r, t)$ depends on $\phi(D)$. It is thus clear that

the original Gaussian spatial distribution (eq. [2]) of the population density can be modified by the impact of population structure, as given by $\phi(D)$. Indeed, the larger D is, the larger the typical dispersal distance of the given rank is; thus, it is intuitively clear that a slower rate of decay in $\phi(D)$ may result in a slower rate of decay in the population density n .

Now, the question is, what can actually be the properties of $\phi(D)$? Perhaps the first semi-intuitive idea about $\phi(D)$ is that it should be a normal distribution:

$$\phi(D) = \phi_1(D) = A_0 \exp\left[-\left(\frac{D - D_0}{\mu}\right)^2\right], \quad (5)$$

where $A_0 = 1/(\mu\pi^{1/2})$ is a coefficient, D_0 is the distribution center, and $\mu \ll D_0$ is the half-width. In order to take into account the fact that diffusivity is nonnegative, we may additionally define $\phi(D) \equiv 0$ for $D < 0$, which does not make any essential difference because under condition $\mu \ll D_0$, the values of ϕ at $D < 0$ are negligibly small anyway.

Having plugged equation (5) into equation (4), we obtain

$$n(\mathbf{R}, t) = \frac{N_0 A_0}{4\pi t} \exp\left(-\frac{\eta^2}{4}\right) \int_0^\infty \frac{1}{z} \exp\left(-\frac{p}{z} - z^2 + \eta z\right) dz, \quad (6)$$

where $z = D/\mu$, $p = r^2/(4\mu t)$, and $\eta = 2D_0/\mu$. In order to calculate the rate of decay of population density n at large distances, we need to know how n depends on p . Unfortunately, an exact analytical expression for the integral on the right-hand side of equation (6) is not available. However, it appears possible to obtain an estimate of its behavior for large values of p , which is exactly what we need.

Having applied a relevant asymptotical analysis (for the calculation details, see app. A in the online edition of the *American Naturalist*), from equation (6) we arrive at the following expression for the population density:

$$n(\mathbf{R}, t) \approx C \times \left(\frac{p}{2}\right)^{-1/3} \exp\left[-3\left(\frac{p}{2}\right)^{2/3} + \eta\left(\frac{p}{2}\right)^{1/3}\right], \quad (7)$$

where $C = \{N_0 A_0 / [4t(3\pi)^{1/2}]\} \exp(-\eta^2/4)$, which is valid when $p = r^2/(4\mu t) \gg 1$; the larger p is, the higher is its accuracy.

Therefore, from equation (7) we obtain that, for any given moment of time,

$$n(\mathbf{R}, t) \sim r^{-2/3} \exp\left[-\frac{3r^{4/3}}{4(\mu t)^{2/3}}\right], \quad (8)$$

which is obviously a fatter tail than that of the Gaussian distribution. A question that immediately arises here is whether this theoretical prediction of a fat-tailed distribution is robust with respect to variations in the properties of function ϕ . One particular point of concern is that the normal distribution is feasible only under the assumption $\mu \ll D_0$. In a more general case, the following Maxwell-type distribution should be more appropriate:

$$\phi(D) = A_1 D^k \exp\left[-\left(\frac{D}{\mu}\right)^2\right], \quad (9)$$

where $A_1 = 1/(C(k)\mu^{k+1})$ is the scaling factor, $k > 0$ is an auxiliary parameter, and $C(k) = \int_0^\infty z^k \exp(-z^2) dz$ is a numerical coefficient. Note that, although both equations (5) and (9) have Gaussian tails (up to a different preexponential factor) for large values of diffusivity, at small and intermediate D , their behavior is significantly different.

Having taken equation (4) together with equation (9) and omitting calculation details, we obtain the large-distance population distribution:

$$n(\mathbf{R}, t) \approx \frac{N_0}{4\sqrt{3}\pi C(k)\mu t} \times \left(\frac{r}{2}\right)^{(k-1)/3} \exp\left[-3\left(\frac{r}{2}\right)^{2/3}\right], \quad (10)$$

so that, for any given t ,

$$n(\mathbf{R}, t) \sim r^{2(k-1)/3} \exp\left[-\frac{3r^{4/3}}{4(\mu t)^{2/3}}\right]. \quad (11)$$

Remarkably, equation (11) nearly coincides with equation (8), with both of them showing a fatter tail than that of a normal distribution. Note that parameter k affects only the preexponential factor but not the exponent itself.

Mechanisms of Diffusivity Distribution

We have shown that the existence of statistical structure in the dispersing population makes the rates of population decay at large distances lower. A question remains, however, as to what are the processes and mechanisms that can possibly result in different diffusivity distributions, that is, in ϕ of different shapes. The generic case that we have considered in the previous section is that the large- D asymptotics of function $\phi(D)$ are described by a normal distribution. That seems to be biologically reasonable, but is it the only possible case? We will follow a simple chain of arguments to argue that the situations when ϕ has an

exponential or a power law rate of decay at large D are not at all exotic. A key to the understanding is the observation that population diffusivity is not a “first-principle” property but actually appears as a result of interplay between various factors affecting individual motion.

To begin with, we recall that microscopic analysis of the random walk (e.g., see Okubo and Levin 2001, p. 13) leads to the following equation for the diffusion coefficient:

$$D = \frac{l^2}{2\tau}, \quad (12)$$

where l is length of a separate step and τ is the time required to make this step. The time-continuous case is reached in the limit $\tau \rightarrow 0$ and $l \rightarrow 0$, provided the ratio l^2/τ remains constant. It is clear, however, that the time-discrete random walk with finite values of l and τ will have properties close to those of the time-continuous diffusion if l and τ are much smaller compared with, respectively, the temporal and spatial scales of a given dispersal process. Therefore, equation (12) can be used to calculate the distribution function of D if the corresponding information is available on l and/or τ .

Case 1

We assume that all insects have trajectories of their motion with the same value of l . As for τ , we assume that it can be different for different individuals, which means that a given population is described by a distribution of τ rather than by a single value.

One could then speculate in what way the distribution of step times $\psi(\tau)$ should be related to a distribution of some more basic individual parameters, such as the body mass. Although detailed consideration of this issue lies beyond the scope of this note, the existence of such relation looks plausible. Indeed, considering, for instance, body mass m , a heavier body requires a larger force and a larger energy expense to change the direction of flight. Therefore, it may be expected that heavier individuals would prefer to change direction less often, thus having larger typical values of τ . The simplest case is given by a linear relation between m and τ ; assuming that the value of the individual body mass is distributed normally, we arrive at a normal distribution for τ :

$$\psi(\tau) = \frac{1}{\sqrt{\pi}\delta\tau} \exp\left[-\left(\frac{\tau - \tau_0}{\delta\tau}\right)^2\right] \quad (13)$$

(where τ_0 and $\delta\tau$ are parameters with obvious meaning, $\delta\tau \ll \tau_0$), so that $\psi(\tau)d\tau$ gives the probability that a ran-

domly caught individual is doing its random walk with the single step time between τ and $\tau + d\tau$.

Because τ is a random variable, diffusion coefficient $D \sim 1/\tau$ also becomes a random variable but with a different probability distribution function $\phi(D)$. A standard probability theory technique then leads to the following result:

$$\phi(D) = \psi(\tau(D)) \left| \frac{d\tau(D)}{dD} \right|, \tag{14}$$

where $\tau(D) = l^2/(2D)$. From equations (13) and (14), we then immediately arrive at

$$\phi(D) = \frac{l^2}{2\sqrt{\pi}\delta\tau D^2} \exp\left[-\frac{1}{(\delta\tau)^2}\left(\frac{l^2}{2D} - \tau_0\right)^2\right]. \tag{15}$$

For sufficiently large D (i.e., for $D \gg l^2/\tau_0$), from equation (15) we obtain

$$\phi(D) \approx \frac{l^2}{2\sqrt{\pi}\delta\tau D^2} \exp\left[-\left(\frac{\tau_0}{\delta\tau}\right)^2\right] \sim D^{-2}, \tag{16}$$

so that the probability distribution function $\phi(D)$ has a power law decay.

Case 2

In order to have insight into other possible types of diffusivity distribution, let us note that equation (12) can be written as

$$D = \frac{v^2\tau}{2}, \tag{17}$$

where $v = l/\tau$ is the speed of motion of a given individual along its trajectory. It is readily seen that an assumption that the time τ of a single step is distributed normally (see eq. [13]) would now result in a normal distribution for diffusivity D , provided v is the same for all insects in the given population.

However, available data indicate that v is also a distribution rather than a parameter. In particular, Okubo and Chiang (1974), having measured and analyzed the speed of individual motion of flying insects, arrived at the conclusion that it is very well described by a Maxwell-type distribution:

$$\chi(v) = Cv \exp(-bv^2), \tag{18}$$

where b is a certain empirical parameter and $C = 2b$ is a coefficient.

Equation (18) gives the distribution of v , so that $\chi(v)dv$ gives the probability that a randomly chosen insect will have its typical flight speed between v and $v + dv$. The distribution of v^2 can be obtained if we rewrite equation (18) as follows:

$$2bv \exp(-bv^2)dv = b \exp(-bv^2)dv^2. \tag{19}$$

The predifferential factor on the right-hand side then gives the probability distribution for v^2 .

In contrast to the previous case, we now assume that $\tau = \text{const}$; then, taking into account equation (17), we obtain the following distribution function for D :

$$\phi(D) = \frac{2b}{\tau} \exp\left(-\frac{2bD}{\tau}\right). \tag{20}$$

We want to emphasize here that the results by Okubo and Chiang (1974) are not unique, and a Maxwell-type distribution of the individual speed has been observed for some other invertebrate species as well (see Jopp 2006).

Therefore, a simple observation that diffusivity D is not a “first-principle” parameter but can be expressed through microscopic characteristic of the individual insect’s flight leads to the conclusion that the diffusivity distribution function must not necessarily be Gaussian. Correspondingly, its rate of decay at large D can be much slower, for example, either exponential or power law.

We also want to mention that another argument in favor of $\phi(D)$ with a tail fatter than the normal distribution can possibly be found if we place the population statistical structure into the evolutionary context. A mathematical theory of speciation recently developed by Volpert and coworkers (see Genieys et al. 2006a, 2006b) predicts that, within a given phenotype, the statistical distribution of species’ traits should have an exponential tail. Consider, for instance, the characteristic time τ of a single step along the trajectory to be the trait; then, even the simplest case $D \sim \tau$ results in $\phi(D)$ with a fat (exponential) tail.

In order to reveal the impact of these different statistical structures on the dispersal tail, we now consider the population density, as given by equation (4), with function $\phi(D)$ having either exponential or power law rates of decay at large D . Table 1 summarizes all our findings; calculation details can be found in appendixes A and B in the online edition of the *American Naturalist*. Note that, in order to keep the model tractable, we need to make additional assumptions about the properties of $\phi(D)$ at small D . That results in additional factors such as D^β for the exponential case and $\exp(-\alpha/D)$ for the power law case, where α and

Table 1: Exact expressions for the population density $n(r, t)$ (where available), as given by the model (4), and its large distance asymptotics for different types of the statistical structure described by $\phi(D)$

$\phi(D)$	Exact expression	Large-distance asymptotics for a given t
$A_0 \exp\left[-\left(\frac{D - D_0}{\mu}\right)^2\right]$	NA	$r^{-2/3} \exp\left[-\frac{3r^{4/3}}{4(\mu t)^{2/3}}\right]$
$A_1 D^k \exp\left[-\left(\frac{D}{\mu}\right)^2\right]$	NA	$r^{2(k-1)/3} \exp\left[-\frac{3r^{4/3}}{4(\mu t)^{2/3}}\right]$
$A_2 D^\beta \exp\left(-\frac{D}{\nu}\right)$	$\frac{N_0}{2\pi\nu\Gamma(\beta + 1)t} \times q^{\beta/2} K_\beta(2\sqrt{q}),$ $q = \sqrt{\frac{r^2}{\nu t}}$	$r^{\beta-1/2} \exp\left(-\frac{r}{\nu t}\right)$
$A_3 D^{-\gamma} \exp\left(-\frac{\alpha}{D}\right)$	$\frac{N_0}{4\pi t} \times \frac{\alpha^{\gamma-1}\Gamma(\gamma)}{\Gamma(\gamma-1)} \left(\alpha + \frac{r^2}{4t}\right)^{-\gamma}$	$r^{-2\gamma}$

Note: Here $\Gamma(z)$ is the gamma function, $K_\beta(z)$ is the modified Bessel function of the second kind, and A_0, \dots, A_3 are the scaling factors ensuring that $\int_0^\infty \phi(D)dD = 1$. NA, not available.

β are auxiliary parameters, with α having the meaning of characteristic diffusivity (similar to that of μ in the second row and ν in the third row of table 1). We want to emphasize that we have not found a single case where the large-distance rate of decay in population density would be described by the thin Gaussian tail. On the contrary, the tail is predicted to be much fatter, being either exponential or power law if the rate of decay in $\phi(D)$ is exponential or power law, respectively.

Comparison with Field Data

A question of immediate interest is whether the predictions of our theoretical approach comply with field data. Field data on insect dispersal usually show the number of (re)captured individuals at different distances from the place of their initial release. The first remark that we make here is that, depending on the way the captured insects are treated, trapping can induce a considerable perturbation to the spatial distribution of the dispersing population (see Yamamura et al. 2003). For instance, if the captured insects are killed during the trapping, they are removed from the population. It means that those captured at a short distance do not have the possibility of a longer-distance travel. As a result, the properties of the long-distance dispersal can be considerably distorted. Therefore, since our approach does not take into account the impact of trapping, it means that not all data sets on insect dispersal are suitable for comparison with the theory developed in this note.

However, we have identified two types of field studies when trapping is unlikely to cause any significant bias to

the data. In particular, studies on butterfly dispersal (Brakefield 1982; Wilson and Thomas 2002) often treat the captured insects in a less harsh way, just having them marked and released again. Not only does this approach significantly decrease the perturbation introduced into the dispersing system, but also it effectively increases the sample because the released butterflies can, after some time, be captured again at a different position. The distance between their release and the second recapture can then be interpreted in exactly the same way as the distance between the initial release and the first recapture.

The second remark that we make here is that the variable $n(\mathbf{R}, t)$ calculated in “Model” and “Mechanisms of Diffusivity Distribution” for different cases (see table 1) is actually a function of a position $\mathbf{R} = (r, \theta)$, not just of a distance r . The assumption of spatial isotropy, that is, $n(\mathbf{R}, t) = n(r, t)$, does not help because a fixed value of θ would correspond to a transect in space along a given direction. However, the field data available from literature often provide only a cumulative value of the captures at a certain distance, without specifying the direction of the dispersal. In order to obtain the spatial distribution $\hat{n}(r, t)$ over the distance, we should integrate $n(r, t)$ over θ , even if n does not depend on θ explicitly. Assuming that all directions are equivalent, we then arrive at $\hat{n}(r, t) = 2\pi r n(r, t)$, and it is this expression that should be used for comparison with the field data.

The third remark is that the field data consist of numbers (of animal captures), and our theoretical results are obtained in terms of population density. To the best of our knowledge, how the population density is transformed into captures is an issue that has not yet been properly

studied and is not yet fully understood. Here we use a very simple approach assuming that the number of captures at a certain distance r arises as a result of integration of the population density over a certain “window,” that is, between $r - \Delta r$ and $r + \Delta r$, where Δr is a parameter that can be interpreted as the “sampling range” of the trap (see Wall and Perry 1987). Therefore, the theoretical prediction of the total number of recaptures at a distance r from the place of release is given by the following expression:

$$N_{\text{recap}}(r) = 2\pi \int_{r-\Delta r}^{r+\Delta r} rn(r, t)dr \approx 4\pi(\Delta r)rn(r, t), \quad (21)$$

where the approximation is valid if the population density $n(r, t)$ (as given by table 1 or by eq. [4] in a general case) varies slowly over the range $(r - \Delta r, r + \Delta r)$, which is always the case with the dispersal tail.

Figure 1 shows the data from Brakefield (1982) for the cumulative number of the first-day captures of dispersing butterflies over two seasons, that is, 1977 and 1978 (respectively, the right-hand panels in the middle and bottom rows of fig. 4 in Brakefield 1982). The thick line (line 1) shows the theoretical prediction as given by equation (21),

with $n(r, t)$ decaying as a power law; see the last row of table 1. The exact value of the characteristic diffusivity for the butterfly *Maniola jurtina* is not available; we used a hypothetical value $\alpha = 600 \text{ m}^2 \text{ day}^{-1}$, which is consistent with a typical diffusivity of flying insects (see Shigesada and Kawasaki 1997). As for the sampling range, its value $\Delta r = 7 \text{ m}$ was defined by the spatial resolution of the experimental setting used in that field study. The value of parameter $\gamma = 2.63$ (proportion of variance explained $R^2 = 0.955$, $\text{SE} = 0.14$) was obtained by nonlinear regression (Dennis et al. 1981) using the NLREG statistical package (P. H. Sherrord; demonstration version available at <http://www.nlreg.com>). Interestingly, the theory appears to be in good agreement with the data not only at the tail of the dispersal curve but also at small and intermediate distances. We want to emphasize that this agreement is obtained for biologically reasonable parameters.

Remarkably, the power law decay appears to provide the best possible fit of the data. To compare, line 2 in figure 1 shows the theoretical prediction in the case of exponential decay (see third row of table 1). The corresponding value of β was obtained by nonlinear regression ($\beta = 0.03$; $R^2 = 0.952$, $\text{SE} = 0.14$). Obviously, it fails to catch the tail of the distribution; also, the statistical error

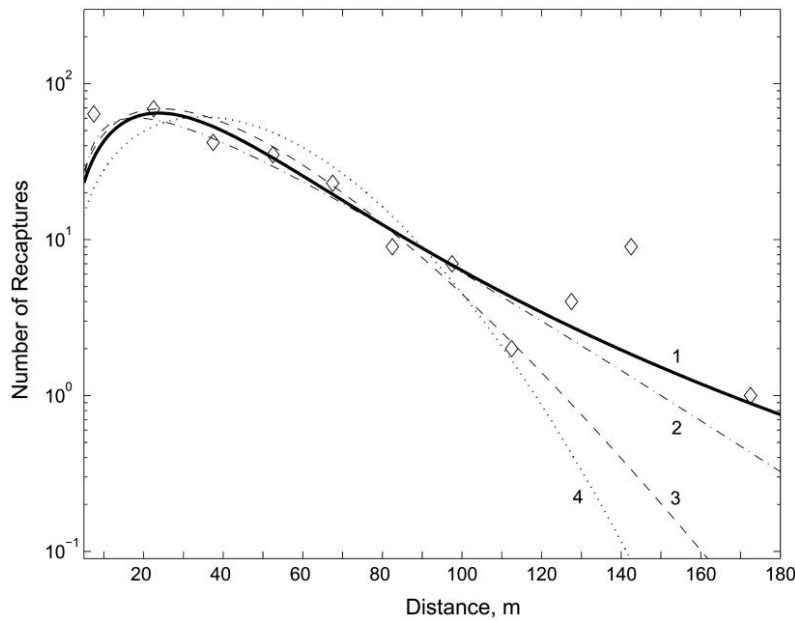


Figure 1: Comparison with field data. Diamonds show the data on butterfly dispersal from Brakefield (1982; day 1 recaptures, total numbers for males during 1977 and 1978 experiments). Lines 1–3 show the theoretical predictions as given by equations (4) and (21) for different cases of $\phi(D)$ (see table 1, bottom three rows, respectively). Line 4 shows the population density of the corresponding unstructured population (see eq. [2]). The characteristic diffusivity is considered to be the same for all four cases, $\alpha = \nu = \mu = D = 600 \text{ m}^2 \text{ day}^{-1}$. The total number of recaptures is assumed to be $N_0 = 250$.

is very large. Other cases make it even worse. Line 3 is obtained in the case of the Maxwell-type distribution with $k = 1$ (second row in table 1), and line 4 shows the unstructured case given by equation (2). We want to mention here that variation of parameter values, such as diffusivity and/or sampling range (with new values of β and γ adjusted by nonlinear regression), does not change the hierarchy of the curves, with the power law always being the best fit and the normal/Maxwell-type always being the worst.

The second type of field data on species dispersal that allows comparison with our theoretical result is given by the studies when the number of recaptured individuals were deliberately kept small. As one particular example, figure 2 shows the data on the southern pine beetle dispersal from Turchin and Thoeny (1993; see upper left panel of their fig. 3). The data were obtained for a few transects in space, along a few chosen directions; therefore, integration of the population density over the angles is not needed in this case. The traps were open for the whole duration of the experiment, and hence the data show the cumulative counts. Therefore, in order to provide a theoretical prediction, $n(r, t)$ should be integrated over the time. For the sake of simplicity, we assume as above that the population density varies in space slowly and the in-

tegration over the sampling area can be changed to multiplication; then, we arrive at

$$N_{\text{recap}}(r) \approx \pi(\Delta r)^2 \int_0^t n(r, \tau) d\tau. \quad (22)$$

Turchin and Thoeny (1993) found that their data can be fitted by an exponential function. Indeed, line 1 in figure 2 shows the prediction of our theory obtained for the exponential decay (see third row in table 1); obviously, it is in good agreement with the data. For the diffusivity and the sampling range, we used hypothetical values $\nu = 2,000 \text{ m}^2 \text{ day}^{-1}$ and $\Delta r = 6 \text{ m}$, respectively. The total number of dispersing beetles was assumed to be $N_0 = 4,000$. For these values, the auxiliary parameter β was found by nonlinear regression, resulting in $\beta = 5.4$ ($R^2 = 0.965$, $\text{SE} = 0.4$).

Interestingly, a closer look reveals that fitting by an exponential function is not the only possible one. The matter is that the value of the parameters for the southern pine beetle experiment is known very approximately. In particular, Turchin and Thoeny (1993) gave just a rough estimate (up to the order of magnitude) of the total number of beetles. Also, their experimental settings give only an

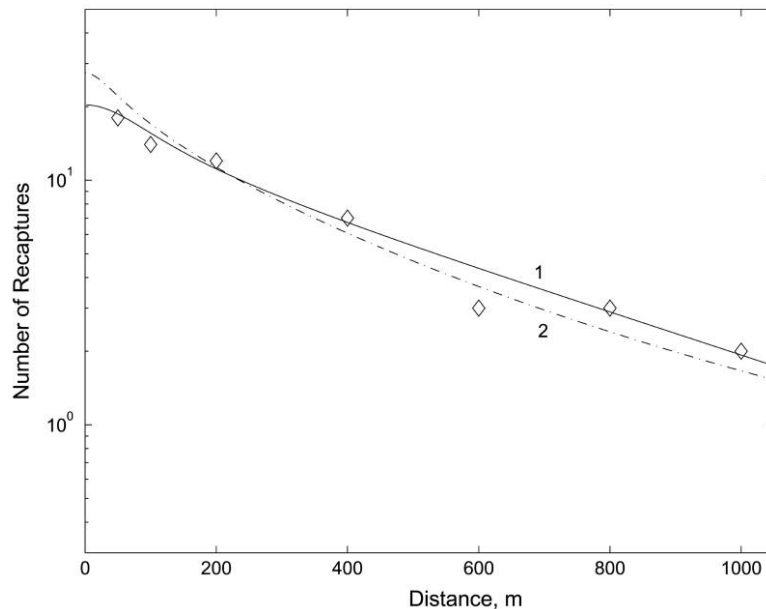


Figure 2: Comparison with field data. Diamonds show a data sample on southern pine beetle dispersal from Turchin and Thoeny (1993). Line 1 shows the theoretical prediction as given by the exponential decay (third row in table 1) for $\nu = 2,000 \text{ m}^2 \text{ day}^{-1}$ and $\beta = 5.4$. The duration of the experiment is estimated to be $t = 50$ days. Line 2 shows the power law decay (fourth row in table 1) obtained for a slightly different value of the characteristic diffusivity $\alpha = 2,500$ and $\gamma = 1.045$.

upper bound for the sampling range of the traps. Correspondingly, we observe that, using somewhat different parameter values, the data can also be fitted by our theory with the power law function (fourth row in table 1). Line 2 shows it as obtained for $\alpha = 2,500 \text{ m}^2 \text{ day}^{-1}$, $\Delta r = 10 \text{ m}$, and $N_0 = 10,000$. Note that the higher diffusivity value that we used in this case is still within the biologically reasonable range. The value of $\gamma = 1.045$ ($R^2 = 0.931$, $\text{SE} = 0.005$) was found by nonlinear regression.

Therefore, low accuracy of the southern beetle experiment (Turchin and Thoeny 1993) does not make it possible to distinguish confidently between the exponential and power law types of decay. However, we want to emphasize that the fat tail of the beetle dispersal data is well described by our theoretical predictions obtained for biologically reasonable parameter values. We also want to mention here that other types of function $\phi(D)$ (rows 1 and 2 in table 1), as well as the unstructured case (eq. [2]), either result in an unacceptably low quality of data fitting or require unrealistic parameter values.

Discussion and Concluding Remarks

Fat tails of population dispersal are often regarded as a “fingerprint” of non-Brownian diffusion. In this note, we have shown that the existence of population density distributions with exponential or power law rates of decay at large distances is just an intrinsic property of the standard random walk scenario, provided that the inherent statistical variation of individual parameters in the dispersing population is taken into account. We quantified this variation by introducing a diffusivity distribution function $\phi(D)$, where D is the diffusion coefficient. Having analyzed a few cases of ϕ with different properties, we have not found a single case where the population density tail would exhibit a Gaussian rate of decay.

It should be mentioned that there have previously been other attempts to explain the phenomenon of fat-tailed dispersal. For instance, the dispersal distances observed in field studies may arise as a result of the interplay between different processes because the insects do not move all the time but instead alternate periods of movement with periods of rest (e.g., for feeding). The distribution of dispersal distances and the large-distance rate of decay in population density are then modulated by the distribution of the rest times and can of course differ significantly from a normal distribution, even if the motion is perfectly Brownian.

Therefore, our approach is surely not the only possible one to provide an explanation of the fat-tailed population dispersal. However, we want to emphasize that, while the impact of other factors can vary from case to case—being either present/prominent or absent/negligible—our ap-

proach takes into account a fundamental, inherent feature of the population biology, that is, the existence of individual variations. Therefore, we expect that the mechanism of fat tails formation considered here is always present, even if it can sometimes be blurred by or tangled with other processes.

A question that then becomes important concerns what the mechanistic processes behind the diffusivity distribution $\phi(D)$ can be and whether the distributions other than normal are biologically plausible. A “microscopic” analysis of the random walk shows that the diffusion coefficient can be expressed through individual motion values, such as the time required for each step along the trajectory and the length of the step and/or the speed of motion. We have considered two hypothetical cases when (1) the length step is the same for all insects at all time but the time is distributed normally and (2) the time is the same but the speed of individual flight is distributed according to a Maxwell-type distribution, with the latter being in very good agreement with some available data (Okubo and Chiang 1974). A simple analysis shows that these two cases result in a non-Gaussian diffusivity distribution with a power law tail and an exponential tail, respectively.

Note that, when considering the distribution of the individual speed, as given by equation (18), we actually assumed that its value is “fixed” to individuals. The differential probability $dP_{v, dv} = \chi(v)dv$ then gives the probability that a randomly chosen insect has its individual typical speed of motion between v and $v + dv$ but not the probability that a given individual would take this speed after making another turn in its trajectory. The value of speed can be different for different insects, but for any given individual it does not change with time (up to a reasonably small variation, if thinking about real populations).

The question thus arises whether this assumption of the individually fixed speed is realistic. In order to look for an answer, we first observe that the “reason” for a given insect to move with a particular value of speed can be of either physiological or behavioral origin. In the former case, the speed would obviously depend on parameters such as body mass and wing length, which are fixed for any adult individual. Therefore, a “preferable” or characteristic value of speed can also be expected to be fixed, of course up to some variations.

What may happen in the case when the individual speed is mostly controlled by behavioral factors? Although the first impression might be that, in this case, there should be a wider spectrum of options, surprisingly, this is not so. Many recent studies in behavioral ecology indicate that, quite often, types of behavior are fixed to individuals (Richards and Packer 1996; Reale et al. 2000; for a fuller

list of references, see Petrovskii et al. 2008). Therefore, the typical value of speed would be fixed as well.

Effects of Diffusivity Boundedness

The analysis in “Model” was done under the assumption that diffusivity is distributed over the semi-infinite domain $D \geq 0$. In reality, this is not so; obviously, for any given population, diffusivity cannot be arbitrarily large. One physical limitation resulting in the boundedness of possible diffusivity values is the finiteness of the individual speed (see eq. [7]). A question arises as to how the finiteness of the diffusivity distribution domain may possibly affect the results. Intuitively, it seems that, at sufficiently large distances, one should then expect a spatial distribution close to the normal distribution.

Technical details can be found in appendix C in the online edition of the *American Naturalist*. Our theory predicts that the fat-tailed decay in the population density at large distances appears to be an “intermediate asymptotics” (see Barenblatt 1996) rather than the actual asymptotics. The whole space where dispersal takes place consists of a few regions (see fig. 3). Because of the diffusivity boundedness, the region with the lower rate of decay—such as exponential or power law dependence on the distance from the point of insect release—eventually changes to the faster rate of decay corresponding to the Gaussian distribution. The characteristic distance r_* where the transition between these two types of decay takes place is found analytically.

Note that this prediction of our approach can, in principle, be tested in the field, even if it would mean con-

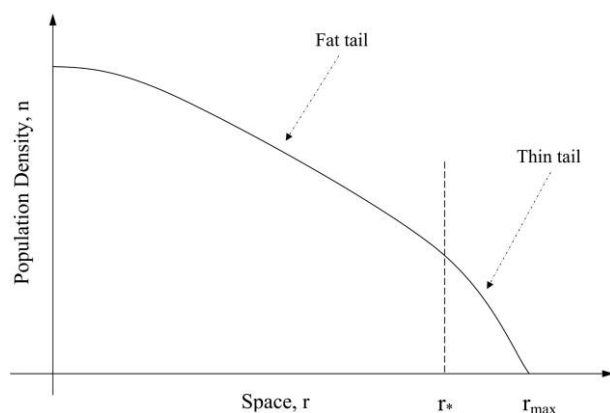


Figure 3: Structure of the dispersal curve as given by the statistically structured population approach. The spatial domain where the curve possesses a fat tail is predicted to eventually give way to the spatial domain with the thin Gaussian tail.

siderable experimental difficulty, because the population density at large distance is usually very low, and a lot of effort is required to make the data statistically reliable in order to distinguish between different types of asymptotics. We want to mention here that, even if the number of individuals recaptured over a certain distance becomes very small, this fact by itself by no means proves that the asymptotics are reached. By definition, asymptotics require comparison between different data sets obtained at different (large) distances, and that implies a much larger database than is usually available from dispersal experiments. Also, in order to calculate the characteristic distance r_* , a separate study is necessary to obtain a reliable estimate of the maximum diffusivity D_* for a given species.

Finally, we should not forget that the prediction for the population density to be positive at any position in space is an artifact of the linear diffusion. In reality, the (thin) dispersal tail will not go infinitely far either: there exists a maximum theoretical distance $r_{\max}(t)$ so that no individual of the given dispersing population can possibly be found at $r > r_{\max}(t)$ at time t .

Acknowledgments

We are thankful to B. Blasius, J. Freund, A. Gorban, H. Malchow, and J. Walters for fruitful discussions and helpful comments.

Literature Cited

- Abramowitz, M., and I. A. Stegun. 1972. Handbook of mathematical functions. National Bureau of Standards, Washington, DC.
- Barenblatt, G. I. 1996. Scaling, self-similarity, and intermediate asymptotics. Cambridge University Press, Cambridge.
- Bartumeus, F., F. Peters, S. Pueyo, C. Marrase, and J. Catalan. 2003. Helical Lévy walks: adjusting searching statistics to resource availability in microzooplankton. *Proceedings of the National Academy of Sciences of the USA* 100:12771–12775.
- Blasius, B., and L. Stone. 2000. Nonlinearity and the Moran effect. *Nature* 406:846–847.
- Brakefield, P. M. 1982. Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution and dispersal. *Journal of Animal Ecology* 51:713–726.
- Bullock, J. M., R. E. Kenward, and R. S. Hails, eds. 2002. Dispersal ecology. Blackwell, Oxford.
- Cantrell, R. S., and C. Cosner. 2003. Spatial ecology via reaction-diffusion equations. Wiley, Chichester.
- Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, et al. 1998. Reid’s paradox of rapid plant migration. *BioScience* 48:13–24.
- Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist* 157:537–554.
- Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols, eds. 2001. Dispersal. Oxford University Press, Oxford.
- Dennis, J. E., D. M. Gay, and R. E. Welsch. 1981. An adaptive non-

- linear least-squares algorithm. *ACM Transactions on Mathematical Software* 7:348–368.
- Dobzhansky, T., and S. Wright. 1943. Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. *Genetics* 28:304–340.
- Edwards, A. M., R. A. Phillips, N. W. Watkins, M. P. Freeman, E. J. Murphy, V. Afanasyev, S. V. Buldyrev, et al. 2007. Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature* 449:1044–1048.
- Etienne, R., B. Wertheim, L. Hemerik, P. Schneider, and J. Powell. 2002. The interaction between dispersal, the Allee effect and scramble competition affects population dynamics. *Ecological Modelling* 148:153–168.
- Fagan, W. F., M. Lewis, M. G. Neubert, C. Aumann, J. L. Apple, and J. G. Bishop. 2005. When can herbivores slow or reverse the spread of an invading plant? a test case from Mount St. Helens. *American Naturalist* 166:669–685.
- Fedoryuk, M. V. 1987. Integrals and asymptotic expansions. Nauka, Moscow.
- Fisher, R. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* 7:355–369.
- Genieys, S., V. Volpert, and P. Auger. 2006a. Adaptive dynamics: modelling Darwin's divergence principle. *Comptes Rendus Biologies* 329:876–879.
- . 2006b. Patterns and waves for a model in population dynamics with nonlocal consumption of resources. *Mathematical Modelling of Natural Phenomena* 1:63–80.
- Holmes, E. E. 1993. Are diffusion models too simple? a comparison with telegraph models of invasion. *American Naturalist* 142:779–795.
- Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* 75:17–29.
- Jansen, V. A. A. 1995. Regulation of predator-prey systems through spatial interactions: a possible solution to the paradox of enrichment. *Oikos* 74:384–390.
- Jongejans, E., O. Skarpaas, and K. Shea. 2008. Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology, Evolution and Systematics* 9:153–170.
- Jopp, F. 2006. Comparative studies on the dispersal of the great ramshorn (*Planorbis corneus* L.): a modelling approach. *Limnologia* 36:17–25.
- Jopp, F., and H. Reuter. 2005. Dispersal of carabid beetles: emergence of distribution patterns. *Ecological Modelling* 186:389–405.
- Kareiva, P. M. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia* (Berlin) 57:322–327.
- Kot, M., and W. M. Schaffer. 1986. Discrete-time growth dispersal models. *Mathematical Biosciences* 80:109–136.
- Kot, M., M. A. Lewis, and P. van der Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77:2027–2042.
- Lomnicki, A. 1988. Population ecology of individuals. *Monographs in Population Biology*. Vol. 25. Princeton University Press, Princeton, NJ.
- Lutscher, F., and S. V. Petrovskii. 2008. The importance of census times in discrete-time growth-dispersal models. *Journal of Biological Dynamics* 2:55–63.
- Malchow, H., S. Petrovskii, and E. Venturino. 2008. Spatiotemporal patterns in ecology and epidemiology: theory, models, and simulations. Chapman & Hall/CRC, Boca Raton, FL.
- Marell, A., J. P. Ball, and A. Hofgaard. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology* 80:854–865.
- Nathan, R. 2001. The challenges of studying dispersal. *Trends in Ecology & Evolution* 16:481–483.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613–1628.
- Neubert, M. G., M. Kot, and M. A. Lewis. 1995. Dispersal and pattern formation in a discrete-time predator-prey model. *Theoretical Population Biology* 48:7–43.
- Okubo, A. 1980. Diffusion and ecological problems. Springer, New York.
- . 1986. Dynamical aspects of animal grouping: swarms, schools, flocks, and herds. *Advances in Biophysics* 22:1–94.
- Okubo, A., and H. C. Chiang. 1974. An analysis of the kinematics of swarming of *Anarete pritchardi* Kim (Diptera: Cecidomyiidae). *Researches on Population Ecology* 16:1–42.
- Okubo, A., and S. A. Levin. 2001. Diffusion and ecological problems: modern perspectives. Springer, New York.
- Petrovskii, S. V., and B. L. Li. 2006. Exactly solvable models of biological invasion. Chapman & Hall/CRC, Boca Raton, FL.
- Petrovskii, S. V., R. P. Blackshaw, and B. L. Li. 2008. Consequences of the Allee effect and intraspecific competition on population persistence under adverse environmental conditions. *Bulletin of Mathematical Biology* 70:412–437.
- Polyanin, A. D., and V. F. Zaitsev. 1995. Handbook of exact solutions for ODEs. CRC, Boca Raton, FL.
- Ramos-Fernandez, G., J. L. Mateos, O. Miramontes, and G. Cocho. 2004. Lévy walk patterns in foraging movements of spider monkeys. *Behavioral Ecology and Sociobiology* 55:223–230.
- Reale, D., B. Y. Gallant, M. Leblanc, and M. Festa-Bianchet. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour* 60:589–597.
- Richards, M. H., and L. Packer. 1996. The socioecology of body size variation in the primitively eusocial bee, *Halictus ligatus* (Hymenoptera: Halictidae). *Oikos* 77:68–76.
- Root, R. B., and P. M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65:147–165.
- Schofield, P. 2002. Spatially explicit models of Turelli-Hoffmann *Wolbachia* invasive wave fronts. *Journal of Theoretical Biology* 215:121–131.
- Shigesada, N., and K. Kawasaki. 1997. Biological invasions: theory and practice. Oxford University Press, Oxford.
- . 2002. Invasion and the range expansion of species: effects of long-distance dispersal. Pages 350–373 in J. M. Bullock, R. E. Kenward, and R. S. Hails, eds. *Dispersal ecology*. Blackwell, Oxford.
- Shlesinger, M. F. 2006. Search research. *Nature* 443:281–282.
- Skarpaas, O., and K. Shea. 2007. Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. *American Naturalist* 170:421–430.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196–218.
- Turchin, P. 1998. Quantitative analysis of movement. Sinauer, Sunderland, MA.

- Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecological Applications* 3:187–198.
- Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Lévy flight search patterns in wandering albatrosses. *Nature* 381:413–415.
- Wall, C., and J. N. Perry. 1987. Range of action of moth sex-attractant sources. *Entomologia Experimentalis et Applicata* 44:5–14.
- Wilson, R. J., and C. D. Thomas. 2002. Dispersal and the spatial dynamics of butterfly populations. Pages 257–278 in J. M. Bullock, R. E. Kenward, and R. S. Hails, eds. *Dispersal ecology*. Blackwell, Oxford.
- Yamamura, K., M. Kishita, N. Arakaki, F. Kawamura, and Y. Sadoyama. 2003. Estimation of dispersal distance by mark-recapture experiments using traps: correction of bias caused by the artificial removal by traps. *Population Ecology* 45:149–155.

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