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ARE DIFFUSION MODELS TOO SIMPLE? A COMPARISON WITH TELEGRAPH MODELS OF INVASION

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Abstract.—Diffusion models of animal movement are often criticized because they assume animals have infinite velocity and completely random motion. To investigate the impact of these assumptions, I compared a diffusion model with a telegraph model of dispersal. The telegraph model assumes organisms have finite velocity and tend to maintain their direction. I compared the models in two settings: (i) as models for dispersal of nonreproducing organisms and (ii) as models for range expansion of organisms that simultaneously disperse and reproduce (so-called reaction-diffusion or reaction-telegraph models). Both models predict very similar dispersal patterns for nonreproducing organisms. In the case of reproducing organisms, however, they predict grossly different rates of range expansion for all but a small range of parameter values. The disparity is greatest for organisms with high population growth and low movement rates. To assess the magnitude of disparity for different organisms, I used published data to estimate model parameters for the cabbage butterfly (*Pieris rapae*), gypsy moth (*Lymantria dispar*), European starling (*Sturnus vulgaris*), collared turtledove (*Streptopelia decaocto*), Black Death (*Yersinia pestis*), and for rabies. All six cases fell within the narrow parameter range where the diffusion and telegraph models yield indistinguishable predictions regarding the rate of range expansion.

To understand how dispersal affects the evolution, population dynamics, and distribution of organisms, mathematical biologists have commonly employed models in which movement is represented by a simple diffusion process. These models have their origins in the studies of Fisher (1937) on the spread of novel mutations and Skellam (1951) on dispersal in animal populations. More recently, diffusion models have been applied to the spread of diseases, the invasion of exotic organisms, the efficiency of biocontrol agents, and the spread of transgenic genes (Weinberger 1978; Murray et al. 1986; Kareiva and Odell 1987; Manasse and Kareiva 1991). Although diffusion models represent one of the classic areas of mathematical biology (Toft and Mangel 1991), they are subject to criticism because diffusion is a simplified model of organism movement that entails assumptions based on conditions that no organism satisfies (Skellam 1973; Stinner et al. 1983; Turchin 1989). The most troubling are the assumptions that organisms proceed at infinite velocity along infinitely random paths. Although these are commonly cited objections, they sound misleadingly drastic. These assumptions are only realized on infinitesimal scales. On a practical scale, these assumptions have subtle implications: (1) The assumption of infinite velocity means there is some probability—albeit infinitesimal—that an organism will move an infinite

distance from its present position in an infinitely small amount of time. (2) The assumption of infinitely random paths (in other words, zero momentum) implies that the organism motion is unpredictable even on the shortest scales. In contrast, organisms can only move a finite distance in a finite amount of time, and, on smaller and smaller scales, organism movement becomes more and more predictable. In other words, organisms have finite velocity and inertia—the tendency to resist changes in direction.

To investigate the implications of these differences between biologically realistic motion and motion described by a diffusion model, I compared a diffusion model to another random-walk model, a telegraph model (Goldstein 1951; Okubo 1980). In the telegraph model, organisms have a finite velocity and tend to move in the direction in which they were previously moving; in other words, they have inertia. Although many models have been proposed to correct the deficiencies of the diffusion model, the telegraph equation represents a simple and fundamental alternative to diffusion that specifically allows one to address the impact of the assumptions of infinite velocity and zero momentum—two oft-cited objections to diffusion models.

I begin by discussing the random-walk models of animal movement upon which the diffusion and telegraph equations are based and compare the spatial distribution for a population of nonreproducing organisms that disperse according to these two movement models. Next, to model organisms invading unoccupied habitat, I develop a telegraph counterpart to the classical reaction-diffusion model (reaction refers to the local population change) and ask to what extent the “improved” telegraph description of movement changes predictions concerning pattern and rate of range expansion of invading organisms. Finally, because the differences between the models’ predictions depend on fundamental rates of movement and population growth, I compare the two models using biologically relevant parameters for a variety of species.

TELEGRAPH DISPERSAL

The simplest model of locomotion assumes that organisms make hops of fixed length and duration. At each jump, the organism randomly chooses a new direction. Such a model is called a simple random walk. If the jump length and duration are reduced toward zero, and, at the same time, the organism velocity is taken to infinity, this “random walk” leads to the simple diffusion model for the expected change in the population density of randomly dispersing organisms,

$$\frac{\partial S}{\partial t} = D \left[\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2} \right], \quad (1)$$

where S is the density of organisms at spatial coordinates x , y , and time t , and D , known as the coefficient of diffusion, is a measure of how quickly the organisms disperse.

If we assume instead that the organism has some tendency to jump in a direction similar to its previous direction, we have a correlated random walk, so named

because the direction of motion is correlated between jumps. This type of motion has also been described as a velocity jump process and a Poisson random walk (Dunbar and Othmer 1986; Othmer et al. 1988). Reducing the step length and duration toward zero and using a finite organism velocity, we obtain a special case of the telegraph equation (Goldstein 1951),

$$\frac{\partial S}{\partial t} = -\frac{1}{2\lambda} \frac{\partial^2 S}{\partial t^2} + \frac{\gamma^2}{2\lambda} \left[\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2} \right], \quad (2)$$

where γ is the organism's finite velocity and λ is the organism's rate of changing direction. Thus, the larger λ is, the less inertia the organism has. The derivation of equation (2) from a discrete correlated walk is straightforward and is analogous to the derivation of the diffusion equation from a discrete random walk (App. A).

In order to compare the predictions of diffusion versus telegraph dispersal, it is useful to focus on a summary statistic of an animal's movement. Following the lead of Skellam (1951) and Okubo (1980), I consider the mean squared displacement (MSD) for a population of organisms after time t has elapsed. I used the simplest constructions of the diffusion and telegraph equations in order to address the basic changes caused by the two models' contrasting descriptions of organism movement. I assumed a one-dimensional, homogeneous environment where D , γ , and λ are constant in time and space. In both these models, the organisms move independently of one another and have no preference to go in one particular direction; in other words, there is no drift.

The expected mean squared displacement for a population of organisms dispersing by simple diffusion in one dimension is

$$\text{MSD}_{\text{diff}} = 2Dt, \quad (3)$$

whereas, for a population dispersing according to the telegraph equation, it is

$$\text{MSD}_{\text{tele}} = \gamma^2 \left[\frac{t}{\lambda} - \frac{1}{2\lambda^2} (1 - e^{-2\lambda t}) \right]. \quad (4)$$

We can see the similarity of the two models by noting that, as t gets large, both equations predict a linear increase in the MSD. If we define D as $\gamma^2/2\lambda$ in the telegraph equation, MSD_{diff} and MSD_{tele} approach each other as t gets large. Indeed, the predictions regarding MSD_{diff} and MSD_{tele} are within 5% of each other by time $10.5/\lambda$. The best fit of the diffusion model to the telegraph model is $D = \gamma^2/2\lambda$.

Of course, mean squared displacement is not the only prediction of interest when modeling dispersal. In addition, plots of the frequency distribution of organisms about the central release point are commonly used to describe dispersal and gene flow. By examining the predicted frequency distribution, we gain a more detailed picture of the differences and similarities between diffusion and telegraph dispersal. These frequency distributions are obtained by solving the model by assuming that all the organisms are released at position $x = 0$ and time $t = 0$. The solution to the diffusion equation is a Gaussian distribution. The assumption

of infinite organism velocity is reflected in the infinite tails of the distribution. In figure 1, I contrast the frequency distributions of the two models. Note that the frequency distributions become similar as time increases and that the frontal edge of the telegraph frequency distribution is abrupt, unlike that for diffusion. The edge is abrupt because, in the telegraph model, the organisms move at the finite velocity, γ ; therefore, at time t , the maximum distance that an organism can be from the release point is γt . In contrast, organisms in the diffusion model have infinite velocity; thus, at any time t , some organisms can be an infinite distance from the release point.

COMPARISON OF REACTION-TELEGRAPH AND REACTION-DIFFUSION MODELS

To model reproducing and dispersing organisms, population growth must be added. The classical model of diffusion plus reproduction, known as "reaction diffusion," is

$$\frac{\partial S}{\partial t} = D \frac{\partial^2 S}{\partial x^2} + F(S), \quad (5)$$

where $F(S)$ is the population growth function and represents the instantaneous rate of change for a population in the absence of dispersal. Reaction-diffusion models have a long and extensive history (Fisher 1937; Skellam 1951; Levin 1974; Fife 1979; Okubo 1980; Murray 1989) and have been used to model the dispersal of such diverse species as sea otters (Lubina and Levin 1988), Neolithic farmers in Europe (Ammerman and Cavalli-Sforza 1971, 1984), muskrats (Skellam 1951), gray squirrels (Okubo et al. 1989), cabbage butterflies and cereal leaf beetles (Andow et al. 1990), Himalayan tahr (Caughley 1970), and a number of passerine birds (Hengeveld 1988; Okubo 1988).

When a population's growth is combined with telegraph dispersal, we obtain the following model, where $F(S)$ is the population growth rate as in equation (5),

$$\frac{\partial S}{\partial t} = -\frac{1}{2\lambda} \frac{\partial^2 S}{\partial t^2} + \frac{\gamma^2 S \partial^2 S}{2\lambda \partial x^2} + \frac{1}{2\lambda} \frac{\partial F}{\partial t} + F(S), \quad (6)$$

which I refer to as the reaction-telegraph model. It is important to note that equation (6) is not simply telegraph dispersal plus the population growth term. One cannot simply tack a population growth function onto the telegraph equation because the telegraph equation (2) includes the $\partial^2 S / \partial t^2$ term (App. A).

Using equations (5) and (6), one can ask at what rate invading organisms will spread upon being introduced into novel territory. The general approach is to search for traveling wave solutions to the models. A traveling wave of invading organisms moves through the environment in such a way that the invasion wave front never changes shape. Figure 2 shows typical traveling wave solutions. At time t , the plot of organism density versus the distance from the release point describes the wave front shape. At later times, the front has an identical shape but is shifted forward in space. I derive and discuss the speed of invasion in one dimension; however, this relates in a simple way to the two-dimensional invasion

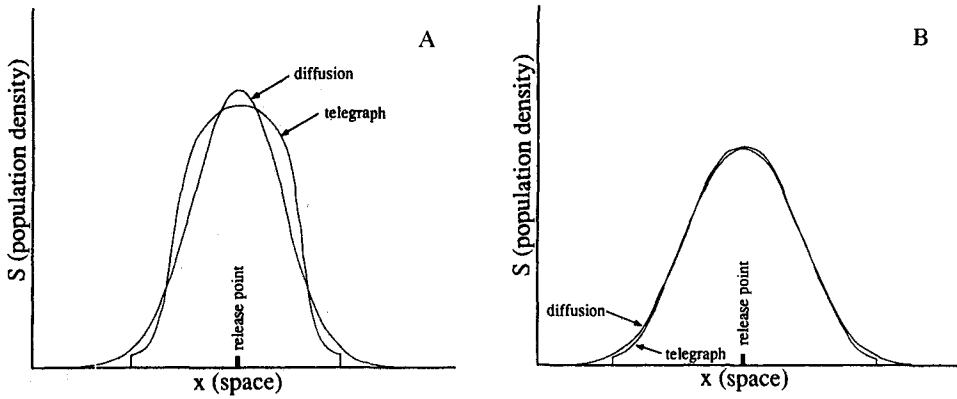


FIG. 1.—Comparison of dispersal from a central release point according to the telegraph and diffusion models ($\lambda = .7$, $\gamma = 1$). A, Five time units after release; B, 7.6 time units after release.

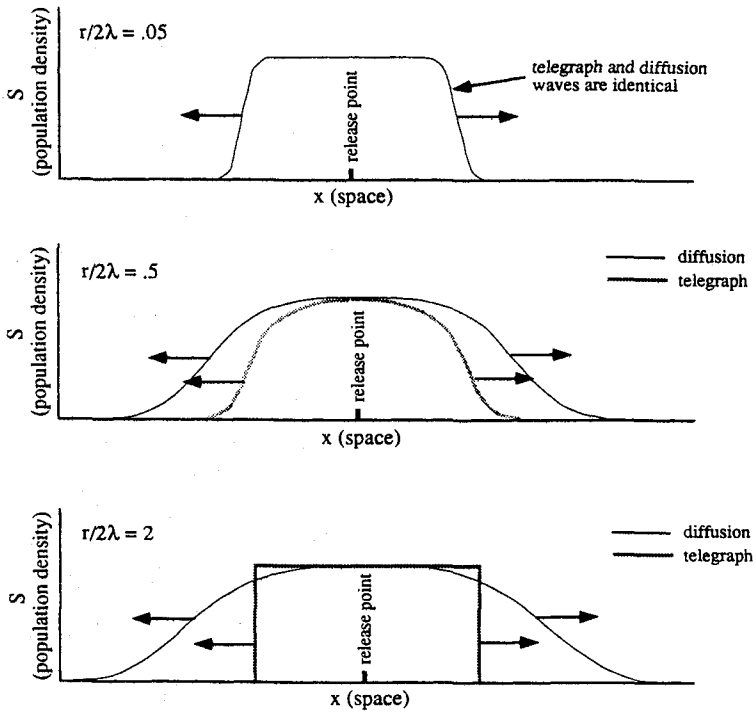


FIG. 2.—Traveling wave solutions to the reaction-telegraph and reaction-diffusion models for varying ratios of reproduction rate to reversal rate, $r/2\lambda$.

speed. When the invasion advances across a two-dimensional landscape in a straight wave front, the invasion velocity is the one-dimensional invasion velocity. When the front is curved outward, the invasion velocity is slower at the leading edge, so that the front gradually becomes straight until it again has the one-dimensional invasion velocity. When the front is curved inward, the velocity at the lagging edge is higher, so that the front also straightens and once straight has the one-dimensional velocity (Lewis and Kareiva 1993).

To calculate rates and patterns of invasion for the two models, I use simple logistic growth, $F(S) = rS(1 - S/K)$, for the population growth function. The "carrying capacity," or equivalently the equilibrium population size, is represented by K , and r is the intrinsic rate of increase. When we use this population growth function in the reaction-diffusion model, equation (5), we find that the invading organisms spread as a traveling wave of velocity. For all biologically reasonable releases of organisms, the velocity of the invasion wave asymptotically approaches the velocity, $\sqrt{4rD}$ (Fisher 1937; Kolmogoroff et al. 1937; Uchiyama 1978).

Using the logistic growth function in my reaction-telegraph model, equation (6), I found that traveling wave solutions also exist, and at the following velocities (App. B):

$$c_{\text{tele}}^2 \geq \frac{8r\lambda}{(r + 2\lambda)^2} \gamma^2 \quad \text{for } 0 < \sqrt{r/2\lambda} \leq 1 \quad (7)$$

$$\geq \gamma^2 \quad \text{for } \sqrt{r/2\lambda} \geq 1. \quad (8)$$

Numerical simulation of equation (6), with $0 < \sqrt{r/2\lambda} \leq 1$, indicates that the invasion waves travel at the minimum velocity. Under the conditions of equation (8), equation (6) resists numerical simulation because the solution is discontinuous; however, the maximum velocity of the organisms is γ , and the invasion speed certainly cannot be greater than speed of the individual organisms. Thus, the invasion waves of equation (8) must travel at γ . Which equation to use to predict the invasion velocity depends on the value, $r/2\lambda$. This critical factor is the ratio of the time to reverse direction over the time to produce a new individual.

If we substitute $D = \gamma^2/2\lambda$ (the best fit of diffusion to telegraph) into the equation for the reaction-diffusion wave velocity, $c_{\text{diff}}^2 = 4rD$, we can compare the wave velocities for the reaction-diffusion and reaction-telegraph models. One immediately obvious distinction between the wave velocities of the two models is the dependence on r . Whereas reaction-diffusion predicts a rate of spread that increases linearly with r , the reaction-telegraph model predicts a rate of spread that asymptotically approaches the organism velocity, γ , as r increases (fig. 3). This means that, for large r relative to λ , modeling locomotion by simple diffusion will lead to a gross overestimate of the expected velocity of invasion; whereas, for small r , the error is minor.

The disparity between the predicted traveling wave speeds can be summarized by the ratio

$$\frac{c_{\text{tele}}}{c_{\text{diff}}} = \frac{1}{(r/2\lambda + 1)}. \quad (9)$$

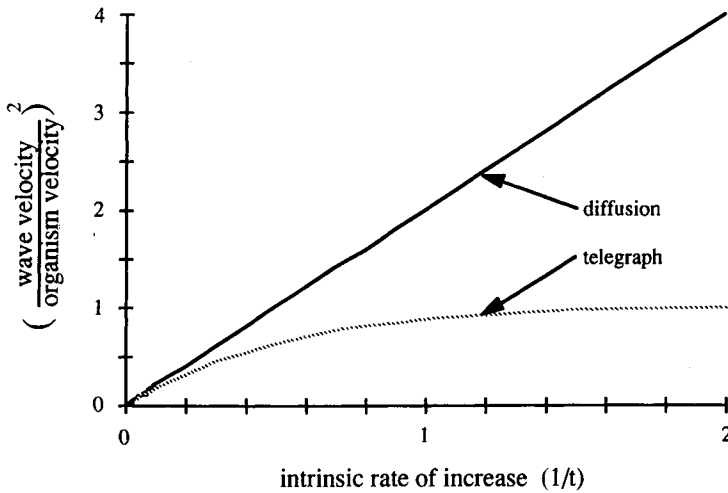


FIG. 3.—Traveling wave speed versus the reproductive rate for the reaction-telegraph and reaction-diffusion models ($\lambda = 1$).

For $r/2\lambda < .052$, the wave speeds are within 5% of each other, and for $r/2\lambda < .11$, the wave speeds are within 10% of each other.

Another way to compare the predicted wave speeds of diffusion and telegraph reaction is to consider the case in which one knows the mean squared displacement and the intrinsic rate of increase—the normal circumstance when applying such models to field data. The mean squared displacement gives a measure of D for diffusion and a measure of $\gamma^2/2\lambda$ for the telegraph equation. For organisms with differing speeds but with the same mean squared displacement, how do the predicted wave speeds compare? As the organisms' velocity increases, the organisms resemble randomly moving particles with infinite velocity, and the predicted wave speed approaches that for reaction diffusion (fig. 4).

The wave-front shapes of the reaction-telegraph and reaction-diffusion models also differ (fig. 2). The diffusion wave front broadens as r increases, whereas the telegraph wave front first broadens as r increases to moderate values and then steepens as r becomes very large. When r is greater than 2λ , the organisms are reproducing faster than they are reversing direction. As a result, they "pile up" at $x = \gamma t$, the maximum distance that the organisms can disperse from their release point by time t . The invasion wave, therefore, looks like a square wave when $r > 2\lambda$. In all cases, the telegraph equation predicts a steeper front than that predicted by the diffusion model.

COMPARISON OF TELEGRAPH DISPERSAL AND DIFFUSION WITH DATA

The theoretical analysis identifies some potentially dramatic disagreements between the reaction-diffusion and reaction-telegraph models of invading organisms. One key question is whether these differences commonly arise in nature.

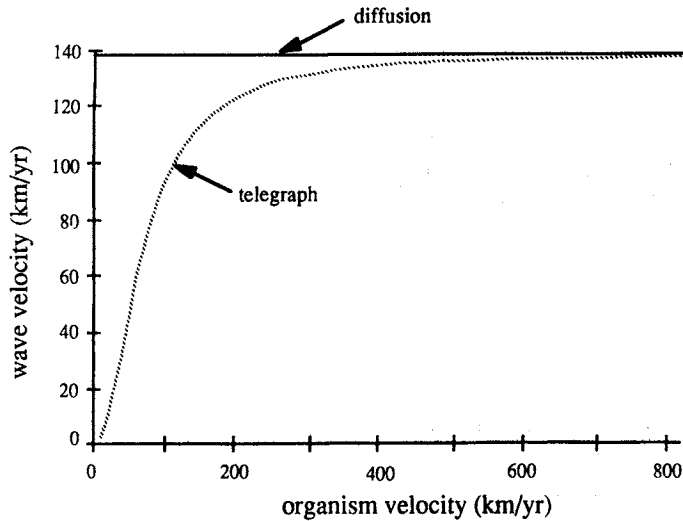


FIG. 4.—Comparison of the predicted wave speeds for reaction-telegraph and reaction-diffusion models given a fixed rD and $r\gamma^2/2\lambda$ ($r = .51/\text{yr}$ and $D = 9,402 \text{ km}^2/\text{yr}$). These values are typical for collared turtledoves. The average yearly velocity of collared turtledoves is at least 650 km/yr.

If organisms invariably have a higher ratio of the intrinsic rate of population increase to the rate of direction reversal, diffusion models are doomed to misrepresent organism spread. Conversely, if this ratio, given by $r/2\lambda$, is low, for example, $<.1$, the telegraph model will provide only minor improvement over the simple diffusion model. To compare the two models' performance on a variety of organisms, I calculated or otherwise obtained parameter estimates from the literature for the cabbage butterfly (*Pieris rapae*), rabies in red foxes (*Vulpes vulpes*), gypsy moths (*Lymantria dispar*), European starlings (*Sturnus vulgaris*), collared turtledoves (*Streptopelia decaocto*), and Black Death (*Yersinia pestis*). I sought organisms that disperse by a variety of mechanisms and that have high intrinsic rates of increase (since large rates of increase accentuate the dissimilarities between the two models).

Estimating Parameters

Rabies in foxes.—I calculated D and γ for rabies using data on three radio-collared rabid foxes in the wild (Andral et al. 1982). For D , I followed the formula by Murray et al. (1986):

$$D = \frac{1}{N} \sum_{j=1}^N \frac{(\text{straight line distance from the start})^2}{4 (\text{time from start})}, \quad (10)$$

which gives $D \approx 50 \text{ km}^2/\text{yr}$. Given that two of the three foxes died closer to their origin than their mean distance from it, Murray believes that this D is a lower bound. He calculates an upper bound using the maximum distance that one fox

traveled from its starting point, $D = (2.7 \text{ km})^2/4 (2 \text{ d}) \approx 330 \text{ km}^2/\text{yr}$. For the velocity, I used the average distance traveled per day, 9 km/d (Andral et al. 1982).

I calculated an upper bound for the exponential rate of increase of rabies by using the rate of rabies increase at the moment the disease enters the population (at this point, the susceptible population is at its maximum) and by assuming that foxes go directly from susceptible to rabid with no incubation period. With these assumptions, the rate of increase is

$$r = (\text{maximum rate at which susceptibles become rabid}) \\ - (\text{natural} + \text{disease-induced mortality rates}).$$

The maximum rate at which susceptibles become rabid is βS_0 , where β is the disease transmission coefficient and S_0 is the population density before infection (the maximum density of susceptibles). I obtained the disease transmission coefficient ($79.69 \text{ km}^2/\text{foxes} \cdot \text{yr}$), maximum density of susceptibles ($1 \text{ fox}/\text{km}^2$) and natural and disease-induced mortality rates ($.5 \text{ foxes}/\text{yr}$ and $73 \text{ foxes}/\text{yr}$) from Anderson et al. (1981).

Cabbage butterflies.—Jones et al. (1980) determined the average overland distance that a cabbage butterfly travels per day (700 m) and the mean distance flown in 1 d (450 m) and over a 16-d life span (2,000 m). On individual days, the butterflies tend to travel in a straight line; however, they travel in a random direction on each new day. Thus, while their movement is very directed on individual days, over several days, it resembles a random walk. To calculate D , I used the formula

$$D = \frac{2(\text{MD})^2}{\pi t}, \quad (11)$$

where MD is the mean distance traveled and t is the time during which this distance is covered. Following Andow et al. (1990), I converted the diffusion coefficients and overland velocity from daily to yearly by multiplying by the adult life expectancy (10–20 d) and the number of generations per year (three to seven). I also used Andow et al.'s (1990) low and high estimates for r (9 and 31.5/yr).

Collared turtledoves.—I estimated D from ring recovery data on the distance that offspring nest from their parents (Hengeveld 1989, p. 100). I calculated the mean displacement, MD, as

$$\text{MD} = \frac{\sum (\text{number of birds recovered}) \times (\text{distance from release site})}{(\text{total number of birds recaptured})}, \quad (12)$$

which gave 121.5 km, and used equation (11) with $t = 1 \text{ yr}$ to determine D . For γ , I used the maximum ring recovery distance after 1 yr (650 km). This is certainly an underestimate of the average overland distance traveled during dispersal. I calculated r from life table data (Hengeveld 1989, p. 100).

Gypsy moths.—Although adult gypsy moths are winged, they are mostly sedentary and the larvae are considered the dispersal agents. Long-distance dispersal of larvae after being carried to high altitudes by updrafts is well documented (Campbell 1981, p. 161); however, I consider the dispersal below the forest can-

opy—this is the mechanism for local dispersal from a tree. Weseloh (1985) calculated diffusion coefficients from mark release data for the first 5 d of a 10-d dispersal period. To convert this from daily to yearly, I multiplied by the length of the dispersal period (10 d) and by the number of generations per year (one). Weseloh never observed larvae more than 200 m from the release site. Thus, I used 200 m/yr as the maximum yearly velocity.

Data from yearly records of two gypsy moth infestations (Campbell 1981, p. 70) gives ratios of egg densities from year to year. At low egg densities, the ratios ranged from 10 to 1,000. If we assume that populations are growing exponentially at this time, the ratio of egg densities from one year to the next, $E_1/E_0 = e^r$. We can then determine r from $r = 1/t \ln E_1/E_0$, where t is the generation time (1 yr).

Starlings.—I estimated rD from range expansion maps (Wing 1943; Kendeigh 1974), using Skellam's (1951) relation

$$\sqrt{\pi R^2} = 2t(\pi rD)^{1/2}, \quad (13)$$

where R is the distance to the edge of the range. Skellam derived this relation for a two-dimensional random walk with exponential growth. A plot of the square root of the range area versus time will be linear, and the slope is $2(\pi rD)^{1/2}$. In the period from 1915 to 1930, the slope of the graph is 83.3 km/yr, which gives $rD = 552.2 \text{ km}^2/\text{yr}^2$. During early starling expansion, the birds were invading empty habitats where competition and crowding effects were limited, thus we can suppose that the growth was, in fact, exponential. To calculate the maximum yearly velocity, I used the maximum distance between overwintering sites in consecutive census periods (1,800 km in 9 yr; Hengeveld 1989, p. 40).

Black Death in humans.—I used Noble's (1974) rough estimate of D for humans infected with *Yersinia pestis* in 1347. He obtained D by roughly estimating that news and minor gossip spread 160 km in 1 yr. Thus, D is of order $\text{length}^2/t = 25,600 \text{ km}^2/\text{yr}$. He estimated the transmission rate to be $\beta = 1.024 \text{ km}^2/\text{yr}$ and the disease-induced mortality rate to be 15/yr (corresponding to a 2-wk infectious period). The population density was approximately 20 persons/ km^2 . Using the same method as for rabid foxes and ignoring the natural mortality, we have $r = 5.5/\text{yr}$. For comparison, measles, a highly infectious disease, has a value for r between 5/yr and 18/yr. If we assume that villages were on average 16 km apart, then, given that $D = 25,600 \text{ km}^2/\text{yr}$, the average yearly velocity traveling between villages was 1,600 km/yr (velocity $\approx D/\text{mean distance between villages}$) (Landahl 1953; Rashevsky 1968, p. 12).

Comparison of the Wave Speeds

Taking equation (9) and substituting $D = \gamma^2/2\lambda$, we obtain an equation with r , D , and γ for the ratio of the velocity of invasion predicted by the reaction-telegraph model to that predicted by the reaction-diffusion model:

$$\frac{c_{\text{tele}}}{c_{\text{diff}}} = \frac{1}{(rD/\gamma^2 + 1)}. \quad (14)$$

In table 1, the predicted invasion velocities of the two models are compared through the parameters for the above-mentioned organisms. It is striking that,

TABLE 1

PARAMETER ESTIMATES AND THE PERCENTAGE DIFFERENCE BETWEEN THE INVASION WAVE SPEED PREDICTED BY THE REACTION-TELEGRAPH AND REACTION-DIFFUSION MODELS

	r (1/yr)	D (km ² /yr)	γ (km/yr)	$\frac{C_{tele}}{C_{diff}}$	% Difference between Models
<i>Yersinia pestis</i>	5.0	25,600	1,600	.952	4.8
Cabbage butterfly (day)*	9.0	3.87	21	.927	7.3
Cabbage butterfly (day)†	31.5	18.05	98	.944	5.6
Cabbage butterfly (generation)*	9.0	.298	21	.994	.6
Cabbage butterfly (generation)†	31.5	1.39	98	.995	.5
Collared turtledove	.51	9,402	650	.989	1.1
European starling	. . . ‡	. . . ‡	200	.986	1.4
Fox rabies§	6.19	50	3,285	> .999	< .1
Fox rabies¶	6.19	330	3,285	> .999	< .1
Gypsy moth	7	4.57×10^{-5}	.2	.992	.8

* Adult life expectancy, 10 d; generations/year, three (a low intrinsic rate of increase).

† Adult life expectancy, 20 d; generations/year, seven (a high intrinsic rate of increase).

‡ For starlings, $rD = 552.2$ km²/yr.

§ Low diffusion coefficient.

¶ High diffusion coefficient.

for all of the cases, the diffusion model predicts invasion wave speeds that are very close to those predicted by the telegraph model. I deliberately chose examples in which diffusion was likely to fail, that is, organisms with high reproduction and low velocity; however, the greatest differences between the predicted wave speeds of the models were 7.3% and 5.6%. These worst cases occurred with cabbage butterflies when I used the daily movement parameters. During a single day, the butterflies move nearly in straight lines, but, each new day, they pick a new random direction in which to fly. Thus, over a generation, the movement is not directed. If, instead, movement parameters for a generation are used, the disparity between telegraph and diffusion wave speeds is less than 1%. For most suites of biologically meaningful parameters, the invasion velocity predictions of the reaction-diffusion model differed by less than 5% from the predictions of the reaction-telegraph model. Clearly these data do not support the need for the refinement of a correlated random-walk model if the question of interest involves predicting the rate of spread of invading organisms.

DISCUSSION

As a mechanistic model of animal movement, the diffusion model is highly unrealistic. It assumes that animals move infinitely randomly with infinite velocity. Despite this fact, the dispersal of intelligent animals with highly nonrandom movement and finite velocity may be well described by diffusion. Although an animal's dispersal pattern would be unlike a diffusion pattern shortly after dispersal begins, as time increases the pattern approaches a simple diffusion pattern (i.e., a Gaussian frequency distribution). When a diffusion model is used to describe mere dispersal, the assumptions of the model are reflected in the predic-

tion that some animals will move an infinite distance—albeit with an infinitely small probability—and that on small time scales an animal's movement is still unpredictable. These differences are not discernable if one chooses a large enough time scale. For example, for an animal moving in one dimension and changing direction three times per day, the predicted mean square displacements for diffusion and telegraph movement differ by only 5% after $10.5/(3/d) = 3.5$ d. When the diffusion approximation of an organism's movement is incorporated into more complex models—models that address not only dispersal but also, for example, the population dynamics and the interactions with other individuals or the environment—the impact of approximating an organism's movement by diffusion is not obvious. The dissimilarity between the diffusion model of locomotion and real organism locomotion can, in fact, create serious errors.

In this article, I examined the implications of using the diffusion approximation in the classic reaction-dispersal model for the invasion of reproducing organisms into unoccupied habitat. "Reaction" refers to the reproduction of the invading organisms. Using the classical diffusion equation and the telegraph equation, I examined the effect of dissimilar descriptions of organism locomotion on the predicted pattern and rate of invasion. The telegraph equation models organisms that move at finite velocities and whose direction from one step to the next is correlated. Without the reproduction term, the telegraph and diffusion models give almost identical dispersal patterns, after an initial transition period. With the reproduction term, both models show organisms moving into the new environment as an advancing traveling wave; however, the diffusion model predicts that the speed of invasion will increase without bound as the reproductive rate of the organism increases, while the telegraph model predicts that, as the reproductive rate increases, the velocity of the invasion wave increases to the organism maximum velocity and does not increase beyond that upper limit.

For organisms with a high rate of reproduction relative to their rate of changing direction, the diffusion model predicts much higher invasion velocities than those predicted by the telegraph model and would, therefore, be inappropriate for studying invasions by such organisms; however, for organisms with low ratios of reproductive rate to reversal rate, the two models give very similar invasion speeds. It is pertinent, therefore, to determine where parameter values for actual organisms fall between these two extremes. For this purpose, I extracted parameters from the literature for six species with high reproductive rates and a wide variety of dispersal mechanisms. In the cases in which movement was not extremely correlated, the speed of invasion calculated with the diffusion model was within 5% of that calculated by the telegraph model. In general, the difference was less than 2%. In the one case in which the animals' movement was extremely correlated (only 3.8 direction changes/d), the difference was still less than 8%. The examples I examined are typical for organisms with medium to high reproductive rates and moderate to low reversal rates. The motion of these organisms would be described as nonrandom (or highly nonrandom). Yet these results indicate that, for these examples, using a telegraph model, which allows finite organism velocity and nonrandom motion, offers minor improvement over the classic diffusion model, which assumes infinite organism velocity and completely

random motion. It is obvious that, while, theoretically, there can be significant errors from using the simple diffusion model to describe ecological invasions, these errors are small when using moderate biological parameters.

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APPENDIX A

DERIVATION OF THE TELEGRAPH AND REACTION-TELEGRAPH EQUATIONS

Before describing the derivation of the reaction-telegraph equation, I briefly review the derivation of the telegraph equation from a correlated random walk. The derivation of the telegraph equation is simpler than, yet analogous to, the derivation for the reaction-telegraph equation; thus, presenting the former will make the latter more obvious. Furthermore, by contrasting the two derivations, one can clearly see the effect of adding reproduction to the telegraph equation.

The derivation of the telegraph equation in one dimension is covered in mathematical detail by Goldstein (1951) and is also covered by Othmer et al. (1988); however, the following is adapted from Zauderer (1989). Imagine a large number of animals moving in a correlated walk on a line. The animals make steps of length, δ , and duration, τ . An animal continues in its previous direction with probability p and reverses direction with probability q . At all times, animals move with velocity γ . For small τ , $p = 1 - \lambda\tau$ and $q = \lambda\tau$, where λ is the rate of reversal. The reversal process can be thought of as a Poisson process with intensity λ .

Let $\alpha(x,t)$ be the density, at coordinate x at time t , of animals that arrived from the left. The definition of β is similar, except that it refers to animals that arrived from the right:

$$\alpha(x,t + \tau) = p\alpha(x - \delta,t) + q\beta(x - \delta,t) \tag{A1}$$

and

$$\beta(x,t + \tau) = p\beta(x + \delta,t) + q\alpha(x + \delta,t). \tag{A2}$$

We can use the Taylor series to expand equations (A1) and (A2) to obtain

$$\alpha + \tau\alpha_t + o(\tau) = p(\alpha - \delta\alpha_x + o(\delta^2)) + q(\beta - \delta\beta_x + o(\delta)) \tag{A3}$$

and

$$\beta + \tau\beta_t + o(\tau) = p(\beta + \delta\beta_x + o(\delta^2)) + q(\alpha + \delta\alpha_x + o(\delta)). \tag{A4}$$

The subscript x or t indicates the partial derivative with respect to x or t . Substituting $p = 1 - \lambda\tau$ and $q = \lambda\tau$ and taking the limit as δ and τ go to zero, we have

$$\alpha_t + \frac{\delta}{\tau}\alpha_x = \lambda\beta - \lambda\alpha = \alpha_t + \gamma\alpha_x \tag{A5}$$

and

$$\beta_t - \frac{\delta}{\tau}\beta_x = \lambda\alpha - \lambda\beta = \beta_t - \gamma\beta_x, \tag{A6}$$

where γ is the velocity. The density of animals at point x and time t is represented by $S(x,t)$; thus, $S(x,t) = \alpha(x,t) + \beta(x,t)$, since an animal must have arrived at point x from the left or the right.

After differentiating the sum of equations (A5) and (A6) with respect to t and differentiating the difference of equations (A5) and (A6) with respect to x after multiplying by γ , we obtain

$$(\alpha + \beta)_{tt} + \gamma(\alpha - \beta)_{xt} = 0 \quad (\text{A7})$$

and

$$\gamma(\alpha - \beta)_{xt} + \gamma^2(\alpha + \beta)_{xx} = -2\gamma\lambda(\alpha - \beta)_x. \quad (\text{A8})$$

Subtracting equations (A8) from (A7) and using the sum of equations (A5) and (A6), that is, $2\gamma\lambda(\alpha - \beta)_x = -2\lambda(\alpha + \beta)_x$, we arrive at the telegraph equation

$$S_{tt} - \gamma^2 S_{xx} + 2\lambda S_t = 0. \quad (\text{A9})$$

The derivation of the reaction-telegraph equation in one dimension from a correlated random walk is analogous to the above with a population growth term added. At each step, animals move as before, but also increase in number at the rate $F(S)$. As in the previous derivation, $\alpha(x,t)$ and $\beta(x,t)$ are the densities of animals that arrive at x from the left and right, respectively. After adding the growth term to the equations for α and β for a simple correlated walk (eqq. [A1] and [A2]), the new equations for α and β are

$$\alpha(x,t + \tau) = p\alpha(x - \delta,t) + q\beta(x - \delta,t) + \frac{1}{2}\tau F(S(x - \delta,t)) \quad (\text{A10})$$

and

$$\beta(x,t + \tau) = p\beta(x + \delta,t) + q\alpha(x + \delta,t) + \frac{1}{2}\tau F(S(x + \delta,t)). \quad (\text{A11})$$

In the interval, τ , $\tau F(S(x,t))$ animals are produced at time t at point x . The new animals have equal probability of going left or right, which leads to the $1/2$ in the above equations.

As in the derivation of the telegraph equation, we substitute $p = 1 - \lambda\tau$ and $q = \lambda\tau$, use the Taylor series to expand, and take the limit as δ and τ go to zero to obtain

$$\alpha_t + \gamma\alpha_x = \lambda\beta - \lambda\alpha + \frac{1}{2}F(S) \quad (\text{A12})$$

and

$$\beta_t - \gamma\beta_x = \lambda\alpha - \lambda\beta + \frac{1}{2}F(S), \quad (\text{A13})$$

where $\gamma = \delta/\tau$ is the animal velocity.

The $S(x,t)$ is composed of two parts, the density of animals that arrived from the left or the right and the density of newly produced animals (as a result of reproduction). Thus, $S(x,t) = \alpha(x,t) + \beta(x,t) + \tau F(S(x,t))$; however, since we take the limit as τ goes to zero, this reduces to $S(x,t) = \alpha(x,t) + \beta(x,t)$.

Now, as before, we differentiate the sum of equations (A12) and (A13) with respect to t and differentiate the difference of equations (A12) and (A13) with respect to x after multiplying by γ , to obtain

$$(\alpha + \beta)_{tt} + \gamma(\alpha - \beta)_{xt} = F_t(S) \quad (\text{A14})$$

and

$$\gamma(\alpha - \beta)_{xt} + \gamma^2(\alpha + \beta)_{xx} = -2\gamma\lambda(\alpha - \beta)_x. \quad (\text{A15})$$

Subtracting equation (A15) from (A14) and using the sum of equations (A12) and (A13), that is,

$$2\gamma\lambda(\alpha - \beta)_x = -2\lambda(\alpha + \beta)_t + 2\lambda F(S), \tag{A16}$$

we arrive at the reaction-telegraph equation,

$$\frac{\partial^2 S}{\partial t^2} + 2\lambda \frac{\partial S}{\partial t} = \gamma^2 \frac{\partial^2 S}{\partial x^2} + \frac{\partial F(S)}{\partial t} + 2\lambda F(S). \tag{A17}$$

Dunbar and Othmer (1986) also derived this equation for a velocity jump process with reproduction using a different approach. (Note, however, that their equation contains a slight error; $v_0 r(n)$ should be $2\lambda r(n)$.)

APPENDIX B

TRAVELING WAVE ANALYSIS OF THE REACTION-TELEGRAPH EQUATION

I use phase-plane analysis to determine the existence and minimum velocity of traveling wave solutions to the reaction-telegraph equation. Murray (1989) gives a clear summary of phase-plane analysis in his appendices. Haderler (1988) solved a similar telegraph equation by transforming the hyperbolic equation into a nonhyperbolic equation. His results on wave speeds are different because he used the approach of McKean (1975) and Dunbar and Othmer (1986) summarizing dispersal by the probability that the rightmost animal is to the right of x . In contrast, I summarize dispersal as the density of particles at x , following the approach of Fisher (1937) and Kolmogoroff et al. (1937).

Substituting a logistic growth function, $F(S) = rS(1 - S/K)$, into the general reaction-telegraph equation (A17), we have

$$\frac{\partial^2 S}{\partial t^2} + 2\lambda \frac{\partial S}{\partial t} = \gamma^2 \frac{\partial^2 S}{\partial x^2} + \frac{\partial}{\partial t} [rS(1 - S/K)] + 2\lambda rS(1 - S/K), \tag{B1}$$

where K is the ‘‘carrying capacity’’ or equilibrium population size, and r is the intrinsic rate of increase.

We can nondimensionalize the equation with the following substitutions:

$$t = t\sqrt{2r\lambda}, \quad x = x\frac{\sqrt{2r\lambda}}{\gamma}, \quad \text{and } S = S/K, \tag{B2}$$

giving a reaction-telegraph equation with only one parameter:

$$\frac{\partial^2 S}{\partial t^2} + \left(\rho - \frac{(1 - 2S)}{\rho}\right) \frac{\partial S}{\partial t} = \frac{\partial^2 S}{\partial x^2} + S(1 - S), \tag{B3}$$

where $\rho = \sqrt{2\lambda/r}$. In one dimension, ρ measures the ratio of the time to produce a new individual over the time to reverse direction.

To look for traveling wave solutions to equation (B3), we introduce the moving coordinate system $z = x - ct$, $c > 0$, which gives

$$c^2 \frac{\partial^2 S}{\partial z^2} - \left(\rho - \frac{(1 - 2S)}{\rho}\right) c \frac{\partial S}{\partial z} = \frac{\partial^2 S}{\partial z^2} + S(1 - S). \tag{B4}$$

We now have an eigenvalue problem to determine the values of c such that a nonnegative solution of S exists that satisfies $\lim_{z \rightarrow \infty} S(z) = 0$ and $\lim_{z \rightarrow -\infty} S(z) = 1$. Equation (B4) is equivalent to the system

$$\begin{aligned} \frac{\partial S}{\partial z} &= U \\ \frac{\partial U}{\partial z} &= \frac{1}{c^2 - 1} \left[(\rho^2 + 2S - 1) \frac{c}{\rho} U + S(1 - S) \right], \end{aligned} \tag{B5}$$

with singular points $(S, U) = (0, 0)$ and $(0, 1)$. From linear stability analysis the eigenvalues at the steady state points are

$$\begin{aligned} (0, 0) \quad \lambda_{\pm} &= \frac{1}{2} \left\{ \frac{(1/\rho - \rho)c}{1 - c^2} \pm \left[\frac{(1/\rho - \rho)^2 c^2}{(1 - c^2)^2} - \frac{4}{1 - c^2} \right]^{1/2} \right\} \\ (1, 0) \quad \lambda_{\pm} &= \frac{1}{2} \left\{ \frac{-(1/\rho + \rho)c}{1 - c^2} \pm \left[\frac{(1/\rho + \rho)^2 c^2}{(1 - c^2)^2} + \frac{4}{1 - c^2} \right]^{1/2} \right\}. \end{aligned} \quad (\text{B6})$$

In order for right-moving waves to be possible, strictly positive heteroclinic orbits must exist for which $\lim_{z \rightarrow \infty} S(z) = 0$ and $\lim_{z \rightarrow -\infty} S(z) = 1$. The eigenvalues indicate that such heteroclinic orbits can exist for

$$\text{Any } \rho \quad c^2 \geq 1 \quad (\text{B7})$$

$$\rho \geq 1 \quad c^2 \geq \frac{4}{(\rho + 1/\rho)^2}. \quad (\text{B8})$$

I used an ordinary differential equation solver to plot the phase-plane trajectories and showed that these orbits do exist for these parameter values.

The existence of these heteroclinic orbits indicates that traveling wave solutions exist but does not indicate what wave speeds are stable. To investigate the stability of these solutions, I numerically simulated equation (B1) to find the wave speeds that are stable to the small errors introduced by a numerical simulator. I was able to show that, for $\rho \geq 1$, traveling waves form and travel at the speed $\sqrt{4/(\rho + 1/\rho)^2}$.

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