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Discrete random walk model to interpret the dispersal parameters of organisms

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Abstract

Most models for describing the dispersal of organisms have been developed by using diffusion equations with a diffusion coefficient. These equations, however, do not yield information that is readily interpretable in biological terms, because the biological meaning of the diffusion coefficient is not always clear. Discrete random walk models, in which organisms move into adjacent positions by a specific probability, seem to be superior in their biological tractability, although they have not been as widely used as diffusion equations because of their mathematical intractability. We reconstructed discrete random walk models of one-dimension based on two assumptions: (1) moving organisms settle by a constant probability and (2) settled individuals are captured by traps by a constant probability. We also constructed a model that is applicable for a directional movement caused by environmental factors such as wind. We applied the model to a one-dimensional dispersal experiment on the ragweed beetle, *Ophraella communa* LeSage, an insect of the size of about 4 mm in adults. Both larvae and adults of this species preferably eat ragweed, *Ambrosia artemisiifolia* L. We planted ragweed plants at a place in a linear field of 100 m length and 20 m width. In mid August, adult beetles dispersed actively along the linear field to find new food plants after they almost defoliated ragweed plants. Assuming a non-directional random walk, we performed the linear regression, which indicated that the movement of the adult *O. communa* in this season is approximately described by a discrete random movement in which an individual travels next 10 m with a probability of 0.906 during its life. The dispersion parameter estimated by the Poisson regression was much larger than 1, indicating that there is a considerable amount of fluctuation in the probability of capture or in other parameters. It is shown that a similar model is also applicable to a situation in which individuals are directly removed by traps from the moving population before settlement.

Key words: Difference equation; Diffusion equation; *Ophraella communa*; Random

dispersal; Trap efficiency

1. Introduction

Quantitative evaluation of the dispersal ability of organisms is of critical importance in designing and evaluating management strategies for highly mobile insects (Turchin and Thoeny, 1993), as well as in predicting the spatial spread of invading organisms (Shigesada and Kawasaki, 1997). Most models for describing the dispersal of organisms have been developed using diffusion equations that are based on continuous random walk models. Various behaviour of movements has been incorporated into continuous differential models (Shigesada, 1980; Kareiva and Odell, 1987; Lewis and Kareiva, 1993; Lewis, 1994; Shigesada, et al., 1995; Kot, et al., 1996; Blackwell, 1997; Clark, et al., 1999; Shiyomi and Tsuiki, 1999; Okubo and Levin, 2001; Yamamura, 2002). In contrast, discrete random walk models are not as widely used, mainly because models with continuous variables are generally easier to solve analytically (Turchin, 1998). Let us consider the simplest case that M individuals disperse at random along a line, starting at position 0. Also suppose that the probability of leaving the dispersing population and settling down is a constant, independent of time and space. Let $n(x, t)$ and $f(x, t)$ be the density of moving individuals and that of settled individuals at a position, x , at a time, t , respectively. Then, we usually use differential equations to obtain $n(x, t)$ and $f(x, t)$:

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} - \delta n, \quad (1)$$

$$\frac{\partial f}{\partial t} = \delta n, \quad (2)$$

where δ is the rate of settlement, and D is the diffusion coefficient that measures the dispersal rate that has a dimension of distance²/time. By solving Eqs. (1) and (2), we

obtain the density of settled individuals at a position, x , which is denoted by $f_1(x)$, by a simple form (Okubo, 1980; Müller-Herold and Nickel, 2000):

$$f_1(x) = \frac{M}{2} \sqrt{\frac{\delta}{D}} \exp\left(-\sqrt{\frac{\delta}{D}} |x|\right). \quad (3)$$

For a two-dimensional model, the density of settled individuals at a distance, r , is given by:

$$f_2(r) = \frac{M\delta}{2\pi D} K_0\left(\sqrt{\frac{\delta}{D}} r\right), \quad (4)$$

where K_0 is a zero order modified Bessel function of the second kind (Broadbent and Kendall, 1953; Williams, 1961; Shigesada, 1980).

The shape of $f_1(x)$ and $f_2(r)$, is solely determined by $\sqrt{\delta/D}$. However, the numerical estimate of $\sqrt{\delta/D}$ is not readily interpretable in biological terms, since the biological meaning of the diffusion coefficient (D) is not clear (Turchin, 1998). Let us consider a discrete random walk in which the spatial step length is λ , and the time step is τ . In a limiting argument, one imagines a series of processes in which organisms make progressively smaller and more frequent steps: $\lambda \rightarrow 0$ and $\tau \rightarrow 0$. Then, the diffusion coefficient is defined by $D = \lim \lambda^2/\tau$, assuming that λ^2 goes to zero by the same order of magnitude as τ . However, there is no biological foundation about why we must take limits in such a strange way, apart from the trivial observation that any other way of taking limits will not lead to a diffusion equation (Turchin, 1998). The speed of the dispersing organisms is given by λ/τ . By substituting $D = \lambda^2/\tau$, we can describe the speed by D/λ . This quantity approaches infinity as λ approaches zero. Thus, we are implicitly assuming that the speed of the organisms is infinity in applying Eq. (1), although actual organisms have finite speed. In this respect, it may be preferable to use

a telegraph equation, in which we assume that organisms move at finite velocities and that the direction from one step to the next is correlated (Holmes, 1993). The telegraph and diffusion equations yield a similar pattern after an initial transition period.

However, a telegraph equation is not tractable in deriving an analytical solution of $f_1(x)$.

Parameters in a discrete random dispersal model are biologically more interpretable than those in a diffusion equation and a telegraph equation, since a discrete model does not rely on a limiting argument; it assumes that an organism moves by a fixed step length with a fixed probability. However, some arbitrariness may arise for the choice of step length in applying a discrete model. In this article, we show that a discrete random dispersal model in one dimension yields a $f_1(x)$ that is identical to Eq. (3), independent of the choice of step length. Thus, an arbitrary choice of step length does not influence the shape of $f_1(x)$. Therefore, a discrete random dispersal model enables us to obtain a more biologically tractable interpretation from Eq. (3) without forcing any artificial distortion. We applied the model to a dispersal experiment on the ragweed beetle, *Ophraella communa* LeSage.

2. Model

2.1. Non-directional movement

We considered a linear random walk with a step length of 1. Individuals are released at the origin ($x = 0$). Let us assume that an individual that entered a position settles by a constant probability at that position without emigrating from it. We first assume that the direction of movement is random; an individual moves to the right and left positions by an equal probability. Let d be the probability that an individual settles at a position, and s be the probability that an individual moves to the adjacent position during its life. If there is no artificial removal of individuals, s is equal to $(1 - d)$. Let M be the total number of individuals that are released at the origin. Let N_x be the

expectation of the cumulative number of entrances into position x , including multiple entrances by the same individual. Individuals that entered a position $(x + 1)$ enter the position x by a probability of $(s/2)$ if $x \geq 0$. Individuals that entered a position $(x - 1)$ enter the position x by a probability of $(s/2)$ if $x \geq 1$. Thus, we have the difference equation:

$$N_x = \frac{s}{2} N_{x-1} + \frac{s}{2} N_{x+1}. \quad (x = 1, 2, 3, 4, \dots) \quad (5)$$

The same equation holds for the negative range of x ($x = -1, -2, -3, \dots$). However, we have another relation around the origin of release ($x = 0$):

$$N_0 = \frac{s}{2} N_{-1} + M + \frac{s}{2} N_1, \quad (6)$$

since M individuals directly enter at this position. The general solution of a homogeneous difference equation such as Eq. (5) is given by

$$N_x = C_1 \beta_1^x + C_2 \beta_2^x, \quad (7)$$

where C_1 and C_2 are constants. β_1 and β_2 are the roots of the characteristic equation that is given by replacing N_{x-1} , N_x , and N_{x+1} in the difference equation by 1, β , and β^2 , respectively (Goldberg, 1958, p 136). In our case, the characteristic equation is given by

$$\beta = \frac{s}{2} + \frac{s}{2} \beta^2, \quad (8)$$

which yields the roots:

$$\beta_1 = \frac{1 - \sqrt{1 - s^2}}{s}, \quad (9)$$

$$\beta_2 = \frac{1 + \sqrt{1 - s^2}}{s} = \frac{1}{\beta_1}, \quad (10)$$

where $\beta_1 < 1$ and $\beta_2 > 1$. Conversely, we obtain

$$s = \frac{2\beta_1}{1 + \beta_1^2}. \quad (11)$$

N_x must converge to zero for $x \rightarrow \infty$ and $x \rightarrow -\infty$. Therefore, the appropriate solution has a form

$$N_x = \alpha\beta_1^x, \quad (x \geq 0) \quad (12)$$

$$N_x = \alpha\beta_2^x, \quad (x \leq 0) \quad (13)$$

where α is a constant. By substituting Eqs. (9) and (10) for Eq. (6) by using Eqs. (12) and (13), we obtain

$$\alpha = \frac{M}{\sqrt{1 - s^2}}. \quad (14)$$

Eqs. (12) and (13) can be expressed by

$$N_x = \alpha\beta_1^{|x|}. \quad (15)$$

Then, expectation of the cumulative number of individuals that settled at a position x , which is denoted by Z_x , is given by

$$Z_x = d\alpha\beta_1^{|x|}. \quad (16)$$

If we capture settled individuals (but not moving individuals) by a constant probability c , the expected number of individuals captured at the position x , which is denoted by T_x , is given by

$$T_x = cd\alpha\beta_1^{|x|}. \quad (17)$$

Let t_x be the observed number of individuals captured at the position x . Eq. (17) becomes a linear form about $|x|$ in a logarithmic scale. Hence, we can estimate the parameters by the linear regression assuming a model:

$$\ln(t_x) = \ln(cd\alpha) + |x|\ln(\beta_1) + e_{x1}, \quad (18)$$

where e_{x1} is an error that follows a normal distribution with constant variance. We obtain the estimates, $\hat{\beta}_1$ and $\widehat{cd\alpha}$, from the slope and intercept of the regression, respectively. Then, we obtain the estimate of s by substituting the estimate $\hat{\beta}_1$ for Eq. (11). If we have an estimate of M , we can estimate α by using Eq. (14). The probability of settlement, d , is estimated by $(1 - \hat{s})$.

We have some trouble performing the linear regression in a logarithmic scale when some data are equal to zero, since we cannot calculate the logarithm of zero. In such a case, we can use a nonlinear least squares method by assuming a model:

$$t_x = cd\alpha\beta_1^{|x|} + e_{x2}, \quad (19)$$

where e_{x2} is an error that follows a normal distribution with constant variance.

However, the variance of e_{x_2} usually decreases as the expected number of captures decreases, which contradicts the standard assumption in the least squares method. If the proportion of captured individuals is small, we can assume that t_x follows the Poisson distribution with a mean of T_x . In this case, we can use the maximum likelihood estimation based on the Poisson distribution. Fortunately, Eq. (19) becomes a linear form by using a logarithmic transformation as discussed before. Hence, we can use a generalized linear model for the estimation of parameters, where error distribution is the Poisson distribution and link function is the logarithmic link (McCullagh and Nelder, 1989). The probability of capture, c , will fluctuate in an actual field, and hence the expected number of captures, T_x , may fluctuate around the number predicted from the model. Then, it will be preferable to assume an overdispersed Poisson distribution in estimating the parameters.

2.2. Directional movement

If the wind is blowing in a specific direction, an advection movement occurs for the dispersal of insects; the probability of their moving to the right is then different from that for their moving to the left. Thus, some modifications are required for the above equations. Let p be the conditional probability that an individual moves to the right, given that it moves to an adjacent position. Then, Eqs. (5) and (6) are modified to

$$N_x = psN_{x-1} + (1-p)sN_{x+1} \quad (x = \dots, -3, -2, -1, 1, 2, 3, 4, \dots) \quad (20)$$

$$N_0 = psN_{-1} + M_0 + (1-p)sN_1 \quad (21)$$

By using a similar argument as that used above, we obtain Eqs. (12) and (13) with

$$\beta_1 = \frac{1 - \sqrt{1 - 4p(1-p)s^2}}{2(1-p)s} \quad (22)$$

$$\beta_2 = \frac{1 + \sqrt{1 - 4p(1-p)s^2}}{2(1-p)s} \quad (23)$$

By substituting Eqs. (22) and (23) for Eq. (21) by using Eqs. (12) and (13), we obtain

$$\alpha = \frac{M}{\sqrt{1 - 4p(1-p)s^2}} \quad (24)$$

Then, if we capture settled individuals after the dispersal period by a constant probability c , the expected number of captured individuals at the position x is given by

$$T_x = cd\alpha\beta_1^x \quad (x \geq 0) \quad (25)$$

$$T_x = cd\alpha\beta_2^x \quad (x \leq 0) \quad (26)$$

By solving Eqs. (22) and (23), we obtain

$$s = \frac{1 + \beta_1\beta_2}{\beta_1 + \beta_2}, \quad (27)$$

$$p = \frac{\beta_1\beta_2}{1 + \beta_1\beta_2}. \quad (28)$$

We can obtain the estimates, $\widehat{cd\alpha}$, $\hat{\beta}_1$, and $\hat{\beta}_2$ by using Eqs. (25) and (26). Then, we can estimate s and p by using Eqs. (27) and (28). If we have an estimate of M , we can obtain the estimate $\hat{\alpha}$ by using Eq. (24).

3. Example

We applied the above model to a dispersal experiment on the ragweed beetle,

Ophraella communa LeSage, an insect of the size of about 4 mm in adults. Both larvae and adults of this species preferably eat ragweed, *Ambrosia artemisiifolia* L. The ragweed beetle was unintentionally introduced into Japan recently; it was first found in 1996 in Chiba prefecture (Takizawa, et al., 1999), and the range of distribution is currently expanding year by year (Moriya and Shiyake, 2001). We used a linear field to evaluate the dispersal ability in one dimension (Fig. 1). Ragweed seeds were drilled with 1m spacing in a plot (10×20 m) in early spring in 1999. Wild overwintering adults immigrated into the ragweed field from late April to May, and reproduced in an exponential manner. The ragweed plants were almost defoliated in mid-August when the third and fourth generation adults emerged. Then, adult beetles dispersed actively along the linear field to find new food plants. We placed ragweed plants (about 30 cm in height) as trap plants at 10 m intervals from the edge of the ragweed field along two lines (Fig. 1) at 17 o'clock on 19 August, 1999. Afterwards, adult beetles around the trap plants walked onto the plants to eat them. One hour later, we brought these plants to the laboratory and counted the number of beetles on the plants. We assumed that the trees along the field formed a reflecting barrier for the dispersal. Although the south end of the field will also be a reflecting barrier, we used Eq. (17) as an approximation. We cannot evaluate the directionality in movement in our experimental field since we placed traps only in one-direction. If we place traps in both direction in a linear field, we will be able to evaluate the directionality in movement by using Eqs. (25) and (26).

Observed $\ln(t_x)$ decreased approximately linearly with increasing distance from the ragweed field within 100 m (Fig. 2). The linear regression based on Eq. (18) yielded a relation:

$$\ln(T_x) = 8.182 - 0.451 x. \quad (r^2 = 0.910) \quad (29)$$

where x is distance measured by 10 m unit. The standard errors were 0.311 and 0.050

for the intercept and slope, respectively. Then, we obtain $\hat{\beta}_1 = \exp(-0.451) = 0.637$. By substituting $\hat{\beta}_1 = 0.637$ for Eq. (11), we obtain $\hat{s} = 0.906$. It indicates that the movements of adult *O. communa* are described by a random movement in which an individual travels a distance of next 10 m by a probability of 0.906 during its life. The estimates (\pm asymptotic SE) based on the nonlinear regression using Eq. (19) were $\widehat{cd\alpha} = 3686 \pm 884$ and $\hat{\beta}_1 = 0.675 \pm 0.073$. In this case, we obtain an estimate, $\hat{s} = 0.927$. We used the Marquardt method in the procedure NLIN of SAS for this calculation (SAS Institute, 1989). The maximum likelihood estimates based on the Poisson distribution were

$$\ln(T_x) = 8.378 - 0.473 x. \quad (30)$$

The asymptotic standard errors adjusted by the dispersion parameter were 0.240 and 0.076 for the intercept and slope, respectively. In this case, we obtain an estimate, $\hat{s} = 0.898$. The dispersion parameter was 11.93, which was much larger than 1, indicating that there is a considerable amount of fluctuation in the probability of capture or in other parameters. We used the procedure GENMOD of SAS for this calculation (SAS Institute, 1997).

4. Discussion

The distribution of settled individuals that was derived from a discrete random dispersal model (Eq. 16) has the same form as that derived from a diffusion equation (Eq. 3). However, Eq. (16) enables an interpretation that is biologically more tractable than Eq. (3). The parameter β_1 in Eq. (16) is interpreted as the probability of movement by using Eq. (11), whereas the parameter $\sqrt{\delta/D}$ in Eq. (3) is not readily interpretable. Although we used 10 m as the step length in the above example for simplicity, it will be

preferable to adopt a step length based on biological observations. For example, in the case of the flight movement of the female small white butterfly, *Pieris rapae crucivora*, 1.3 m will be a reasonable step length when we describe the movement in densely planted cabbage fields (Yamamura, 1999).

In several mark-release experiments, we sometimes used traps that continuously removed the dispersing organisms during the dispersal period (e.g., Wakamura, et al., 1992; Miyatake, et al., 2000). The probability of movement (s) becomes smaller near a trap, since individuals captured by traps cannot move to adjacent positions. If traps are placed uniformly in a lattice pattern, the probability of movement will uniformly decrease, keeping s independent of time and space. Hence, Eqs. (12) and (13) hold in this situation. Then, the expected number of individuals captured at a position x is given by

$$T_x = g\alpha\beta_1^{|x|}, \quad (31)$$

where g is a probability that an individual entered at a position is captured by traps. We can estimate s and g by a similar manner as described before. Let us assume that organisms that escape trapping move to adjacent positions by a constant probability ($1 - d$). Then, we have a relation: $s = (1 - g)(1 - d)$. Hence, we can estimate d by $(1 - \hat{g} - \hat{s}) / (1 - \hat{g})$. By substituting the estimate of d for Eq. (16), we obtain the distribution of Z_x . Thus, we can predict the natural distribution of settled individuals from an artificial distribution of trap catches that is obtained from a release experiment.

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Figure legends

Fig. 1. Experimental field for evaluating the dispersal distance of adult *Ophraella communa*. Circles indicate the position of trap plants (ragweed) that were placed at 10 m intervals from the edge of the ragweed field.

Fig. 2. Number of individuals captured by the trap plants, showing the spatial distribution of the density of settled individuals. Circles show the sum of captures on two trap plants placed at the same distance. Linear regression based on Eq. (18) is shown.

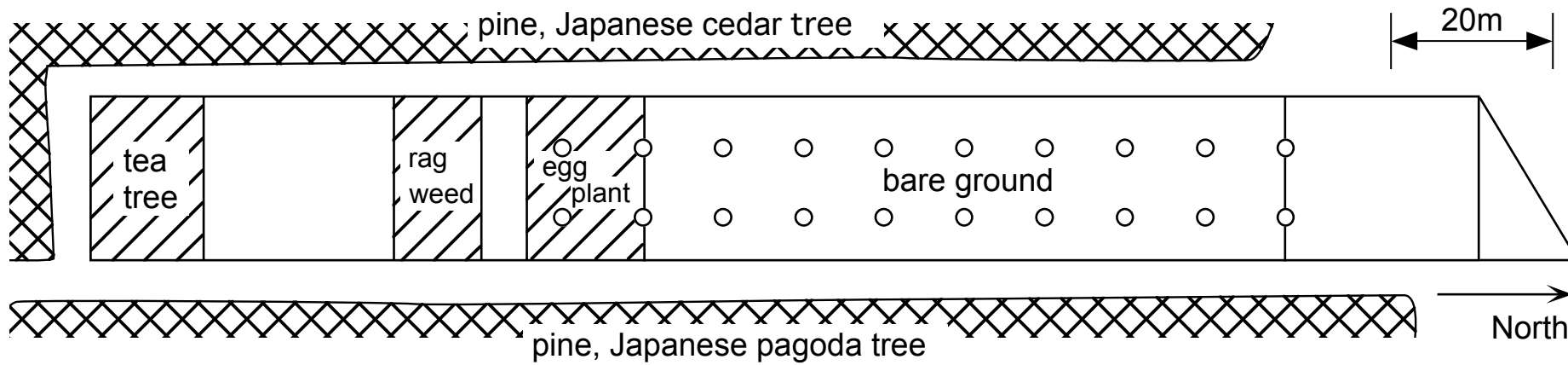


Figure 1
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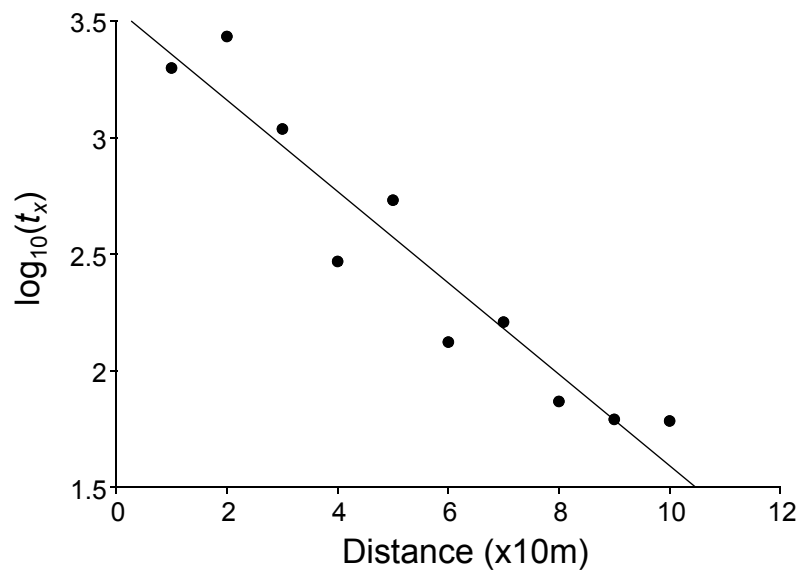


Figure 2
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