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Dispersal distance of heterogeneous populations

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Abstract Heterogeneity among individuals in a population is one of the important factors that influence the rate of population spread. To incorporate the population heterogeneity into dispersal rate, we assume that the traveling duration varies following a gamma distribution with a shape parameter k, where $(1/k)$ indicates the heterogeneity in the traveling duration. The resultant distribution of the traveling distance, which is called dispersal function, is then expressed by using a modified Bessel function of the second kind of order $(k - 1)$. It is shown that the front of the distribution spreads with time in an accelerated manner during an early phase of expansion if the heterogeneity is sufficiently large, which is consistent with the results from previous studies of biological invasions. By using the data obtained from mark–recapture experiments using traps, we can obtain the maximum likelihood estimates of three parameters: heterogeneity in the traveling duration, which is defined by $(1/k)$; the mean dispersal ability, which is defined by the product of the diffusion coefficient and the mean traveling duration; and the trap efficiency. The usefulness of this model is shown by using the data of mark–recapture experiments with the common cutworm, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae).

Key words Biological invasion · Diffusion equation · Gamma distribution · Maximum-likelihood estimation · Spatial expansion · *Spodoptera litura*

Introduction

Quantitative evaluation of the dispersal ability of organisms is critically important 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). Skellam (1951) analyzed the spread of an invading species when growth is Malthusian, showing that the rate of spread is approximately constant. However, this prediction does not always match the data. Andow et al. (1990, 1993) have shown that several species, such as the rice water weevil (*Lissorhoptrus oryzophilus*), expand the range of distribution in an accelerated manner, suggesting the importance of macroscale jumps provided by air currents or human transport. The asymptotic rate of spread generally depends on the probability distribution of the dispersal distance (i.e., dispersal function) and the reproduction rates of individuals. Kot et al. (1996) have suggested that the rate of spread changes, depending critically on very long distance dispersal events, that is, on the length of the tails of the dispersal function. Long tails of the dispersal function can occur due to several factors, one of which is heterogeneity in the dispersal tendencies within population.

To incorporate the population heterogeneity into dispersal rate, Inoue (1978) assumed that a dispersing population consists of two subpopulations that have different diffusion coefficients. For describing the dispersal function of each subpopulation, he used a bivariate normal distribution, which is yielded when a population randomly moves in a two-dimensional space for a fixed traveling duration. In describing the dispersal of stream fish, Skalski and Gilliam (2000) also assumed two subpopulations, i.e., “fast fish” and “slow fish.” For describing the dispersal function, they used a univariate normal distribution, which is yielded when a population randomly moves along a line for a fixed traveling duration. In describing the long-range movement of a checkered beetle, *Thanasimus dubius*, Cronin et al. (2000) also assumed two subpopulations, i.e., slow-moving and fast-moving form. For describing the dispersal function of each subpopulation, they used an approximated equation for zero-order modified Bessel function of the second kind, which is yielded when a population randomly moves in a two-dimensional space with a constant rate of settlement. Although these authors assumed that the dispersing population consists of only two subpopulations, the population

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may actually consist of three or more subpopulations that have different dispersal tendencies. It is therefore reasonable to assume that the dispersal tendencies of individuals vary, following a probability distribution. Clark et al. (1999) incorporated the heterogeneity into the diffusion model by implicitly assuming that the inverse of traveling duration follows a gamma distribution. In this article, we incorporate the heterogeneity in another way; we assume that the traveling duration varies following a gamma distribution. The model is applied to the data of mark-recapture experiments with the common cutworm, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae), conducted by Wakamura et al. (1990, 1992).

Model

Let us assume that the movement of individuals follows a Brownian random motion, the rate of which is invariant in time and space. We assume that the behavior of individuals is mutually independent. The number of individuals at time t at coordinate (x,y), which is denoted by $n(x,y,t)$, is then described by a partial differential equation (Okubo 1980; Shigesada and Kawasaki 1997):

$$\frac{\partial n(x,y,t)}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) \tag{1}$$

where D is the diffusion coefficient measuring the dispersal rate with units (distance^2/time). When n_0 individuals are released at time 0 from the origin (0,0), the solution is given by

$$n(x,y,t) = \frac{n_0}{4\pi Dt}\exp\left[-\frac{(x^2+y^2)}{4Dt}\right] \tag{2}$$

which is a bivariate normal distribution with mean zero, correlation coefficient zero, and variance $2Dt$ in each variate. Let us denote the distance from the origin by $r = \sqrt{x^2+y^2}$. Equation 2 can then be rewritten in a simpler form:

$$n(r,t) = \frac{n_0}{4\pi Dt}\exp\left[-\frac{r^2}{4Dt}\right] \qquad (r \geq 0) \tag{3}$$

Let us first assume that the traveling individuals settle at a position by a rate λ, which is independent of time, space, and the density of individuals. The probability distribution of the traveling duration, which is denoted by $p(t)$, is then given by an exponential distribution:

$$p(t) = \lambda\exp(-\lambda t) \tag{4}$$

The expected number of settled individuals at a distance r, which is denoted by $f(r)$, is given by the following equation because we are assuming that the behavior is independent of the density of individuals.

$$f(r) = \int_0^\infty n(r,t)p(t)dt = \frac{n_0\lambda}{2\pi D}K_0\left(r\sqrt{\frac{\lambda}{D}}\right) \tag{5}$$

where $K_0(\cdot)$ is a modified Bessel function of the second kind of order zero (Broadbent and Kendall 1953; Williams 1961; Shigesada 1980). The shape of $f(r)$ is solely determined by $\sqrt{\lambda/D}$.

If the probability of settlement is not a constant that is invariant in time and space, the probability density function of traveling duration will have a larger variance than that of an exponential distribution. We should use a more flexible distribution to describe such distributions. Yasuda (1975), studying the dispersal of human beings, used a gamma distribution:

$$p(t) = \frac{\lambda}{\Gamma(k)}(\lambda t)^{k-1}\exp(-\lambda t) \tag{6}$$

where k and λ are the shape parameter and scale parameter, respectively. Equation 6 reduces to the exponential distribution (Eq. 4) when $k = 1$. The mean and variance are given by k/λ and k/λ^2, respectively. The variance of a gamma distribution is larger than that of the exponential distribution with the same mean if k is smaller than 1. Therefore, we can use $(1/k)$ as an index of heterogeneity in the dispersal duration. The quantity of $(1/k)$ will be larger than 1 in many cases because of heterogeneity, but it will sometimes be smaller than 1 if the probability of settlement becomes larger after a specific duration due to the consumption of traveling energy. If the behavior of individuals is mutually independent (i.e., density independent), the expected number of settled individuals at a distance r is given by

$$f(r) = \int_0^\infty n(r,t)p(t)dt = \frac{n_0}{2^k\pi\Gamma(k)}\left(\sqrt{\frac{\lambda}{D}}\right)^{(k+1)} r^{(k-1)}K_{(k-1)}\left(r\sqrt{\frac{\lambda}{D}}\right) \tag{7}$$

where $K_{(k-1)}(\cdot)$ is a modified Bessel function of the second kind of order $(k - 1)$, which can be described by an integral form:

$$K_\nu(z) = \int_0^\infty \cosh(\nu t)\exp[-z\cosh(t)]dt \tag{8}$$

We define the mean dispersal ability, which is denoted by m, by multiplying the mean traveling duration and the diffusion coefficient: $m = Dk/\lambda$. Equation 7 is then rewritten as

$$f(r) = \frac{n_0}{2^k\pi\Gamma(k)}\left(\frac{k}{m}\right)\left(r\sqrt{\frac{k}{m}}\right)^{(k-1)}K_{(k-1)}\left(r\sqrt{\frac{k}{m}}\right) \tag{9}$$

When $(1/k)$ equals 1, Eq. 9 reduces to Eq. 5, where (λ/D) is replaced by $(1/m)$. If all individuals settle just after traveling for the same duration, $(1/k)$ becomes zero, keeping the mean traveling duration constant. In such a case, Eq. 9 reduces to Eq. 3 where Dt is replaced by m. The mean dispersal distance and mean squared distance in Eq. 9 are given by

$$E(r) = \frac{1}{n_0}\int_0^\infty r\cdot 2\pi r f(r)dr = \sqrt{\frac{m}{k}}\frac{\sqrt{\pi}\,\Gamma(k+0.5)}{\Gamma(k)} \tag{10}$$

$$E\left(r^2\right) = \frac{1}{n_0}\int_0^\infty r^2 \cdot 2\pi r f(r)\,dr = 4m \tag{11}$$

where E indicates the expectation.

It is convenient to use an approximation for Eq. 9, as the calculation of a Bessel function is sometimes troublesome. A modified Bessel function is approximately given by the following formula if z is large (see Jeffrey 2000, for example):

$$K_v(z) \approx \sqrt{\frac{\pi}{2z}}\exp(-z) \tag{12}$$

Exact equality holds for $v = -0.5$ and 0.5. By using Eq. 12, Turchin and Thoeny (1993) derived an approximation of Eq. 5:

$$f(r) \approx \frac{n_0}{\sqrt{8\pi r}}\left(\frac{\lambda}{D}\right)^{0.75}\exp\left(-r\sqrt{\frac{\lambda}{D}}\right) \tag{13}$$

In a similar way, we obtain an approximation of Eq. 9:

$$f(r) \approx \frac{n_0}{2^k\sqrt{2\pi}\,\Gamma(k)}\left(\frac{k}{m}\right)\left(r\sqrt{\frac{k}{m}}\right)^{(k-1.5)}\exp\left(-r\sqrt{\frac{k}{m}}\right) \tag{14}$$

Several authors have indicated the usefulness of an empirical equation, a generalized gamma distribution (Taylor 1980; Portnoy and Willson 1993; Turchin 1998):

$$f(r) = \alpha r^{-\varepsilon}\exp\left[-(r/\beta)^{\gamma}\right] \tag{15}$$

where $\alpha, \beta, \varepsilon$, and γ are constants. Equation 14 corresponds to a special case of Eq. 15 where $\beta = \sqrt{m/k}$, $\varepsilon = 1.5 - k$, and $\gamma = 1$.

Figure 1 shows examples of the dispersal function given by Eq. 9 for $(1/k) = (2/3)$, 1, and 2. It seems that the approximation by Eq. 14 is satisfactory when $(1/k)$ lies between (2/3) and 2. The curve for $(1/k) = 2$ has a much larger density than the curve for $(1/k) = 1$ in a large distance range, although these curves resemble each other in a small distance range.

Rate of spread

The expansion rate of the front of distribution is calculated by a simple manner in the foregoing model. For simplicity, let us assume that each settled individual yields R_0 adults of the next generation at the settled position. Also assume that

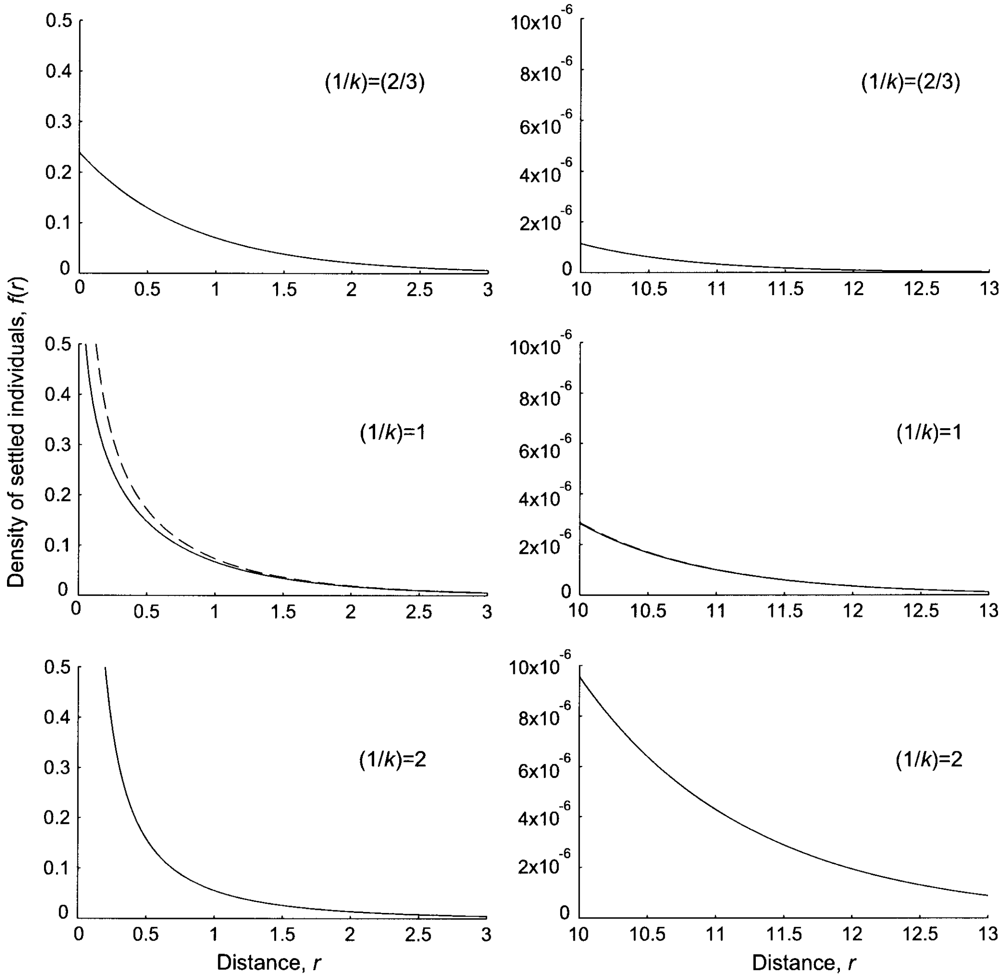

Fig. 1. Examples of the dispersal function for small (*left figures*) and large distances (*right figures*). *Solid curves* indicate the curves given by Eq. 9; *broken curves* indicate the approximation given by Eq. 14. $n_0 = 1$; $m = 1$. Equation 14 coincides exactly with Eq. 9 for $(1/k) = (2/3)$ and 2

the traveling duration of new adults independently follows Eq. 6. We again assume that k, λ, and D are invariant in time and space. For simplicity, we ignore the density-dependent effects that may occur during the process of dispersal, although several authors have indicated the potential importance of these effects (Shigesada 1980; van den Bosch et al. 1990; Mollison 1991; Lewis and Kareiva 1993; Wang et al. 2002). Due to the reproducibility in the convolution integrals of a gamma distribution, the distribution of the cumulative traveling duration from generation 1 to generation τ, which is denoted by $p_\tau(t)$, is given by a gamma distribution with a shape parameter τk and a scale parameter λ:

$$p_\tau(t)=\frac{\lambda}{\Gamma(\tau k)}(\lambda t)^{\tau k-1}\exp(-\lambda t) \qquad (16)$$

We can then simply obtain the density of individuals at a distance r after reproduction of the τ generation by multiplying $n_0R_0^\tau$ by the proportion of individuals settling at the distance r after traveling the cumulative duration. Let n_c be the critical density of individuals that is detected. Then, by replacing k and n_0 in Eq. 9 with τk and $n_0R_0^\tau$, respectively, we obtain the distance between the origin and the dispersal front after reproduction of the τ generation by numerically solving the following equation for r:

$$\frac{n_0R_0^\tau}{2^{\tau k}\pi\Gamma(\tau k)}\left(\frac{k}{m}\right)\left(r\sqrt{\frac{k}{m}}\right)^{(\tau k-1)}K_{(\tau k-1)}\left(r\sqrt{\frac{k}{m}}\right)=n_c \qquad (17)$$

Figure 2 indicates the expansion of front calculated by using the FindRoot function of Mathematica (Wolfram 1996). The upper graph in Fig. 2 indicates that the front expands in an accelerated manner if the heterogeneity is sufficiently large, which is consistent with the field observation indicated by Andow et al. (1990, 1993). However, the rate of spread approaches a constant in the later phase of expansion, as shown in the lower graph in Fig. 2. The asymptotic rate of population expansion is larger in a population with higher heterogeneity (larger $1/k$) even if the mean dispersal ability (m) is the same, that is, even if the diffusion coefficient (D) and mean traveling duration (k/λ) are the same. We estimated the asymptotic rate of expansion per generation by the linear regression for the results from 10001 to 10010 generations for $m = 1$ and $R_0 = 2$. The estimates for $(1/k) = 1, 10, 20$, and 50 were 1.899, 3.019, 3.809, and 5.463, respectively. We further estimated the asymptotic rate of expansion for other combinations of the reproduction rate (R_0) and the heterogeneity in dispersal duration ($1/k$) for $m = 1$ (Fig. 3). The actual population process will be influenced by the population density in fields. Hence, our estimates in Fig. 3, which are based on density-independent assumptions in Eqs. 7 and 17, may be biased. According to the "linear conjecture," however, the rate of spread predicted from a density-independent model will be a good approximation for that of the corresponding density-dependent model in several situations (van den Bosch et al. 1990; Mollison 1991; Kot et al. 1996). The approximation seems valid if (i) the rate of reproduction of an individual in

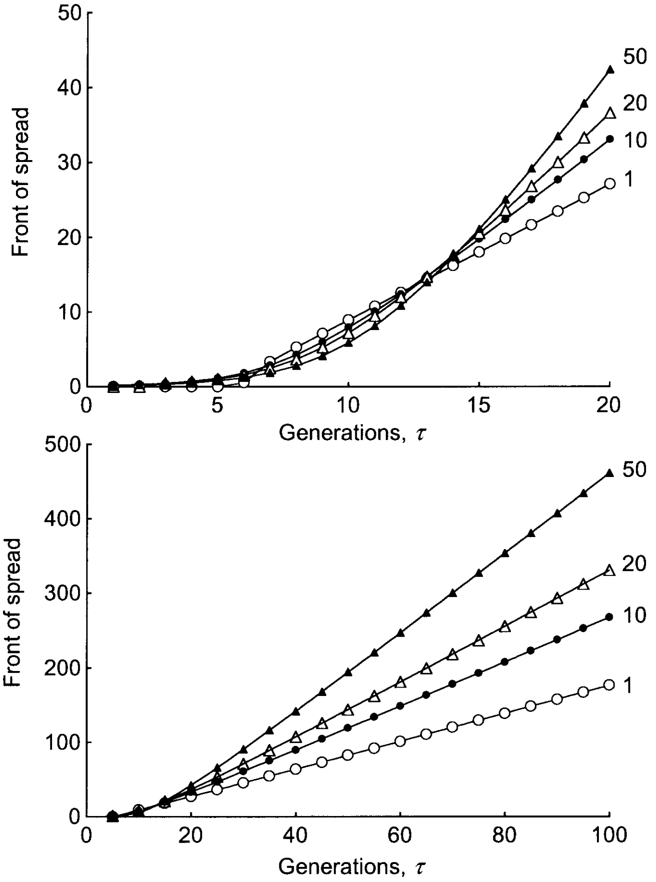

Fig. 2. Expansion of the distribution front calculated by using Eq. 17. The *numbers beside the curves* indicate the heterogeneity in the traveling duration ($1/k$) used in the calculation. $n_0 = 1$; $n_c = 1$; $R_0 = 2$; $m = 1$. *Upper graph*: accelerated increase in an early stage of expansion. *Lower graph*: constant increase in a later stage of expansion

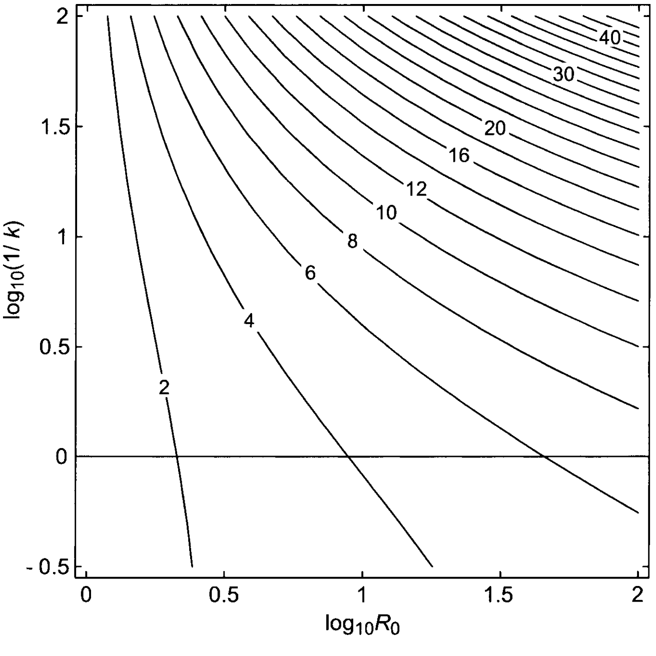

Fig. 3. Influence of the reproduction rate (R_0) and the heterogeneity in dispersal duration ($1/k$) on the asymptotic rate of spread. *Contours* of the rate of spread per generation are shown at intervals of two for $m = 1$

an occupied environment always less than the rate of reproduction in a virgin environment (i.e., no Alle effect), and (ii) the influence of an individual on the environment very far from its present position is negligible (van den Bosch et al. 1990).

van den Bosch et al. (1990) indicated that the asymptotic rate of range expansion that is denoted by C is obtained analytically by solving the following equations about a characteristic function $L(C,\psi)$:

$$L(C,\psi) = 1 \qquad \frac{\partial L(C,\psi)}{\partial \psi} = 0 \tag{18}$$

The characteristic function $L(C,\psi)$ is defined by

$$L(C,\psi) = R_0 \int_{-\infty}^{\infty} \exp(-\psi C + \psi x) f_1(x) dx \tag{19}$$

where $f_1(x)$ is the marginal distribution of $f(r)$. Let us consider a one-dimensional random movement to derive $f_1(x)$. The number of individuals at time t at x, which is denoted by $n(x,t)$, is described by

$$\frac{\partial n(x,t)}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2}\right) \tag{20}$$

When n_0 individuals are released at time 0 from origin, the solution is given by

$$n(x,t) = \frac{n_0}{2\sqrt{\pi D t}} \exp\left[-\frac{x^2}{4Dt}\right] \tag{21}$$

If the density function of traveling duration is given by a gamma distribution defined by Eq. 6, the expected number of settled individuals at a position x is given by

$$\begin{aligned} f_1(x) &= \int_0^{\infty} n(x,t) p(t) dt \\ &= \frac{n_0}{2^{(k-0.5)}\sqrt{\pi}\,\Gamma(k)} \left(\sqrt{\frac{k}{m}}\right)^{(k+0.5)} |x|^{(k-0.5)} K_{(k-0.5)}\left(|x|\sqrt{\frac{k}{m}}\right) \end{aligned} \tag{22}$$

If we use the approximation given by Eq. 12, we obtain

$$f_1(x) \approx \frac{n_0}{2^k \Gamma(k)} \left(\sqrt{\frac{k}{m}}\right)^k |x|^{(k-1)} \exp\left(-|x|\sqrt{\frac{k}{m}}\right) \tag{23}$$

Equation 12 holds exactly for $k = 1$. In this case, Eq. 23 reduces to the exact solution for a one-dimensional random walk with a constant rate of settlement (Williams 1961; Turchin 1998).

$$f_1(x) = \frac{n_0}{2}\left(\sqrt{\frac{1}{m}}\right) \exp\left(-|x|\sqrt{\frac{1}{m}}\right) \tag{24}$$

We substituted Eq. 22 for Eq. 19 and numerically obtained the solution for Eq. 18. If $m = 1$, the solutions of C for $(1/k) = 1, 10, 20$, and 50 were 1.899, 3.019, 3.809, and 5.463, respectively. These solutions for C coincide with the asymptotic rate of expansion estimated by the linear regression stated previously.

Estimation

We can estimate the parameters of the dispersal function if we conduct a mark-recapture experiment. Let s be the number of traps that are used to recapture released individuals, r_i be the distance between the release point and the ith trap, Y_i be the number of individuals recaptured by the ith trap, and y_i be the observed quantity. We tentatively assume that a settled individual is recaptured by a trap at a constant rate and denote the rate by c. This assumption is somewhat restrictive, and hence we discuss the problem in a later section. Under these assumptions, the expected number of individuals recaptured by the ith trap, which is denoted by $g(r_i)$, is given by

$$g(r_i) = c f(r_i) \tag{25}$$

The released individuals fall into one of the $(s + 1)$ categories, which consist of individuals captured by the ith trap $(i = 1,2, \ldots s)$ and individuals not captured by any trap. If each trap has a fixed probability of recapture, and if the behavior of individuals is mutually independent, the distribution of captured individuals follows a multinomial distribution consisting of $(s + 1)$ categories. A multinomial distribution is given by a conditional distribution of a Poisson distribution (Fisher 1922). If the proportion of recaptured individuals is small, it therefore becomes identical to the Poisson distribution approximately. Hence, we obtain the maximum-likelihood estimates of parameters, which are denoted by $\hat{k}$, $\hat{m}$, and $\hat{c}$, by numerically maximizing the log likelihood (l) of the Poisson distribution in such a case:

$$l = \sum_{i=1}^{s} \left\{ y_i \log[g(r_i)] - g(r_i) - \log[y_i!] \right\} \tag{26}$$

We can estimate the asymptotic variance–covariance matrix of estimates, which is denoted by $\mathbf{V}$, by using the Hessian matrix of the log likelihood function evaluated at $\hat{k}$, $\hat{m}$, and $\hat{c}$:

$$\hat{\mathbf{V}} = \begin{bmatrix} \operatorname{var}(\hat{k}) & \operatorname{cov}(\hat{k},\hat{m}) & \operatorname{cov}(\hat{k},\hat{c}) \\ \operatorname{cov}(\hat{m},\hat{k}) & \operatorname{var}(\hat{m}) & \operatorname{cov}(\hat{m},\hat{c}) \\ \operatorname{cov}(\hat{c},\hat{k}) & \operatorname{cov}(\hat{c},\hat{m}) & \operatorname{var}(\hat{c}) \end{bmatrix} = \begin{bmatrix} -\frac{\partial^2 l}{\partial k^2} & -\frac{\partial^2 l}{\partial k \partial m} & -\frac{\partial^2 l}{\partial k \partial c} \\ -\frac{\partial^2 l}{\partial m \partial k} & -\frac{\partial^2 l}{\partial m^2} & -\frac{\partial^2 l}{\partial m \partial c} \\ -\frac{\partial^2 l}{\partial c \partial k} & -\frac{\partial^2 l}{\partial c \partial m} & -\frac{\partial^2 l}{\partial c^2} \end{bmatrix}_{\hat{k},\hat{m},\hat{c}}^{-1} \tag{27}$$

where var(·) and cov(·) indicate the variance and covariance, respectively. If the number of recaptured individuals (Y_i) follows the Poisson distribution with a fixed mean, the variance of Y_i is equal to the mean, i.e., we have $\mathrm{var}(Y_i) = g(r_i)$. However, it is unlikely that each trap has a probability of recapture exactly coinciding with the predicted dispersal curve. Even if the overall probability of recapture exactly follows Eq. 25, the probability of recapture in each trap will fluctuate because of the spatial heterogeneity of environmental conditions. In such a case, the actual variance of the number of recaptured individuals becomes larger than the variance predicted by the Poisson distribution, i.e., we have $\mathrm{var}(Y_i) > g(r_i)$. A standard way of considering such an overdispersion is to assume the following variance function:

$$\mathrm{var}(Y_i) = \phi g(r_i) \tag{28}$$

where ϕ is called the dispersion parameter (McCullagh and Nelder 1989). The quantity of ϕ is usually estimated by Pearson χ^2 statistics divided by the degree of freedom (Aitkin et al. 1989; McCullagh and Nelder 1989; SAS Institute 1997):

$$\hat{\phi} = \frac{1}{(s-p)}\sum_{i=1}^{s}\frac{\left[y_i - g(r_i)\right]^2}{g(r_i)} \tag{29}$$

where p is the number of parameters; $p = 3$ for Eq. 25. We then obtain the adjusted variance–covariance matrix of estimated parameters by $\hat{\phi}\hat{\mathbf{V}}$. We can estimate the variance of $(1/\hat{k})$ by $\mathrm{var}(\hat{k})/(\hat{k}^4)$ through use of the delta method (Stuart and Ord 1994).

We can calculate the maximum-likelihood estimates, $\hat{k}$, $\hat{m}$, and $\hat{c}$, by using the DUD option in the procedure NLIN of SAS (SAS Institute 1989), with the loss function defined by the negative of Eq. 26. The Bessel function is obtained by the numerical integration of Eq. 8 through use of the Legendre–Gauss method. We can calculate the variance–covariance matrix by using Mathematica (Wolfram 1996), where the second derivative ($\partial^2 l/\partial k^2$) in Eq. 27 is calculated by a numerical differentiation (function ND in Mathematica). The estimation procedure is greatly simplified if we avoid calculation of the Bessel function by using the approximation given by Eq. 14.

Several authors have for simplicity used the least-squares method in estimating the parameters of the dispersal function. In this method, we estimate parameters that minimize the square of difference:

$$\sum_{i=1}^{s}\left[y_i - g(r_i)\right]^2 \tag{30}$$

However, the estimates sometimes differ significantly from the maximum-likelihood estimates, as shown by the following example.

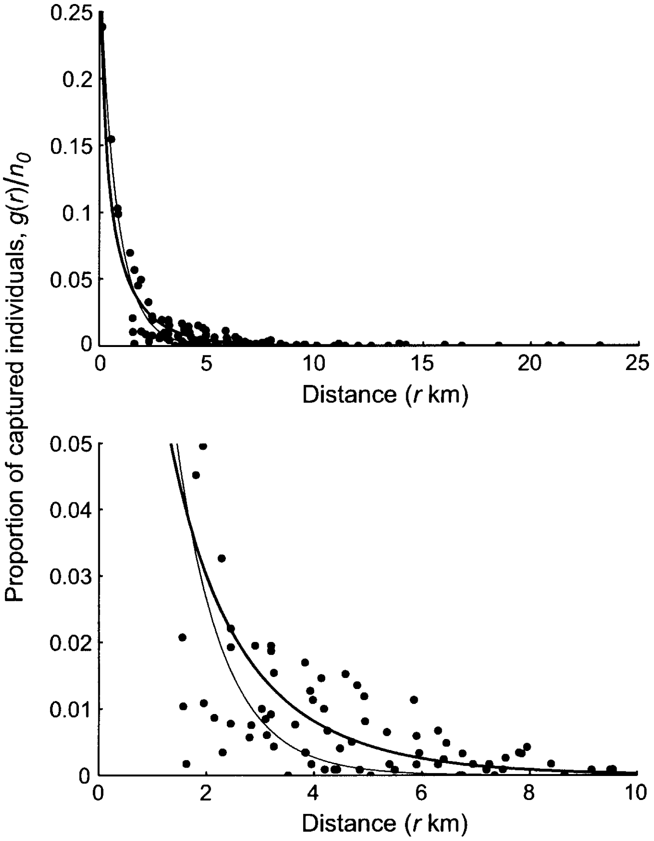

Fig. 4. Dispersal function for *Spodoptera litura* in July. *Upper graph*: the proportion of individuals recaptured by each of the 24 traps. Individuals were released from four points, and hence the 96 plots are shown. *Lower graph*: a magnified figure around the dispersal origin. *Bold curves* indicate the estimates obtained by the maximum-likelihood method. *Thin curves* indicate those obtained by the least-squares method

Example

Wakamura et al. (1990, 1992) conducted mark–recapture experiments with *Spodoptera litura* in Kagawa Prefecture, northern Shikoku, Japan, in 1985. Twenty-four sex pheromone traps (water-pan traps, 30 × 30 × 15 cm; Takeda, Osaka, Japan) were placed in the experimental area to capture male *S. litura*. Male moths reared in the laboratory were marked and released for 3 or 4 days from four release points every month, from May to September. Male catches with sex pheromone traps were continued until 3 days after the last catch of marked males. The total numbers of released males were as follows: May, 5621; June, 7259; July, 4760; August, 5878; and September, 5263.

Figure 4 shows an example of the dispersal function that was estimated using Eq. 9. The estimates obtained by the least-squares method were very different from those obtained by the maximum-likelihood method in the middle range of distance. The maximum-likelihood estimates of parameters changed considerably depending on the season (Fig. 5). Estimates of the dispersion parameter ϕ are much larger than 1, with such a large ϕ indicating that the prob-

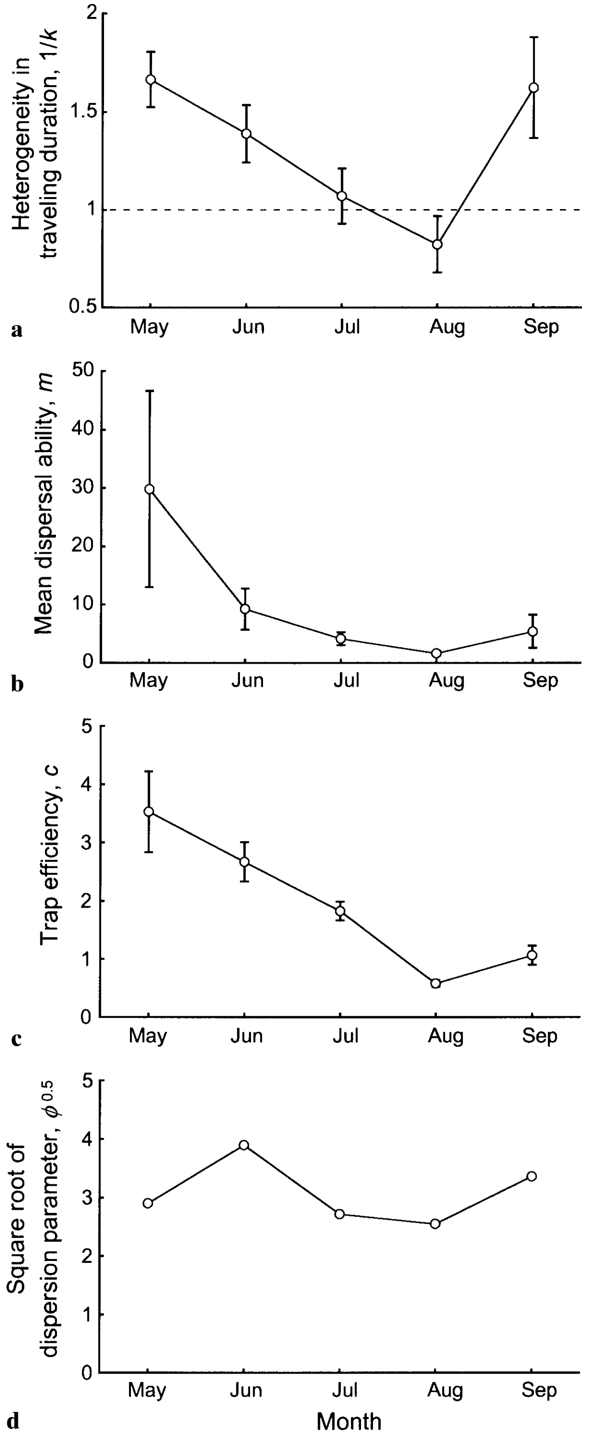

Fig. 5. Seasonal change in the parameters estimated using Eq. 9. **a** *Vertical bars* indicate the asymptotic standard errors estimated using the Delta method. **b**,**c** *Vertical bars* indicate the asymptotic standard errors estimated by the square root of var($\hat{m}$) and var($\hat{c}$). **d** Standard errors cannot be estimated for $\phi^{0.5}$

ability of recapture has considerable spatial fluctuation, although the systematic lack of fit of Eq. 9 might be suspected in several cases.

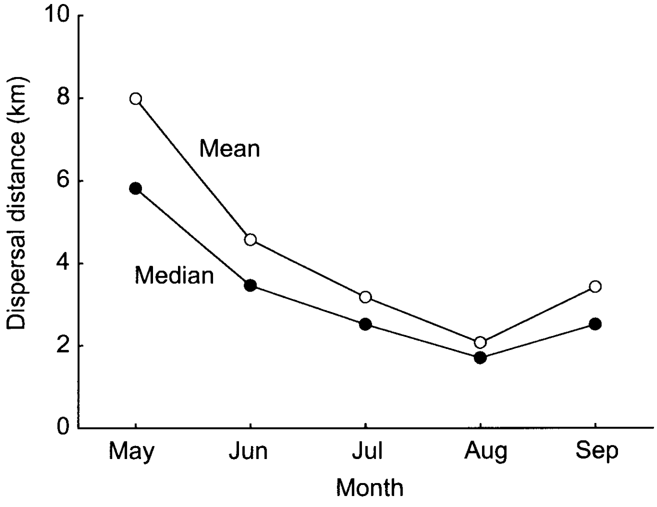

Fig. 6. Seasonal change in the *mean* and *median* dispersal distances for *Spodoptera litura*

Turchin and Thoeny (1993) have suggested the usefulness of the median dispersal distance, $r_{0.5}$, that is, the radius of a circle that encloses 50% of individuals, as an intuitive measure of dispersal. We can obtain $r_{0.5}$ by numerically solving the following equation for $r_{0.5}$:

$$\frac{\int_0^{r_{0.5}} 2\pi r f(r) dr}{\int_0^{\infty} 2\pi r f(r) dr} = 0.5 \qquad (31)$$

Figure 6 shows the estimated seasonal change in the mean dispersal distance calculated by Eq. 10 and that in the median dispersal distance calculated by Eq. 31. The median dispersal distance is consistently smaller than the mean dispersal distance.

Discussion

Shigesada et al. (1995) have provided stratified diffusion models explaining why the speed of invasion is not constant in several species. They considered a situation in which the invading species extends its range into surrounding areas by random diffusion, while at the same time producing individuals that colonize far away. Their model predicted that the range radius increases with acceleration if the colonization rate is sufficiently large. We derived a similar result by assuming that the traveling duration of organisms follows a gamma distribution. The upper graph in Fig. 2 indicates that the distribution front expands with acceleration during an early phase of expansion if the heterogeneity in the traveling duration is sufficiently large.

A gamma distribution is able to describe both heterogeneous and homogeneous traveling durations. When $(1/k) = 1$, a gamma distribution becomes an exponential distribution that corresponds to the diffusion with a constant rate of settlement (Broadbent and Kendall 1953). If $(1/k) > 1$, the traveling duration is heterogeneous in a sense that the variance is larger than that of exponential distribution of the same mean. If $(1/k) < 1$, on the other hand, the traveling duration is homogeneous in a sense that the variance is smaller than that of exponential distribution. The dispersal function of bivariate normal distribution is derived for the extreme case of $(1/k) = 0$, i.e., a case where all individuals settle after traveling the same duration. However, a gamma distribution will not be able to generate a dispersal function having an extremely long tail. Hence, another type of assumption may be more suitable for several situations. Clark et al. (1999) implicitly assumed that the inverse of traveling duration follows a gamma distribution. In this case, by substituting $n(r,1/t)$ for $n(r,t)$ in the left-hand side of Eq. 7, we obtain a distribution called "two-dimensional *t*" (2*Dt*) kernel:

$$f(r) = \int_0^\infty n(r,1/t)p(t)dt = n_0\left(1 + \frac{r^2}{4D\lambda}\right)^{-k-1}\frac{k}{4D\lambda\pi} \qquad (32)$$

which tends to a normal distribution as $(1/k)$ becomes zero and to Cauchy distribution as $(1/k)$ becomes large. Equation 32 is simpler than Eq. 7, but it does not include the standard situation described by Eq. 5.

In deriving Eq. 7, we assumed that D is fixed and that only the traveling duration varies. However, we can obtain a similar result if we assume that the product of diffusion coefficient and traveling duration (Dt) follows a gamma distribution. In this case, the dispersal function is given by Eq. 7 where D is replaced by 1. Similarly, if we assume that $(1/Dt)$ follows a gamma distribution, the dispersal function is given by Eq. 32 where D is replaced by 1. We also obtain a result similar to Eq. 7, if we assume that D varies, following a gamma distribution, among individuals and that all individuals have the same traveling duration. However, we should be careful when we assume the variability in D. In deriving Eq. 3, we implicitly assumed that D does not change in the course of movement. In actual situations, D will change in the course of movement of "each" individual, depending on the local environmental condition such as local wind speed and local barriers to movement. Therefore, we should rather consider a "scaled traveling duration" in which the traveling duration is scaled by D every moment. When a flying individual meets a strong wind at a moment, for example, the individual suffers a large D at that moment, and hence the scaled traveling duration at that moment becomes larger. Then, we can use Eqs. 7 or 9 by assuming that the scaled traveling duration is approximately described by a gamma distribution.

We are sometimes confronted with a dilemma in applying models such as Eq. 25 to field experiments. Although we assumed that a proportion of the settled individuals are captured by traps in applying Eq. 25, these traps will cause additional mortality in mark–recapture experiments. Hence, Eq. 25 will be applicable only in a situation where the proportion of recaptured individuals is small. If the trap efficiency is large, we cannot apply the model, as the traveling duration is influenced by the mortality caused by traps. Conversely, if the trap efficiency is small, we cannot estimate the spatial distribution with sufficient precision because of the large sampling errors. We are thus confronted with a dilemma. When the distribution of the traveling duration is described by an exponential distribution (Eq. 4), that is, when $(1/k) = 1$, we will be able to solve this dilemma by a uniform placement of traps. If traps are placed uniformly in a lattice pattern, the mortality caused by traps is approximately constant, and hence we can assume that the moving individuals are removed by traps at a constant rate, δ. The proportion of individuals captured by traps at time t, which is denoted by $q(t)$, is then given by

$$q(t) = \delta\exp\left[-(\delta + \lambda)t\right] \qquad (33)$$

The expected number of individuals captured by a trap placed at a distance r, which is denoted by $g(r)$, is given by

$$g(r) = \frac{1}{w}\int_0^\infty n(r,t)q(t)dt = \frac{\delta n_0}{2\pi Dw}K_0\left(\sqrt{\frac{\delta + \lambda}{D}}r\right) \qquad (34)$$

where w is the density of traps per unit area; the inverse, $1/w$, indicates the area per trap. In a mark–recapture experiment, we know the released number of individuals (n_0) and the density of traps (w). Therefore, we can estimate δ/D and $\sqrt{(\delta+\lambda)/D}$ by using Eq. 34, and hence we can obtain the estimate of λ/D, although we cannot obtain the estimate of D. We can therefore predict the natural distribution of settled individuals, $f(r)$, by substituting the estimate of λ/D for Eq. 5. If traps are not placed uniformly in space, however, we will not be able to describe $g(r)$ in a simple form, even if $(1/k) = 1$. In the mark–recapture experiment of *S. litura*, traps were placed more densely near the release points. These traps removed the released individuals from the dispersing population to prevent further dispersal. As a result, the tail density of the dispersal function would be smaller than that of the dispersal function without removal. Hence, some bias in the estimates is likely.

Wakamura et al. (1990) have used the dispersal function proposed by Wallace (1966) to describe the dispersal of *S. litura*: $\log_e[f(x)] = a - b\sqrt{r}$. They estimated two parameters from this equation: the trap efficiency and the mean dispersal distance. The trap efficiency, which is denoted by P_4, was defined by the recapture rate at 4 km from the release point. The mean flight distance, d, was calculated by using $d = 20/b^2$ (Hawkes 1972). The seasonal changes in $\hat{P}_4$ and $\hat{d}$ (Figs. 4A and 3B in Wakamura et al. 1990) are similar to the present estimates of seasonal changes in the trap efficiency (c; Fig. 5) and mean dispersal distance (Fig. 6), respectively. Wakamura et al. (1990) have further estimated the mean survival period by plotting the estimated number of released live individuals against days after release using a modified Jackson method (Itô 1973). Seasonal changes in the mean survival period (Fig. 3C in Wakamura et al. 1990) are similar to the seasonal change in the mean dispersal ability (m) shown in Fig. 5. The mean dispersal ability was defined by $m = Dk/\lambda$, and hence it is influenced by the diffusion coefficient (D) as well as the mean traveling duration (k/λ). The similarity between Fig. 3C in Wakamura et al. (1990) and our Fig. 5 indicates that the seasonal change in m would be determined primarily by the seasonal change in the mean traveling duration rather than that of the diffusion coefficient.

When we want to predict the expansion speed of biological invaders, we should more precisely describe the tail shape of the dispersal function, because the speed of invasion is mostly determined by the tail shape (Kot et al. 1996). In this case, we will be able to evaluate the validity of a gamma distribution by calculating several sets of estimates by changing the proportion of tail data used for the estimation. If the estimates change monotonically with a decreasing proportion of tail data, we can conclude that the gamma distribution departs systematically from the data. For example, for the data shown in Fig. 4, we obtained $(1/\hat{k}) = 1.39$, $\hat{m} = 9.3$, and $\hat{c} = 2.67$, if we used all data ($s = 96$). If we used traps that were placed further away than 1 km ($s = 92$), we obtained $(1/\hat{k}) = 2.03$, $\hat{m} = 22.0$, and $\hat{c} = 3.13$. For traps placed further than 2 km away ($s = 84$), we obtained $(1/\hat{k}) = 1.06$, $\hat{m} = 16.4$, and $\hat{c} = 2.57$. For traps placed further than 4 km away ($s = 59$), we obtained $(1/\hat{k}) = 2.55$, $\hat{m} = 26.8$, and $\hat{c} = 3.34$. The estimate of m was smallest when we used all data for the estimation, although the estimates fluctuated greatly depending on the proportion of tail data. Therefore, a systematic departure was indicated for the gamma distribution. When we want to predict the tail distribution in this case, it might be preferable to use estimates obtained from the traps placed further than 1 km away. We should always be careful when we extrapolate the tail distribution from small-distance experiments.

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