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Kohji Yamamura · Mitsunobu Kishita · Norio Arakaki
Futoshi Kawamura · Yasutsune Sadoyama

Estimation of dispersal distance by mark-recapture experiments using traps: correction of bias caused by the artificial removal by traps

Abstract Although in mark-recapture experiments traps are useful to estimate the dispersal distance of organisms, they cause a dilemma that may be called a kind of Heisenberg effect: a large number of traps should be placed to yield a precise estimate of mean dispersal distance, while these traps shorten the mean dispersal distance itself by intercepting organisms that should have dispersed for further distances. We propose a procedure to solve this dilemma by placing traps uniformly in a lattice pattern, and by assuming a random movement and a constant rate of settlement for organisms. We applied this procedure to estimate the dispersal distance of the sugarcane wireworm *Melanotus okinawensis* Ohira (Coleoptera: Elateridae). The estimated mean dispersal distance was 143.8 m. Through the use of a conventional method of estimation, the mean dispersal distance was estimated to be 118.1 m. Thus, it was shown that the conventional estimate of dispersal distance was 18% smaller than the corrected estimate in our experiment.

Keywords Wireworm · *Melanotus okinawensis* · Removal by traps · Dispersal distance · Bias correction

Introduction

Traps are frequently used in mark-recapture experiments for estimating the mean dispersal distance or estimating the dispersal function which is the relation between distance and the density of dispersed individuals. Marked individuals are released from a point source and are recaptured continuously by traps that are placed at various distances from the release point. In these experiments, we are confronted with a dilemma that may be called a Heisenberg effect (Turchin 1998). If we want to reduce the sampling error in the estimates of dispersal distance, we should recapture most of the marked individuals by placing as many traps as possible over the field. However, these traps cause additional mortality during the dispersal of individuals. Individuals captured by traps would have dispersed over longer distances had they not been captured. Thus, the estimate of mean dispersal distance obtained by a mark-recapture experiment becomes inevitably smaller than the actual dispersal distance. To reduce such biases, we should recapture a small fraction of the population by using a small number of traps or less efficient traps. However, the estimate obtained by such an experimental design is subject to large sampling errors and hence less reliable. Such a dilemma will become a serious problem if we want to obtain a precise estimate of dispersal distance.

In this article, we show that, under several assumptions, we can estimate natural dispersal distance if we place traps uniformly in a lattice pattern. We apply this method to the estimation of the dispersal distance of the sugar cane wireworm, *Melanotus okinawensis* Ohira (Coleoptera: Elateridae), conducted in Ikei Island in Okinawa prefecture (Kishita et al. 2003), where funnel-vane traps containing synthetic sex pheromone were placed uniformly in the field in order to recapture male adults.

K. Yamamura (✉)
Laboratory of Population Ecology,
National Institute for Agro-Environmental Sciences,
3-1-3 Kannondai, 305-8604 Tsukuba, Japan
E-mail: yamamura@niaes.affrc.go.jp
Tel.: +81-29-8388253
Fax: +81-29-8388199

M. Kishita · N. Arakaki · F. Kawamura · Y. Sadoyama
Okinawa Prefectural Agricultural Experiment Station,
Naha, Japan

Model

Dispersal distance without artificial removal

We first derive the natural distribution of dispersal distance in which there is no artificial removal. 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 no convection flow. 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:

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

We are using a transformation: $x = r\cos\theta$, $y = r\sin\theta$. Therefore, we have a relation: $n(x,y,t)dxdy = n(r,t)rd\theta dr$, where the Jacobian of transformation (r) is included. Let us 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, since we are assuming that the behavior is independent of the density of individuals (Broadbent and Kendall 1953; Williams 1961; Shigesada 1980):

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

where $K_0(\cdot)$ is a modified Bessel function of the second kind of order zero, and λ_D is defined by λ/D. We refer to λ_D as "rate of settlement scaled by diffusion coefficient".

In the literature, most dispersal experiments using traps are based on the implicit assumption that the influence of artificial removal by traps is negligibly small and that the distribution of captured individuals is proportional to the distribution of naturally settled individuals. Then, the expected number of individuals captured by the ith trap placed at a distance r_i is given by

$$g(r_i) \approx cf(r) = \frac{cn_0}{2\pi}\lambda_D K_0\left(r\sqrt{\lambda_D}\right), \tag{6}$$

where c is a constant.

Dispersal distance with artificial removal

Let us consider a situation where traps are placed for a sufficiently long time until all individuals settle. If traps are placed uniformly in a lattice pattern, the instantaneous mortality caused by traps is nearly constant, and hence we can assume that moving individuals are removed by traps at an approximate constant rate δ. The probability distribution of the traveling duration is given by an exponential distribution:

$$q(t) \approx (\lambda + \delta)\exp\left[-(\lambda + \delta)t\right]. \tag{7}$$

Let w be the density of traps per m^2. A trap then gathers organisms that are captured within $1/w$ m^2 on average. Individuals that stop their movement enter some traps by a rate $\delta/(\delta + \lambda)$. Therefore, the expected number of individuals captured by the ith trap placed at a distance r_i is approximately given by

$$\begin{aligned} g(r_i) &\approx \frac{\delta}{w(\lambda + \delta)}\int_0^\infty n(r_i,t)q(t)dt \\ &= \frac{n_0}{2\pi w}\delta_D K_0\left(r_i\sqrt{\lambda_D + \delta_D}\right), \end{aligned} \tag{8}$$

where δ_D is the "artificial mortality scaled by diffusion coefficient" defined by $\delta_D = \delta/D$. Equation 6 corresponds to a special case of Eq. 8 where $\delta_D \to 0$, $w \to 0$ keeping $c\lambda_D = \delta_D/w$. Let m be the total number of individuals captured by traps. The expected proportion of recaptured individuals is then given by

$$E\left(\frac{m}{n_0}\right) \approx \frac{\delta_D}{\lambda_D + \delta_D}, \tag{9}$$

where E indicates the expectation.

Estimation of parameters

We can estimate λ_D and δ_D by using Eq. 8. We can then estimate the natural dispersal distance, $f(r)$, by substituting the estimate of λ_D for Eq. 5. Let s be the number of traps that are used to recapture released individuals. Let r_i be the distance between the release point and the ith trap, y_i be the observed number of individuals recaptured by the ith trap. 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 multiplicative Poisson distribution (Fisher 1922). If the proportion of recaptured individuals is small, it therefore becomes approximately identical to the multiplicative Poisson distribution. Hence, we obtain the maximum-likelihood estimates of parameters, which are denoted by $\hat{\lambda}_D$ and $\hat{\delta}_D$ by numerically maximizing the log

likelihood (l) of the multiplicative Poisson distribution in such a case:

$$l = \sum_{i=1}^{s} \{y_i \log[g(r_i)] - g(r_i) - \log[y_i!]\}. \tag{10}$$

We can use the Solver of Microsoft EXCEL to iteratively find the parameters that maximize the log likelihood. If the values of parameters λ_D and δ_D are expected to be very small, scaling of parameters, such as multiplying by 10^5 in our case, is preferable to enhance the convergence property of iterative calculation. The Bessel function of order zero is calculated by using BESSELK worksheet function. Logarithmic factorial, $\log[y_i!]$, is calculated by using the logarithmic gamma function of the form GAMMALN($y_i + 1$). Least squares estimates of parameters are useful as initial values for iteration. 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 $\hat{\lambda}_D$ and $\hat{\delta}_D$

$$\hat{\mathbf{V}} = \begin{bmatrix} \mathrm{var}(\hat{\lambda}_D) & \mathrm{cov}(\hat{\lambda}_D, \hat{\delta}_D) \\ \mathrm{cov}(\hat{\lambda}_D, \hat{\delta}_D) & \mathrm{var}(\hat{\delta}_D) \end{bmatrix}$$

$$= \begin{bmatrix} -\dfrac{\partial^2 l}{\partial \lambda_D^2} & -\dfrac{\partial^2 l}{\partial \lambda_D \partial \delta_D} \\ -\dfrac{\partial^2 l}{\partial \lambda_D \partial \delta_D} & -\dfrac{\partial^2 l}{\partial \delta_D^2} \end{bmatrix}_{\hat{\lambda}_D, \hat{\delta}_D}^{-1}, \tag{11}$$

where var($\cdot$) and cov($\cdot$) indicate the variance and covariance, respectively. Standard errors of estimates are given by the square roots of the diagonal elements of the variance-covariance matrix. We can estimate the variance-covariance matrix by employing numerical differentiations using Microsoft EXCEL.

Bias in the estimation of mean dispersal distance

From Eq. 5, we derive the mean dispersal distance:

$$E(r) = \frac{1}{n_0} \int_0^\infty \int_0^{2\pi} r \cdot f(r) \cdot r \, d\theta \, dr$$

$$= \frac{1}{n_0} \int_0^\infty r \cdot 2\pi r f(r) \, dr = \frac{\pi}{2\sqrt{\lambda_D}} \tag{12}$$

Let $\hat{E}(r)$ be the estimate of mean dispersal distance obtained by substituting $\hat{\lambda}_D$ for λ_D in Eq. 12. Let $\hat{\lambda}'_D$ be the apparent estimate of λ_D obtained by fitting Eq. 6 to data, and $\hat{E}'(r)$ be the apparent estimate of $E(r)$ obtained by substituting $\hat{\lambda}'_D$ for λ_D in Eq. 12. Then, we have the following relation, since we have $\hat{\lambda}'_D = \hat{\lambda}_D + \hat{\delta}_D$:

$$\hat{E}'(r) = \sqrt{\frac{\hat{\lambda}_D}{\hat{\lambda}_D + \hat{\delta}_D}} \hat{E}(r). \tag{13}$$

Thus, $\hat{E}'(r)$ becomes much smaller than $\hat{E}(r)$ if the mortality caused by traps (δ_D) is large. We obtain an approximation of Eq. 13 by using Eq. 9.

$$\hat{E}'(r) \approx \sqrt{1 - \frac{m}{n_0}} \hat{E}(r) \tag{14}$$

This equation will be useful in estimating the degree of underestimation, since we can readily obtain the quantity of m/n_0 from field data without estimating λ_D and δ_D.

Materials and methods

The sugar cane wireworm, *M. okinawensis* Ohira (Coleoptera: Elateridae), is a serious pest of sugar cane in the Ryukyu Islands (Ohira 1988). Adults emerge on the ground between March and May on Okinawa Island (Nagamine and Kinjo 1990). The larvae injure underground buds, causing germination failure, death of hearts, and ratooning failure (Hokyo 1980; Nagamine and Kinjo 1981). A large amount of insecticide is applied before planting or during the growth period of the sugar cane in order to control the larvae (Yasuda and Hokyo 1983).

Experiments were conducted on Ikei Island, Yonashiro-cho, Okinawa Prefecture, Japan in 2000. Ikei Island (about 158 ha in its total area) is one of the three stepping-stone islands at the east of Kin Bay, about 12 km distant from Okinawa Island (Fig. 1; 26°23′N, 128°00′E). The cultivated area of this island is 81.4 ha. Sugar cane (21.6 ha) and tobacco (28.6 ha) are the main crops. The total experimental area including farm roads and periphery fields is 95.3 ha.

Pheromone traps were used for gathering the males to be released and also for recapturing the released males. We used polyethylene tubes (60 cm long, 2 mm i.d.) containing 1 ml *n*-dodecyl acetate [>95.0% (GC); Tokyo Chemical Industry, Tokyo] as pheromone lures. Two pheromone lures were attached to each funnel-vane trap (15 cm in diameter, 38.5 cm height with crossed vanes; Trece, Salinas, Calif.). We placed each trap on the ground by wiring it to a rod (0.8 cm in diameter, 90 cm length) that was pushed into the soil to a depth of about 10 cm.

Insects to be released were collected in traps in the field at Itoman and Haebaru, in the southern part of Okinawa. They were kept in plastic boxes and provided with a wad of tissue paper that was soaked with a diluted "sports drink" solution (Otsuka Pharmaceutical Company, Tokyo) as their food. Pieces of sugar cane leaves were supplied as their shelter. One day before the experiments, the pronotum and elytra of beetles were marked with an oily dye using felt-tip pens (Mitsubishi Paint). Three hundred and 500 marked insects were released at the center of the island (Fig. 2), on March 30 (Experiment 1) and April 25 (Experiment 2), respectively.

We placed traps uniformly over the experimental area in order to apply the described method. Traps were placed at 725 sites throughout the experimental area approximately in a lattice pattern. Among these traps, 250 set along roads were used for the estimation of dispersal distance (Fig. 2). Trap catches were examined on 1 and 3 April in Experiment 1, and on 27 and 29 April in Experiment 2.

Results

We estimated the averaged dispersal curve by combining the results of Experiments 1 and 2, since the number of recaptured individuals was not sufficiently large to yield precise estimates for each experiment. We used the cumulative number of insects recaptured 2 and 4 days after release in order to predict the cumulative dispersal distance (Fig. 3). The total number of recaptured indi-
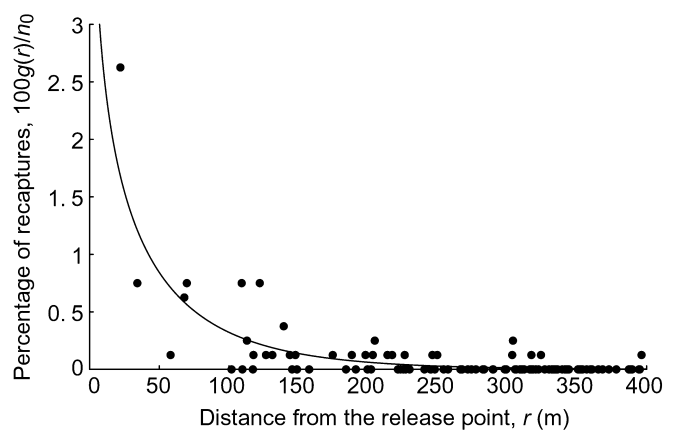
Fig. 1 Location and map of Ikei Island
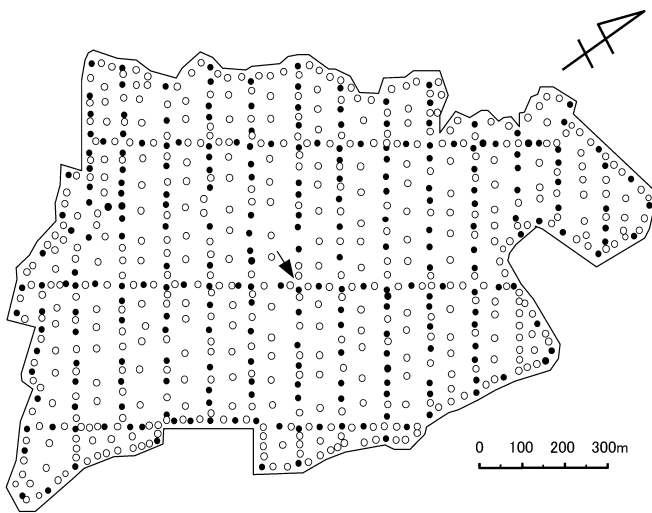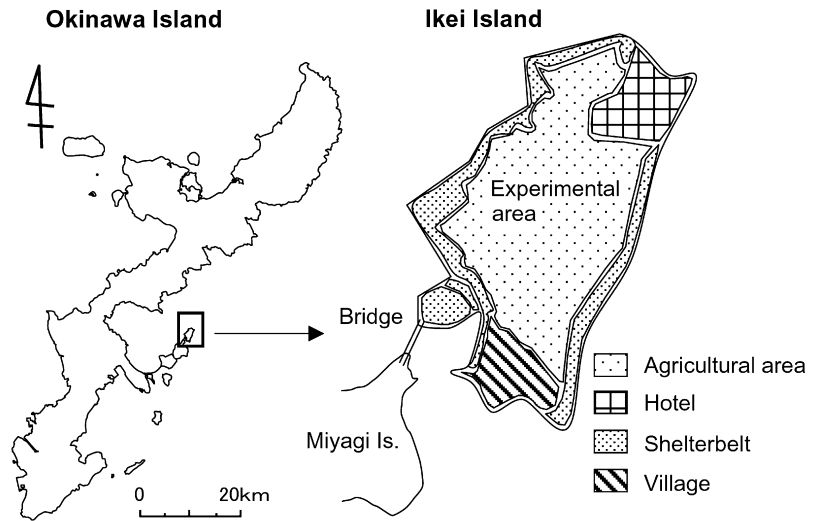
Fig. 2 Arrangement of 250 traps (*solid circles*) for evaluating the dispersal distance of male beetles and 475 traps (*open circles*) for mass trapping. *Arrow* indicates the release point of marked individuals

Fig. 3 The number of recaptured individuals in traps placed at different distances. The *curve* indicates the distribution that was estimated by using Eq. 8. The number of recaptured individuals is not shown for traps that were placed farther than 400 m from the release site

viduals in the 250 traps was 79. The maximum likelihood estimates ($\pm$ asymptotic standard errors) of parameters of Eq. 8 were $\hat{\lambda}_D = 11.93 \times 10^{-5} \pm 2.30 \times 10^{-5}$ and $\hat{\delta}_D = 5.77 \times 10^{-5} \pm 1.20 \times 10^{-5}$. The log likelihood given by Eq. 10 was -89.63. The estimate of mean dispersal distance calculated by Eq. 12 was 143.8 m.

If we adopt the conventional method of estimation by using Eq. 6, we obtain an estimate: $\lambda'_D = (11.93 + 5.77) \times 10^{-5} = 17.70 \times 10^{-5}$. The dispersal curve calculated by using this estimate overestimates the density of settled individuals near the release origin (upper panel of Fig. 4), while it underestimates the density at farther distances (lower panel of Fig. 4). By substituting $\hat{\lambda}_D$ and $\hat{\delta}_D$ for Eq. 13, we obtain the degree of underestimation: $\hat{E}'(r) = 0.821\hat{E}(r)$. Thus, if we use the conventional method, we underestimate the mean dispersal distance by about 18%. Another estimate of

the degree of underestimation is given by Eq. 14. We examined 250 of 725 traps placed in the field and recaptured 79 individuals. Hence, we can estimate the total number of recaptured individuals as $79 \times 725 / 250 = 229$. The estimate of the proportion of recaptured individuals is then $229/800 = 0.286$. By substituting this observed quantity for m/n_0 in Eq. 14, we obtain an estimate of the degree of underestimation: $\hat{E}'(r) \approx 0.845\hat{E}(r)$.

Discussion

We showed that the dilemma caused by traps in mark-recapture experiments is avoidable if we place traps uniformly in a lattice pattern, and if we assume a random movement and a constant rate of settlement for organisms. We can obtain the maximum likelihood estimate of the natural dispersal distance by estimating the parameters of Eq. 8 by using the maximum likeli-
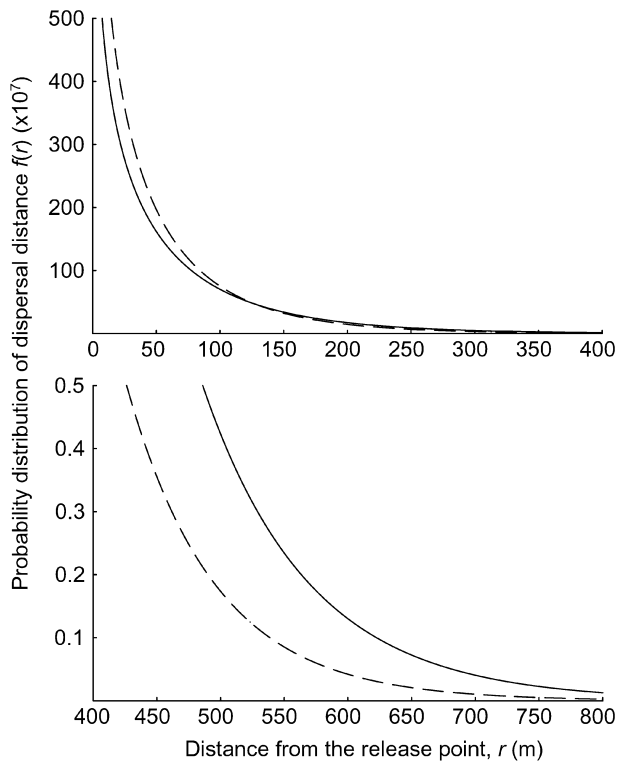
Fig. 4 Influence of artificial removal by traps on the estimate of dispersal distance. *Solid curves* indicate the dispersal curves, $f(r)$, obtained by considering artificial removal by traps $\left(\hat{\lambda}_D = 11.93 \times 10^{-5}\right.$ in Eq. 5). *Broken curves* indicate the estimates obtained by assuming no removal $\left(\hat{\lambda}'_D = 17.70 \times 10^{-5}\right.$ in Eq. 5). *Upper panel* indicates the comparison of curves at shorter distances. *Lower panel* indicates the comparison at longer distances

hood method, and by substituting the parameters for Eq. 12. Microsoft EXCEL is available for this estimation. Equation 14 indicates that the conventional estimate of mean dispersal distance is much smaller than the corrected estimate if the proportion of removal is large. In our experiment for examining the dispersal distance of the sugarcane wireworm *M. okinawensis*, the conventional estimate of mean dispersal distance was 18% smaller than the corrected estimate.

The uniform placement of traps, which is required for the estimation of dispersal distance, will not be easily attainable. Some kind of approximation is necessary, since it is logically impossible to place traps uniformly over infinite space of two dimensions. We placed traps uniformly over an island which is a closed space isolated from other habitats. In this case, both the range of insect dispersal and the range of trap placement are limited within the island, although both ranges are assumed to be infinite in the model. This approximation will be satisfactory if the size of the island is sufficiently large with respect to the dispersal ability of insects. Several experiments have adopted a lattice placement of traps over a specific range (Plant and Cunningham 1991; Schneider 1999; Mo et al. 2003). The labor required for recapturing, however, increases in an accelerating manner with increasing distance, because the number of

traps is in proportion to the square of the distance. Radial trap placements are frequently adopted as an alternative experimental design; that is, the same number of traps (or approximately the same number of traps) are placed at each distance over a specific range (Turchin and Thoeny 1993; Cronin et al. 2000; Sato et al. 2000; Smith et al. 2001). Other experiments have adopted more complicated patterns (Hawkes 1972; Wakamura et al. 1990; Hunt et al. 2001; Showers et al. 2001; Skovgård 2002). If traps are not placed uniformly, however, it will be difficult to solve the dilemma, since the instantaneous proportion of individuals that departs from a dispersing population is not constant even if the rate of natural settlement is constant. If we can assume a random dispersal and a constant rate of natural settlement of organisms, we should place traps in a lattice pattern at least around the release point. Such a placement enables us to eliminate the bias caused by artificial removal.

We can more easily perform the uniform placement of traps if we can release organisms in a one-dimensional space that is sandwiched between two linear reflecting barriers; the number of traps in a one-dimensional space increases in proportion to the maximum trap distance, while in a two-dimensional space it increases in proportion to the square of the maximum distance. We can derive the equation for one dimension by using a method similar to that described earlier. Let $n(x,t)$ be the number of individuals at time t at a distance x. Then, we have a one-dimensional version of Eq. 3:

$$n(x,t) = \frac{n_0}{2\sqrt{\pi Dt}} \exp\left[-\frac{x^2}{4Dt}\right]. \tag{15}$$

The number of settled individuals at a distance x, which is denoted by $f_1(x)$, is given by the following equation (Williams 1961; Turchin 1998):

$$f_1(x) = \int_0^\infty n(x,t)p(t)\mathrm{d}t = \frac{n_0}{2}\sqrt{\lambda_D}\exp\left(-|x|\sqrt{\lambda_D}\right). \tag{16}$$

The mean dispersal distance is given by $1/\sqrt{\lambda_D}$. The expected number of individuals captured by the ith trap placed at a distance x_i is given approximately by

$$
\begin{aligned}
g_1(x_i) &\approx \frac{\delta}{w_1(\lambda + \delta)} \int_0^\infty n(x,t)q(t)\mathrm{d}t \\
&= \frac{n_0 \delta_D}{2w\sqrt{\lambda_D + \delta_D}} \exp\left(-|x|\sqrt{\lambda_D + \delta_D}\right),
\end{aligned} \tag{17}
$$

where w_1 is the density of traps per m. Yamamura et al. (2003) suggested a discrete version of these equations for one dimension. We can estimate the parameters of this equation by a manner similar to that for Eq. 8. Let $E(x)$ be the estimate of mean dispersal distance and $E'(x)$ be the apparent estimate. We then have a relation:

$$\hat{E}'(x) = \sqrt{\frac{\hat{\lambda}_D}{\hat{\lambda}_D + \hat{\delta}_D}}\hat{E}(x) \approx \sqrt{1 - \frac{m}{n_0}}\hat{E}(x). \tag{18}$$

Empirical equations are sometimes superior to theoretical equations in describing the dispersal function, although theoretical equations are necessary if we want to obtain unbiased estimates of the mean dispersal distance. Taylor (1978) compared the descriptive ability of empirical equations having two parameters, and showed that the empirical model proposed by Wallace (1966) is most preferable; that is,

$$\ln[g(r_i)] = a - b\sqrt{r_i}, \qquad (19)$$

where a and b are constants. Plant and Cunningham (1991), in analyzing the dispersal of sterile Mediterranean fruit flies, *Ceratitis capitata*, also concluded that the Wallace model is the most preferable. Kishita et al. (2003) compared the fitness of several empirical equations for the dispersal of *M. okinawensis* by using An Information Criterion (AIC, proposed by Akaike 1973, which is frequently referred as the Akaike Information Criterion). They also concluded that the Wallace model is most preferable; the AIC for the Wallace model was 182.7, the smallest among those of models examined. In the present study we used the same data as that of Kishita et al. (2003). AIC is defined as $-2\ln$ (maximum likelihood) $+2$ (number of parameters in the model). In our model that contains two parameters (λ_D and δ_D), the logarithm of maximum likelihood was -89.63. Hence, we obtain AIC $= -2 \times (-89.63) + 2 \times 2 = 183.3$. Thus, the Wallace model is slightly superior to our model according to AIC. Some assumptions involved in our model will not provide a highly accurate approximation of actual dispersal.

We did not consider the variability that will emerge in actual fields, such as variability of wind speed and wind direction, individual variability of dispersal ability, the spatial heterogeneity of vegetation over the experimental field, and the spatial heterogeneity in barriers against movement such as trees. Such variability will change both the diffusion coefficient and the rate of settlement during the movement of each individual. Skalski and Gilliam (2003) described heterogeneity in a state-structured framework; during their dispersal, individuals change their movement states, such as their diffusion coefficients, in a stochastic manner. Yamamura (2002) described heterogeneity by assuming that the traveling duration of organisms follows a gamma distribution; a gamma distribution is a generalization of an exponential distribution that was used in this article (Eq. 4). Clark et al. (1999) used an inverse gamma distribution instead of a gamma distribution. By assuming that the traveling duration scaled by the diffusion coefficient follows a gamma distribution or an inverse gamma distribution, we can describe the natural dispersal distance under several kinds of variability including variability in the diffusion coefficient and the rate of settlement. However, it will be difficult to solve the aforementioned dilemma in these general models, since the removal by traps influences the distribution of dispersal duration in a complicated manner. Further improvement in the methodology will be required in this respect.

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