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QUANTIFYING DISPERSAL OF SOUTHERN PINE BEETLES WITH MARK–RECAPTURE EXPERIMENTS AND A DIFFUSION MODEL[1]

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Abstract. Pest management decisions should take into consideration quantitative information on dispersal of insect pests, but such information is often lacking. The goal of this study was to measure intraforest dispersal in the southern pine beetle (SPB). We developed an analytical formula for interpreting data from mark–recapture studies of insect dispersal. The formula is obtained by postulating a simple model of diffusion with disappearance (e.g., as a result of death) for the spread of marked insects from the release point. Parameters of the model (assumed to be invariant in space) are estimated by fitting the curve to the cumulative number of recaptured insects as a function of the distance from release. We also derived an expression for the distribution of dispersal distances in terms of the fitted parameters.

The proposed methodology was applied to a mark–recapture study of SPB dispersal. Statistical analysis of recaptures-with-distance curves obtained in 11 replicate releases indicated that the proposed formula provided an accurate description of the data. There were no systematic departures from the functional relationship prescribed by the formula, and the model consistently outperformed another commonly used formula for fitting data on dispersal distances, the exponential curve.

We explored the effect of spatial heterogeneity in the host distribution on SPB movement by regressing the deviation from the recapture rate predicted by the model in each trap on the pine basal area around the trap. This correlation was significantly greater than zero, indicating that beetles tended to aggregate in localities where pines were dense. This result suggests that a diffusion model with spatially varying parameters may provide a more accurate description of the redistribution process in the SPB.

Quantitative results on SPB intraforest dispersal were summarized by calculating radii of circles enclosing a given proportion of SPB dispersal distances. For example, we estimated that one half of released beetles dispersed >0.69 km. This result has important implications for evaluating the area-wide consequences of current or novel control tactics that rely on disrupting SPB movements, e.g., cut-and-leave and treatments with anti-congregation pheromone.

Key words: bark beetles; Dendroctonus frontalis; *diffusion; dispersal; distribution of dispersal distances; forest insects; model; quantitative measure of dispersal; southern pine beetle; spatial heterogeneity.*

INTRODUCTION

Quantitative information on dispersal should be a key element in designing and evaluating management strategies for highly mobile insect pests. However, as Kennedy and Way (1979) remark, "there is a terrible lack of information about the movements of these species." The situation has not improved since 1979. For example, we possess no quantitative information on the dispersal of the southern pine beetle (*Dendroctonus frontalis* Zimm.), even though this beetle is the most destructive insect pest of pine forests in the southern United States. The problem is not a lack of techniques for studying beetle dispersal in the field—indeed, techniques for mass-marking (Gara 1967, Moore et al. 1979, Bridges et al. 1989) and recapturing beetles with pheromone-baited traps (Lindgren 1983) are well known—but rather a lack of analytical tools for extracting practical answers from the data. For example, a previous study has reported the maximum observed dispersal distance for the southern pine beetle (Moore et al. 1979). To make management decisions, however, we need to know not only whether insects can fly as far as x km, but also what proportion of the population will fly that far.

One of the most useful theoretical approaches to quantifying insect dispersal and relating it to insect population dynamics is provided by the diffusion framework (Skellam 1951, Okubo 1980, Kareiva 1986, Turchin 1989*a*). The advantages of the diffusion framework are a compact and precise summary of the spatial redistribution process, and its explicit and mechanistic connection to data (Kareiva 1986). If dispersal from a point source is governed by simple (or

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"passive") diffusion, then the spatial distribution of organisms will be normal (Gaussian), centered at the point of release, and the variance of the distribution will increase linearly with time (Okubo 1980). The Gaussian formula provides an accurate description of the population density in space for a number of insect species (Kareiva 1983). However, several problems prevent direct application of this formula to dispersal of southern pine beetles (SPB), as well as many other economically important insects.

1) Spatial density of flying insects often cannot be assessed directly, and instead marked insects are recaptured with elaborate traps. If spatial density changes rapidly in the period of time between trap collections, then recaptures in traps will not provide an estimate of instantaneous spatial density distribution, but rather a time integral of the density.

2) A related problem arises if the death rate in the population of marked insects is high relative to the temporal scale of the mark–recapture experiment. In this case spatial density will change not only as a result of population redistribution but also as a result of population losses due to death.

3) Finally, the simple diffusion model assumes that space is homogeneous. However, spatial heterogeneity is always present in natural situations, and thus it would be useful to have a measure of its influence on the redistribution process.

The first goal of this paper is to develop a methodology for statistical interpretation of data from mark–recapture experiments in systems for which the problems discussed above preclude direct fitting with the simple diffusion equation. Second, we describe a field mark–recapture study of SPB dispersal. We apply the method to the recaptures data, and use the model to estimate the frequency distribution of SPB dispersal distances.

Methods

A model of diffusion with disappearance, for analyzing mark–recapture data

Our statistical analyses of mark–recapture data are based on the following simple model:

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) - \delta u. \qquad (1)$$

Here $u \equiv u(x, y, t)$ is the density distribution of marked insects as a function of one temporal (t) and two spatial (x, y) coordinates. The model has only two parameters: the diffusion rate, D, which measures the rate of spread of the population of marked insects from the point source, and the disappearance rate, δ, which measures the rate at which insects are lost from the marked population. Disappearance rate in the Southern pine beetle (SPB) is a result of three processes: (1) beetles dying during the process of dispersal, (2) beetles attacking and entering host trees, and (3) beetles leaving the system by flying above the tree canopy, and possibly being carried away by prevailing winds. A similar model was proposed by Williams (1961) for the spatial distribution of larvae of randomly moving insects.

The model makes several simplifying assumptions about the spatial and temporal dynamics of the population of marked insects.

1) It is assumed that the spatial redistribution process of insects is adequately represented by the diffusion equation. In particular, diffusion assumes that insects move in an identical fashion independently of each other. Dispersal of many insects is adequately described by diffusion (Kareiva 1983). In the SPB, however, in addition to dispersal, population redistribution will be affected by congregation and mass attack of host trees. This violates the assumption of simple diffusion that all insects move independently of each other. We will discuss this complication below (see *The study system*).

2) A more important assumption is that the diffusion rate (D) is constant. The influence of spatial heterogeneity on dispersal can be modelled by assuming a spatially varying diffusion rate (e.g., Okubo 1980):

$$\frac{\partial u}{\partial t} = \left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}\right)(D(x, y)u) - \delta u. \qquad (2)$$

However, we do not know of any analytical results that would allow direct estimation of spatial dependence in the diffusion rate using Eq. 2. Thus, we proceed by fitting the model (Eq. 1) in order to determine whether it gives an adequate first approximation to the data, and then assess the effects of spatial heterogeneity statistically, by regressing the residuals from fitting the model on such environmental variables as host density (see *Statistical analyses*, below).

3) The model also assumes that there is no effect of directionality on dispersal, for example, direction towards the sun, or the effect of prevailing winds. The effect of direction on dispersal can be modelled by adding a drift term to Eq. 1. This assumption will be tested below (see *Statistical analyses*).

4) The model assumes that the loss rate (δ) is constant in space and time. This assumption would be violated if, for example, older insects were more likely to succumb to environmental extremes or natural enemies.

5) In addition, we will later need another assumption: when beetles are recaptured with traps, the recapture rate is proportional to the instantaneous density of beetles in the trap locality.

It is clear from the preceding that Eq. 1 is at best a caricature of the actual redistribution process of real insects. In fact, it is the simplest possible model of diffusion with disappearance, since it has only two parameters—one for diffusion (D), and one for disappearance (δ). The empirical question is whether this simple, perhaps simplistic, model will provide an ad-

equate description of the data. We will address this issue by applying the model to data from SPB dispersal.

A formula for analyzing mark–recapture data.—In order to obtain an analytical formula with which to fit data, we need to specify the initial and boundary conditions and solve the Eq. 1. At the beginning of a mark–recapture experiment ($t = 0$), N_0 marked beetles are released at the origin of the coordinate system, that is, at $(x, y) = (0, 0)$. Beetles will spread from the release point in all directions uniformly (this follows from the assumption of no drift). Utilizing the resulting circular symmetry, Eq. 1 can be simplified by rewriting it in polar coordinates:

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial r^2} + \frac{1}{r}\frac{\partial u}{\partial r}\right) - \delta u. \tag{3}$$

Here $r = \sqrt{x^2 + y^2}$ is the distance from the release point. For the boundary conditions, we will assume that there is no flux at $r = 0$, and that the population density is zero at $r = \infty$. The boundary condition at $r = 0$ follows from the assumption of symmetry—the number of insects crossing the origin in any direction is balanced by the number of insects crossing in the opposite direction, leading to zero net movement, or flux.

Beetles are recaptured by traps, and the recapture rate is assumed to be proportional to the instantaneous density of insects in the trap locality, $c(r, t) = \alpha u(r, t)$, where the constant of proportionality, α, is the "attractive area of a trap," or recapture efficiency. The cumulative recaptures over the whole course of the study $C(r) \equiv \int_0^\infty c(r, t)\, dt = \alpha \int_0^\infty u(r, t)\, dt$. Note that we have assumed that the number of beetles captured in traps is small relative to N_0; in other words α, the recapture efficiency, is low. If that were not the case, then traps situated nearest the release point would deplete the population of marked insects, preventing them from reaching more-distant traps, and in doing so would distort the true shape of the $\int_0^\infty u(r, t)\, dt$ curve. Paradoxically this means that, far from attempting to maximize the recapture rate, a typical worry in mark–recapture studies, we should instead attempt to *minimize* it, subject to the constraint of recapturing enough beetles for the statistical analysis. We will return to this point in the following section (*The study system*).

The solution of Eq. 3 is well known (Okubo 1980). Substituting the solution of Eq. 3 into the definition of $C(r)$ and integrating over time, leads to the following formula (Carslaw and Jaeger 1959, Awerbuch et al. 1979):

$$C(r) = \frac{\alpha N_0}{2\pi D} K_0\left(\sqrt{\delta/D}\, r\right), \tag{4}$$

where $K_0(z)$ is a modified Bessel function of the second kind. The Bessel function can be approximated with more familiar transcendental functions (Awerbuch et al. 1979), so that

$$C(r) \approx \frac{\alpha N_0 \exp\left[-\sqrt{\delta/D}\, r\right]}{\sqrt{8\pi r}\sqrt[4]{D^3\delta}}. \tag{5}$$

Note that the above formula is of the form

$$C(r) = A r^{-\frac{1}{2}} \exp[-r/B]. \tag{6}$$

$A \equiv (\alpha N_0)/(\sqrt{8\pi r}\sqrt[4]{D^3\delta})$ is the scale parameter, which is proportional to the product of the total number of beetles released and the recapture efficiency. Parameter $B \equiv \sqrt{D/\delta}$ measures the spatial scale of dispersal, or the width of the recaptures-with-distance curve. A population of insects characterized by a large diffusion rate D will disperse farther than a population with small D. Conversely, a high loss rate δ means that the average "lifetime" of moving individuals is short, leaving little time for the dispersal process and leading to limited population spread.

Eq. 6 provides the basis of the statistical analysis of the recaptures-with-distance data. We note that it is not necessary to assume that beetles were released at a single point in time. The solution of Eq. 3 for the instantaneous release can be used to construct by superposition the solution for the case where beetles were released in several batches, or continuously over a period of time. Eq. 6 is similar to the exponential model that is often used in analyses of dispersal distances (e.g., Taylor 1978):

$$C(r) = a \exp[-br]. \tag{7}$$

However, unlike the phenomenological parameters of the exponential model, the parameters of Eq. 6 have a biological interpretation as combinations of D, δ, α, and N_0. Once parameters A and B have been estimated, one can solve for D and δ, provided that N_0 and α are known. Thus, the model (Eq. 1) can provide a method for distinguishing between redistribution and loss terms in mark–recapture studies. We will not be able to do so, because the parameter α is presently unknown for the SPB system (studies to measure α are under way).

Distribution of dispersal distances.—Although the spatial scale of SPB dispersal is completely characterized by the parameter B, a numerical estimate of B is not readily interpretable in biological terms. However, the following argument shows that we can use B to calculate a more intuitive measure of dispersal, i.e., the radius of a circle encompassing a given percent of dispersers.

The number of beetles per unit area terminating dispersal r kilometres from the release point during a short time interval dt is given by the loss term in Eq. 1 multiplied by dt, i.e., $\delta u(r, t)\, dt$ (termination of dispersal could result from death, or from attacking and entering a host tree). First, we multiply this quantity by the area of an annulus with radius r and width dr, to translate beetle density (numbers per unit area) into the absolute numbers: $2\pi r \delta u(r, t)\, dt\, dr$. Second, we sum over time

to obtain the number of beetles terminating dispersal in the annulus between r and $r + dr$ over the course of the replicate: $2\pi r\delta \int_0^\infty u(r, t)\, dt\, dr$. Another way of describing this quantity is the expected number of dispersal end points lying between r and $r + dr$, which is the same as $N_0 M(r)\, dr$, where $M(r)$ is the probability density function of dispersal end points (or distances) and N_0 is the total number of released beetles. Thus,

$$M(r) = \frac{2\pi r\delta}{N_0} \int_0^\infty u(r, t)\, dt.$$

Next, we substitute $\int_0^\infty u(r, t)\, dt = \alpha^{-1}C(r)$:

$$\begin{aligned} M(r) &= 2\pi\delta N_0^{-1}\alpha^{-1} rC(r)/N_0 \\ &= 2A\pi\delta N_0^{-1}\alpha^{-1} r^{1/2} \exp[-r/B]. \end{aligned}$$

Since at present we do not have estimates of the parameters δ and α, we wish to obtain an expression for $M(r)$ that depends only on r and B. Utilizing the fact that $M(r)$ is a probability distribution, and thus $\int_0^\infty M(r)\, dr = 1$, we obtain

$$M(r) = \frac{2A\pi\delta N_0^{-1}\alpha^{-1} r^{\frac{1}{2}} \exp[-r/B]}{2A\pi\delta N_0^{-1}\alpha^{-1} \int_0^\infty r^{\frac{1}{2}} \exp[-r/B]\, dr} \tag{8}$$

$$= \frac{r^{\frac{1}{2}} \exp[-r/B]}{\int_0^\infty r^{\frac{1}{2}} \exp[-r/B]\, dr}. \tag{9}$$

This relationship can be used to calculate the median dispersal distance $r_{0.5}$, that is, the radius of a circle that encloses 50% of dispersers, by numerically solving the equation

$$\frac{\int_0^{r_{0.5}} r^{\frac{1}{2}} \exp[-r/B]\, dr}{\int_0^\infty r^{\frac{1}{2}} \exp[-r/B]\, dr} = 0.5.$$

Similarly, we can determine $r_{0.67}$, $r_{0.95}$, and $r_{0.99}$, the radii enclosing two-thirds, 95%, and 99% of dispersal distances, respectively (numerical solutions were obtained using Mathematica [Wolfram 1988]). These numbers provide readily interpretable statistics describing the spatial scale of dispersal.

The study system

The southern pine beetle, *Dendroctonus frontalis* Zimm. (Coleoptera: Scolytidae), is the most destructive insect pest of southern forests (USDA 1988). Most of the losses due to the SPB occur during outbreaks (which recur every 5–9 yr). The last outbreak (1984–1986) was more devastating than any previous outbreak, causing timber losses valued at $121 000 000 in 1985 alone (USDA 1987).

Gara and Vité (1962) separated bark beetle movements into two phases, dispersal and concentration (or congregation). Congregation occurs as a result of movements in response to the attractive pheromone, frontalin, released by conspecific beetles burrowing into host trees (Vité et al. 1964). Congregation often results in several adjacent hosts mass-attacked by beetles, a phenomenon termed a spot, or an infestation. Spot growth can occur as a result of immigration, when numerous beetles attracted to the original mass-attacked trees shift the focus of attack to the neighboring trees. Additional spot growth can occur as a result of production of the next-generation beetles within the spot. Within-spot SPB movements have been relatively well studied (Gara and Coster 1968, Coster and Johnson 1979).

Because mass attack is an important feature of the SPB biology, a general model for SPB population redistribution needs to have both dispersal and congregation terms. For example, SPB movements can be modelled using the nonlinear diffusion framework (Turchin 1989*b*). However, the focus of our study was specifically on the dispersal phase of SPB movement. It is possible to study the two phases of SPB movement separately because movements of individual beetles are affected not by numbers of conspecific beetles per se, but by conspecifics that have bored into trees. Thus, congregative movements can be minimized by removing hosts that have become foci for mass attack. In other words, in the absence of mass-attack foci, population redistribution in the SPB will be dominated by dispersal, and thus can be approximately described by Eq. 1.

Our use of frontalin-baited traps for recapturing marked beetles (see *Field procedure*, below) deserves discussion since it may appear to be inconsistent with our goal of studying dispersal only. Using pheromone as bait is necessary to increase the catching power of a trap (without bait, traps do not capture sufficient numbers for statistical analysis). There is a critical difference between pheromone-baited traps and mass-attacked foci, however. The process of mass attack is characterized by a positive feedback in which the more beetles congregate at an attacked tree, the more attractive it becomes to other beetles, which in turn attracts even more congregating beetles (until the tree is full). It is the positive feedback nature of mass attack that leads to nonlinear diffusion as the model for congregation (see Turchin 1989*b*). Attraction to a pheromone-baited trap, by contrast, does not increase as beetles are caught in it. This argument shows that using pheromone traps does not necessitate a change in the mathematical structure of the model from simple to nonlinear diffusion.

From the biological point of view, dispersal flight ends when beetles perceive and react to a pheromone trap. This means that if the sum of the attractive areas of all traps constitutes a large proportion of the study area, then released beetles, instead of dispersing, would

be primarily flying in response to these pheromone sources. We have already raised this point earlier when we discussed the undesirability of recapturing too high a proportion of released beetles. Had we attempted to increase the proportion of recaptured beetles, by either increasing the attractive area of traps or by increasing the number of traps, then we would be studying attraction to traps rather than dispersal. Accordingly, in designing the spatial grid of traps around the release point we attempted to minimize the effect of traps on the dispersing beetle population. We did this by placing no traps closer than 50 m from the point of release, and by reducing the number of traps in the vicinity of the release point (two and four at 50 and 100 m, respectively, instead of eight, as at all other distances). A preliminary study indicated that the attractive radius of a pheromone trap in summer is much less than 50 m (P. Turchin, *unpublished data*). This result suggests that the area sampled by traps was only a small proportion of the total study area.

Field procedure

A supply of beetles for use in the mark–recapture studies was secured by locating SPB infestations and cutting infested pines into 1.2–1.8 m lengths (bolts). Bolts containing SPB brood (in the mid-larval through callow adult stages) were transported to release points located at centers of trapping grids. Bolts were coated with a fluorescent pigment (Day-Glo Color Corporation). A piece of tarpaulin was stretched above dusted bolts to protect them from rain. Beetles emerged from bolts over a period of time ranging from 2 wk in summer to >1 mo in fall or spring. Emerging beetles marked themselves by crawling through fluorescent dust prior to taking flight. Preliminary studies showed that the proportion of emerging beetles that were not marked was similar to that of unmarked beetles (Cook and Hain 1992). Fluorescent dust appears to decrease adult longevity in the SPB (Cook and Hain 1992). Since the majority of bark beetles are recaptured soon after emergence, however, this should not cause problems in utilizing the dusting technique in field experiments on dispersal (Cook and Hain 1992).

The total number of released beetles, N_0, was estimated by cutting 0.4-m bolts from the same SPB-infested trees that were used in releases. These bolts were moved to the laboratory and placed into beetle-rearing containers (Browne 1972). Beetle emergence per unit area of bark was estimated by dividing the total number of beetles emerging from each bolt by the surface area of its bark. The number of beetles released in each study was estimated by multiplying the average beetle emergence per unit of bark area by the combined surface area of all bolts used in each release.

Marked beetles were recaptured on a circular grid of funnel traps (Lindgren 1983) centered on the point of release. Forty-six traps were placed in eight cardinal directions at distances from release ranging from 50 m to 1 km (Fig. 1). We used only two traps at 50 m, and only four traps at 100 m for reasons stated above. Each trap was baited with a 0.5-mL vial of frontalin (99.8% chemically pure 1,5-dimethyl-6,7-dioxabicyclo 3,2,1 octane) and a 120-mL (4 oz) bottle of natural steam-distilled turpentine. Traps were censused three times a week, and captured beetles were collected, brought to the lab, and examined under an ultraviolet lamp for fluorescent mark. A subsample of 20 beetles or the total trap collection, whichever was less, was examined to determine sex ratio.

Releases of marked beetles were replicated spatially and temporally. Trap grids were established at four spatial locations in a 10 × 5 km area within the Catahoula Wildlife Management Reserve, Kisatchie National Forest (Louisiana, USA). There was no spatial overlap between grids. At each location, 2–4 releases were made, for a total of 11 releases in 1989 and 1990 (see Table 1).

Since our study focused on SPB dispersal rather than congregation, we attempted to remove all natural pheromone sources within our grids. In this we were aided by generally low numbers of beetles in the area, because during 1989 and 1990 the SPB population in Louisiana was in an endemic phase. However, we released tens of thousands of beetles within our grids, and thus some infestations were inevitable, especially in the vicinity of pheromone-baited traps that provided a focus for mass attack. Incipient spot infestations were detected by examining pines around each trap for pitch tubes. In some cases spots were first detected by unusually high capture rates in traps. When an incipient spot was detected, we felled and removed all trees undergoing mass attack. Control of infestations, however, usually took several days, and in some extreme instances weeks (due to weather conditions, or the sheer number of incipient spots). Because artificially high recapture rates in traps near mass-attacked trees would bias our model-fitting results, we excluded such traps from the analysis.

Statistical analyses

Directionality.—The first step in the statistical analysis of the data was to test the assumption of no directionality, or no drift in SPB dispersal. Without drift, displacements of insects are equally likely to occur in all directions, so that the average displacement is zero. Population drift will cause a shift in the average displacement from the origin, which in turn will be reflected in the spatial distribution of recaptures. Thus, the hypothesis of no drift can be evaluated by calculating the average displacement of recaptures for each of the 11 replicated releases, and testing whether these average displacements are significantly different from zero. The x component of the average displacement of recaptures in replicate j (the y component is defined analogously) is:

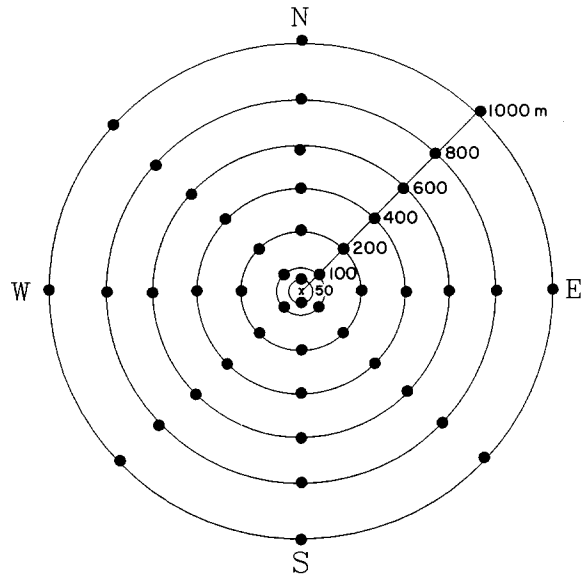

FIG. 1. Recapture grids. Each ● indicates the position of a trap; "x" indicates the point of release.

$$X_j = \frac{\sum_{i=1}^{n} x_i C_{ij}}{\sum_{i=1}^{n} C_{ij}}, \qquad (10)$$

where C_{ij} is the cumulative recaptures in trap i over the course of replicate j, x_i is the x coordinate of the location of trap i, and n is the number of traps. The quantity $x_i C_{ij}$ is the sum of recapture displacements along the x axis of C_{ij} beetles that flew to the trap i. When summed over all n traps, we obtain the sum of x displacements of all recaptures, which is divided by the total number of recaptures to obtain the average x displacement, X_j. When we dropped traps from the analysis due to mass-attack activity, in order not to bias X_j, we have also omitted a trap located at the same distance but in the opposite direction from the release point. The hypothesis that X_j or Y_j were significantly different from zero was evaluated by a t test (Sokal and Rohlf 1981).

Fitting the model.—Assuming no drift, the next step is to fit the model to data using Eq. 6. There are at least two ways of doing this. The first approach we followed was to fit the Eq. 6 directly by means of a nonlinear routine. The problem with this approach was that the data were heteroscedastic, with the variance increasing as the mean increased. Thus, a log transformation was indicated (Sokal and Rohlf 1981).

Our second approach was to log-transform cumulative recaptures before performing regression. This procedure has a desirable side effect of linearizing the relationship (Eq. 6). However, a problem with log-transforming data is dealing with zeros. Adding a small number to the data before log-transforming, the usual procedure in such cases, has an unfortunate effect of changing the functional form of Eq. 6, which would result in the loss of the mechanistic interpretation of the formula parameters in terms of diffusion and loss rates. We avoided this potential problem by first averaging the trap catches for all traps at the same distance from the release point, and then taking log-transforms. This is an especially appropriate procedure for our data set, because the basic statistical unit in the analysis is each replicate release, rather than each trap catch.

Spatial heterogeneity.—As mentioned earlier, we do not know of any analytical results that would allow us to fit the Eq. 2 model with spatially varying diffusion rate to the data. Consequently, we followed a phenomenological, regression approach. The basic idea was to determine whether local stand characteristics have any effect on the recapture rate of a trap. For example, if trap recaptures are higher than expected in traps located in dense pine stands, that would indicate that beetles are aggregating in such localities, either because they engage in area-restricted search (Curio 1976), or possibly because they are attracted to such stands from a distance.

We quantified the local density of host and nonhost trees by measuring the basal area (BA) of pines and the basal area of hardwood species (Husch et al. 1972). Only trees with diameters >10 cm were included in the BA estimate. The effect of stand conditions was evaluated by first calculating for each trap the deviation of its cumulative recapture from the recapture predicted by Eq. 6, and then regressing the deviations on the pine and hardwood basal area in the vicinity of the trap. Both cumulative recaptures and basal areas were transformed prior to the analysis, by adding 0.1 to the data and then taking logs.

RESULTS AND DISCUSSION

Effect of directionality

There was a slight, but apparently significant, shift in the average recapture displacement to the east (Fig. 2). The mean (±1 SE) of X_j, $\bar{X}$, equalled 22 ± 9 m (t = 2.59, df = 10, $P < .05$). The shift in the y direction was not statistically significant ($\bar{Y} = -22 \pm 22$ m, t = 1.0, df = 10, $P > .2$). Even if this drift is real, its effect on dispersal is miniscule—two orders of magnitude less than the scale of diffusion we estimate below (see *Fitting the model*).

Moreover, there is a reason to believe that the result of the t test is of spurious statistical significance. This test assumes that X_js are independent of each other. However, closer inspection of Fig. 2 reveals that the replicate releases conducted at the same spatial grid tend to cluster. In fact, if we exclude the replicate 1-4 (which is an outlier, see *Fitting the model*, below), there is no overlap between the clusters belonging to different

TABLE 1. Summary of replicate releases of southern pine beetles (SPB) and their recaptures, and fits to a model of their movements.

		Numbers of SPB			Model fitting results‡			
					Estimates		R^2 of models	
Replicate	Date	Released	Recaptured*	Used†	A	B	Diffusion	Exponential
1-1	Sep 1989	···§	4569	265	5.20	1.09	0.954	0.945
1-2	Oct 1989	60527	262	119	2.66	0.80	0.946	0.946
1-3	Jun 1990	29460	500	413	8.26	0.68	0.918	0.941
1-4	Jul 1990	4735	77	70	0.64	4.83	0.289	0.198
2-1	Nov 1989	155794	1253	179	4.66	0.87	0.882	0.826
2-2	May 1990	10211	1118	58	···‖	···‖	···‖	···‖
3-1	Jul 1990	···§	110	73	1.99	0.40	0.880	0.871
3-2	Aug 1990	···§	168	123	4.31	0.28	0.975	0.947
4-1	Apr 1990	89861	3805	430	14.48	0.19	0.785	0.722
4-2	Jul 1990	2869	190	190	2.88	0.54	0.628	0.517
4-3	Jul 1990	9143	291	291	6.51	0.33	0.839	0.782

* This number includes beetles recaptured in the vicinity of incipient infestation spots.
† Recaptures used in model fitting.
‡ Model described in *Methods: A model of diffusion . . . : A formula for analyzing mark–recapture data.* The diffusion model is given by Eq. 6, the exponential model by Eq. 7.
§ Estimates not available.
‖ Model was not fitted (see *Results and discussion: Fitting the model*).

grids. This suggests that the apparent directionality in the southern pine beetle (SPB) dispersal may be an artifact of spatial heterogeneity among grids. For example, the apparent drift in grids 1, 3, and 4 could be produced if these grids had a higher concentration of hosts in the east half compared to the west half. We will pursue this idea in *Spatial heterogeneity,* below.

Fitting the model

The replicate 2-2 suffered from a combination of several traps triggering infestations and poor recapture rates in the rest of traps, resulting in 0 average recaptures for two values of r. For this reason replicate 2-2 was omitted from the following analyses.

Before proceeding with estimating model parameters, we asked whether males and females differed in their propensity to disperse. The overall sex ratio of recaptures (the proportion of males) was male-biased, 63%. Regressing the sex ratios of recaptured beetles in each trap on the distance from release revealed no significant trend (F = 1.40, df = 1, 243, P = .25), suggesting that males and females had similar distributions of dispersal distances. Therefore the following analyses did not distinguish between the sexes.

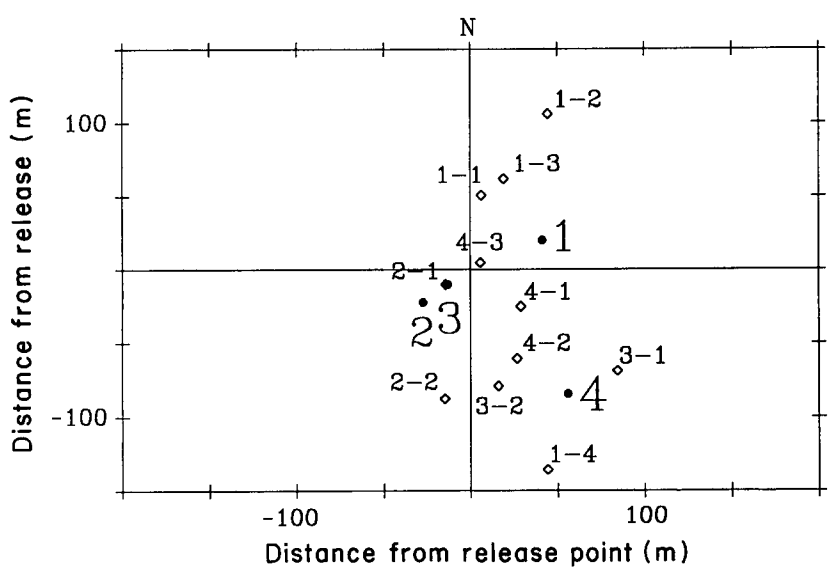

FIG. 2. Directionality effects. Average displacements of recaptures in each replicate release are indicated by ◇. The first number at each diamond represents the number of the spatial grid, while the second number indicates the temporal replicate within each spatial grid. ● with large numbers indicate weighted first moments of the spatial distribution of hosts in each of four grids (see *Results and discussion: Spatial heterogeneity*).

There was a positive relationship between the mean and variance of $C(r)$, the cumulative number of recaptures over the whole course of the study. In fact, plotting the mean of the cumulative number of recaptures in trap i over the course of replicate j, C_{ij}, against their variance for each value of the dispersal distance, r, we obtained an almost perfect linear relationship (linear regression: $R^2 = 0.988$). Thus, it is probably not surprising that fitting the untransformed data with the SAS NLIN routine (SAS 1988) led to some aberrant results. The routine appeared to place most weight on fitting the data at $r = 50$ m (where C_{ij} was greatest), while ignoring the data points at higher r. This led to a systematic bias, in which the fitted curves seriously underestimated C_{ij} at high r, and consequently biased our estimates of dispersal. There is another reason why it is important to obtain good fits at higher r. In order to calculate descriptive statistics, such as radii enclosing x% of SPB dispersal distances, we will need to extrapolate the recaptures-with-distance curve beyond the range of data. For this reason, correct estimation of the shape of the "tail" of $C(r)$ is critical. Because of these problems, we will not report the nonlinear results any further.

The linear regressions using log-transformed data, by contrast, were much better behaved (Fig. 3). Apart from replicate 1-4, the coefficients of determination, R^2, were high (Table 1). Here R^2 is the proportion of variance in log $\bar{C}_{rj}$ explained by the model, where each data point $\bar{C}_{rj}$ is the averaged cumulative number of recaptures in traps at distance r from release point in replicate j. The estimated parameter B in replicate 1-4 was nearly 4½ times as high as the next largest B (Table 1). Combined with an exceptionally low R^2, this suggests that this point is an outlier. Accordingly, we did not use replicate 1-4 in calculating the mean B.

The analysis of residuals showed, first, that the transformation appeared to ameliorate the heteroscedasticity in the data (there was no significant relationship between the mean and the variance). Second, there were no systematic departures in the data from the functional form of Eq. 6. This was investigated by polynomial regressions (up to the cubic order) of residuals on r. In no cases did F values even approach significance. The results of fitting the diffusion model were also compared with the results of fitting the exponential model. The exponential model was fitted to log $\bar{C}_{rj}$, so that the R^2 of both models could be directly compared. Fitting with Eq. 6 resulted in a slight, but significant, improvement over the exponential model (Table 1) ($t = 2.97$, df = 9, $P < .02$). In short, there are no indications in the data that the diffusion model fails in any way to accurately represent SPB dispersal.

We can now use the results of model fitting to quantitatively characterize intraforest dispersal in the SPB. Calculating the radii enclosing x% of dispersal distances, we find that, on the average, an estimated one third of the beetles passed beyond the bounds of our trapping grids (Table 2). This proportion is higher than the one we expected when designing the mark–recapture program, and raises the question of how confidently we can extrapolate recaptures-with-distance curves beyond the distance of 1 km. We believe that in this case extrapolation is justified. First, our approach did not rely on phenomenological curve-fitting of data. Instead, we employed a formula derived by considering the mechanisms determining the shape of the recaptures-with-distance curve. Second, dispersal in mid-summer replicates (July–August; see Table 1) occurred on a shorter spatial scale than fall or spring dispersal. In consequence, in mid-summer replicates trapping grids covered up to 90% of the distributions of dispersal distances. Thus, at least for summer dispersal, extrapolation errors would affect only a small proportion of the population.

Our results show that dispersal is quite variable in the SPB (Table 1). One factor that should influence the distribution of dispersal distances in the SPB is the outbreak status of the area. When infestations are numerous, dispersing beetles will encounter them frequently. This will increase the disappearance rate, δ, because beetles will leave the population of dispersers to join mass attack, and thus shrink the spatial scale of dispersal. Our mark–recapture studies were conducted during the endemic phase of the SPB population in Louisiana, and thus our results are generally relevant to low-density conditions. However, during April 1990 we observed a sudden and short-lived increase in SPB activity, which led to a drastic increase in the number of incipient spots arising during replicate 4-1. As a result, the estimated B for replicate 4-1 was the lowest observed over the whole study.

Another factor affecting SPB dispersal is seasonality. It has been suggested that SPB populations disperse farther during spring and fall months, compared to summer. Indeed, average B (± 1 SE) during the fall months (September through November) was 0.92 ± 0.09, while during the summer months (June through August, but excluding the outlier 1-4) the mean B was half that, 0.45 ± 0.07 (this difference was statistically significant, $t = 4.07$, df = 6, $P < .01$). In terms of the distribution of dispersal distances, this result translates into median dispersal distances of 0.53 km (summer) and 1.09 km (fall). No conclusions can be made about the magnitude of spring dispersal with our data set, because the only replicate that was conducted during the spring was the "outbreak" replicate 4-1.

Spatial heterogeneity

SPB dispersal was also influenced by the spatial distribution of host trees. Regression of deviations from the recaptures-with-distance curve on the local pine basal area indicated a positive, highly significant trend ($F = 8.45$, df = 1, 468; $P < .005$). The coefficient of determination, however, was miniscule: $R^2 = 0.02$.

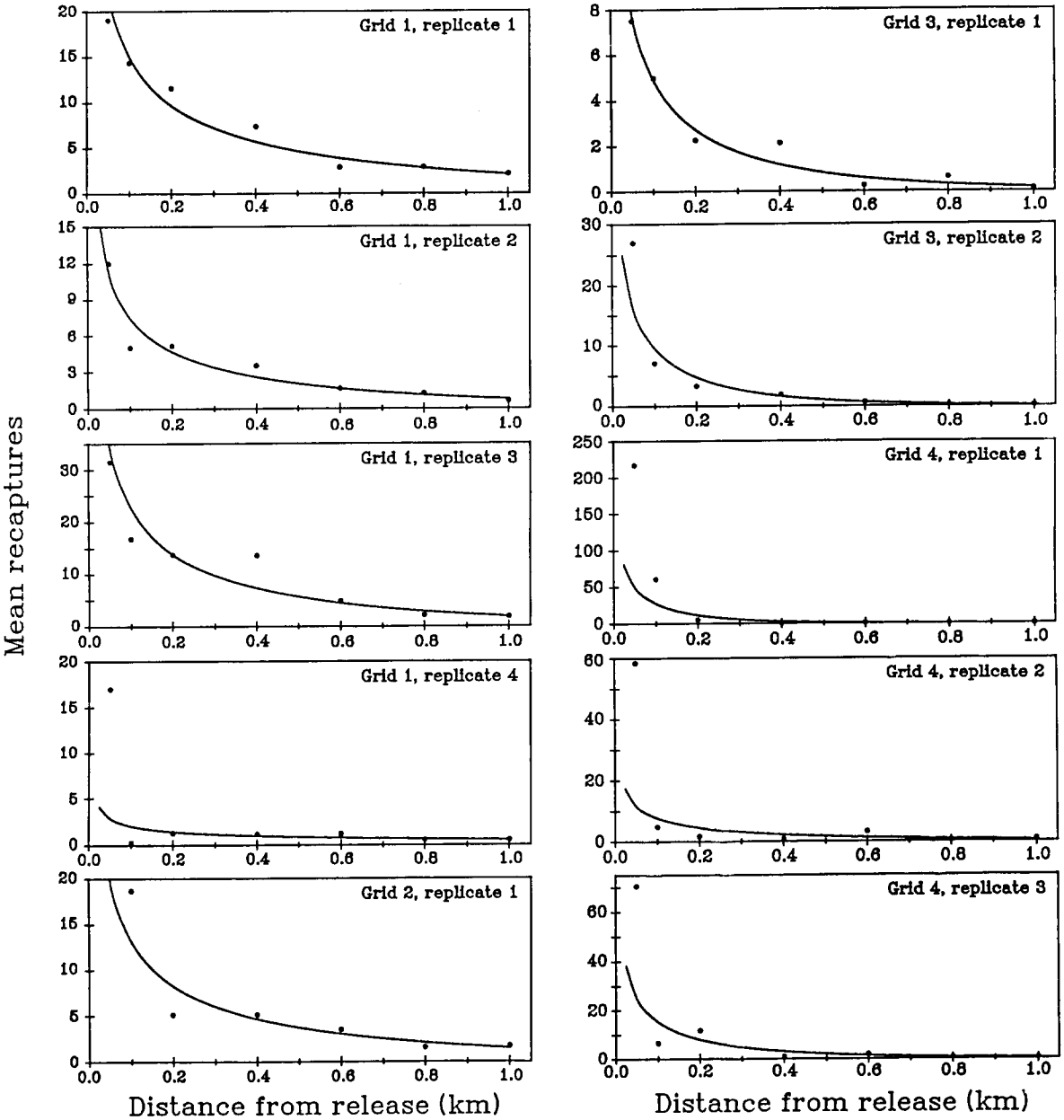

FIG. 3. Recaptures-with-distance curves for each replicate release. The data points are $\bar{C}_{rj}$, cumulative recaptures averaged over all traps r km from release. The solid lines are fitted curves (Eq. 6).

Such a low R^2 indicates that local pine density is only one of many factors affecting trap recapture rate. There was no detectable effect of the hardwood basal area on recaptures.

The significant effect of local pine density on SPB dispersal suggests that at least some of the variation in the average observed displacement (Fig. 2) may be due to a variation in the spatial distribution of hosts. We can approach this question by calculating the spatial coordinates of the center of gravity of pine distribution, in a manner similar to the calculation of the average displacement of recaptures. We cannot use Eq. 10 directly, however, because it gives each spatial position an equal weight, which would imply that the pine density at a point 1 km from the release point exerts an equal influence on the beetle redistribution as does a point 100 m from release. This clearly cannot be true, simply because fewer beetles will pass through a stand at r = 1 km, compared to a stand at r = 100 m. Accordingly, we used a modified formula in which pine basal area was weighted by the recaptures-with-distance curve:

TABLE 2. Estimated radius of a circle enclosing various proportions of southern pine beetle dispersal distances.

Proportion enclosed	Estimated radius (km)	95% confidence interval
0.50	0.69	[0.45, 0.92]
0.67	0.99	[0.65, 1.34]
0.95	2.27	[1.48, 3.05]
0.99	3.29	[2.16, 4.42]

$$X_j = \frac{\sum_{i=1}^{n} x_i \hat{C}(r_i) B_{ij}}{\sum_{i=1}^{n} \hat{C}(r_i) B_{ij}}. \quad (11)$$

Here X_j is the x component of the center of gravity, B_{ij} is the basal area of pines around a trap i in the grid j, $\hat{C}(r_i)$ is the estimated recaptures-with-distance curve, and other variables as before. Plotting these centers of gravity in Fig. 2, we observe that in three out of four grids (1, 2, and 4) the shift in the average displacement of recaptures occurred in the same general direction as the shift in the pine center of gravity. This result provides further evidence that SPB dispersal occurs without drift, and that observed shifts in SPB average displacements were an artifact of spatial heterogeneity between grids.

CONCLUSION

Implications for management of southern pine beetle (SPB)

Our results indicate that the SPB possesses a respectable dispersal ability for an insect only ≈3 mm long: an estimated one third of the population dispersed farther than 1 km in mark–recapture experiments. We found that during summer months beetles dispersed approximately half as far as during fall months, and that beetles were apparently attracted to well-stocked pine stands. Our results are primarily relevant to an endemic situation. During an outbreak dispersal distances will probably be reduced because beetles will not need to fly as far to encounter mass-attacked trees.

These empirical results have important implications for management of the southern pine beetle. Currently the primary objective of all Federally supported SPB suppression projects is to control expanding beetle spots to minimize tree killing and timber resource losses, rather than area-wide management of SPB populations (USDA 1987; 2-1). One of the four spot-control strategies recommended by the U.S. Forest Service (USDA 1987), cut-and-leave, is based on a manipulation of SPB movements. In this method of spot suppression SPB-infested pines and a buffer strip of unattacked trees are felled to prevent the further growth of a spot. The rationale for cut-and-leave is based on the observation that spot growth is disrupted by this treatment (Billings 1980). It has been suggested that "beetles that are forced by the effects of control to fly farther than the next trees are likely to die" (USDA 1987). However, it is also possible that beetles could immigrate to other infestations in the vicinity of the treated spot, especially during epidemic conditions (Kelley et al. 1986). Our data suggest that beetles are capable of dispersing quite far. Even in summer, when cut-and-leave is recommended because dispersal powers of beetles are thought to be lowest, the estimated median dispersal distance was 0.53 km. This result suggests that more research is needed on the consequences of cut-and-leave for SPB dispersal. In particular, future research could directly measure the effect on SPB dispersal of treating a spot with cut-and-leave, as well as on SPBs ability to initiate new spots after dispersing. In addition to traditional control methods, novel techniques using anti-congregation pheromone are currently being tested for their potential to disrupt spot growth (Payne and Billings 1989). However, the fate of beetles emigrating from spots treated with anti-congregation pheromone is unknown, and needs to be determined.

Implications for mark–recapture studies of insect dispersal

Our results also indicate that a simple theoretical model of diffusion with disappearance can provide an accurate and quantitative description of the dispersal process in at least one economically important insect. The analytical formula derived on the basis of the model accurately summarized the observed recaptures-with-distance curves. First, apart from one replicate release, the two-parameter formula described a high proportion of variance in the data. Second, statistical analysis of residuals indicated no systematic departures from the functional form predicted by the model of diffusion with disappearance. Moreover, the model consistently outperformed another formula commonly used in the analysis of dispersal distances, the exponential curve. In sum, the model of diffusion with disappearance provides a robust basis for a methodology for analyzing mark–recapture experiments and estimating the distribution of dispersal distances.

Needs for future mathematical research

The analytical formula describing the relationship between recaptures and distance from release was derived under the assumption of homogeneous space. Assumption of homogeneity appears to provide a good first-order approximation of the overall dispersal in insects (e.g., Dobzhansky and Wright 1943, Dobzhansky et al. 1979, Kareiva 1983, this study). Nevertheless, in many situations the effects of spatial heterogeneity could be of importance. We have attempted to account for spatial heterogeneity by correlating local environmental variables, such as host density, with the deviations in trap recaptures from the expected recapture predicted by the spatially homogeneous model. Our

results were not wholly satisfactory: although we detected highly significant effects of pine density, the R^2 of the relationship was extremely low. It is likely that the density of beetles in a stand will depend not only on the local conditions in the stand, but also on the global spatial distribution of resources.

Estimation of spatially variable diffusion coefficients from mark–recapture data is in its infancy. Dobzhansky et al. (1979) used a computer algorithm that chose values for $D(x, y)$ (the diffusion rate) that resulted in the best fit to observed data. This procedure is highly technical and computationally intensive, since for each set of $D(x, y)$s the partial differential model has to be solved numerically. A similar approach was proposed by Banks et al. (1985, 1987), whose algorithm is so computationally intensive that it had to be solved using the Cray supercomputer. Clearly, there is a need for simpler and more accessible methods for quantifying dispersal in heterogeneous landscapes.

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