

The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey

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Theoretical studies of predator-prey population dynamics have increasingly centered on the role of space and the movement of organisms. Yet, empirical studies have been slow to follow suit. Herein, we quantified the long-range movement of a checkered beetle, *Thanasimus dubius*, which is an important predator of a pernicious forest pest, the southern pine beetle, *Dendroctonus frontalis*. Adult checkered beetles were marked and released at five sites and subsequently recaptured at traps baited with pine and pine beetle semiochemicals and located at distances up to 2 km away from the release point. While the pattern of recaptures-with-distance at each site provided a modest fit to a simple random-diffusion model, there was a consistent discrepancy between observed and expected recaptures: a higher than expected proportion of beetles were recaptured at the more distant traps. To account for this deviation, we developed a model of diffusion that allowed for simple heterogeneity in the population of marked beetles; i.e., a slow and fast moving form of the checkered beetle. This model provided a significantly better fit to the data and formed the basis for our estimates of intra-forest movement. We estimated that on average, one half of the checkered beetles dispersed at least 1.25 km, one third dispersed > 2 km, and 3% dispersed > 5 km. The source of the heterogeneous dispersal rates were partially due to differences in beetle size: smaller beetles (for both males and females) were more likely to be recaptured away from the release site than larger beetles. The southern pine beetle (prey for the checkered beetle) exhibited no significant heterogeneity in dispersal ability and provided a very good fit to the simple diffusion model. The only difference in dispersal between these two species was that checkered beetles were undergoing greater long-distance dispersal than the pine beetles (the radius containing 95% of the dispersing individuals was 5.1 km for the checkered beetle and 1.3 km for the pine beetle). Data on the movement of these two species is used to evaluate a general model of spatial pattern formation in a homogeneous environment, and the potential of the checkered beetle as a biological control agent for the southern pine beetle.

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Numerous theoretical studies have established how spatial patterning can arise in prey and predator populations that exist together within a homogeneous landscape (e.g., Mimura and Murray 1978, Dunbar 1983, Murray 1989, Kareiva 1990, Comins et al. 1992, Hassell and Wilson 1997, Turchin et al. 1998). Among

these models, the movement patterns of the predators relative to their prey appear to play a critical role in determining whether and what types of spatial patterns could form. For example, using a coupled-map lattice or cellular automata model, Comins et al. (1992) found that low host dispersal, coupled with high parasitoid

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dispersal can lead to the formation of spatial chaos or crystal lattice-like (i.e., checker-board) structures in the prey population (see also Hassell et al. 1991, Hassell and Wilson 1997). Similar results were found for models in which the spatial dimension was continuous and movements were described using a diffusion framework (Levin and Segel 1976, Mimura and Murray 1978, Kareiva 1990, Wolkind et al. 1991, Turchin et al. 1998). In these models, "diffusive instability" or permanent spatial patterning arises when, among other things, predators are more dispersive than their prey.

Despite the plethora of models on spatial patterning in predator-prey systems, it is clear that our empirical base of support for these models is disproportionately low: few empirical studies have examined the pattern and process of movement in both predator and prey species in nature (but see Kareiva 1986, 1987, Jones et al. 1996). Its relative lack of empirical support has been attributed to the inherent difficulties in studying the movement of small, short lived and often highly mobile species. We also lack information on the movement of animals at appropriately broad spatial scales. The vast majority of ecological studies, approximately 35%, are performed on the scale of less than 100 m (Kareiva and Andersen 1988, Turchin 1998). In contrast, organisms such as insect pests typically move on the scale of hundreds of meters to tens of even hundreds of kilometers (Southwood 1962, Stinner et al. 1983). Clearly, additional and more broad-scale studies are needed if we hope to test the predictions of this largely untapped wealth of theory.

The southern pine beetle (*Dendroctonus frontalis* Zimmermann; Coleoptera: Scolytidae) is a significant pest of pine forests in the southeastern United States and averages more than \$30 million in timber losses per annum (Price et al. 1992). In National Forest lands that are dominated by suitable pine hosts, Turchin and Thoeny (1993) have found that the movement of the southern pine beetle (SPB) is accurately described by a simple diffusion process and that the range of movement of this pest is quite large (> 1 km). Simple diffusion theory would predict that at equilibrium, the SPB population should be homogeneously distributed throughout the forest (Levitt and Segel 1976, Mimura and Murray 1978, Turchin 1998, Turchin et al. 1998). However, the SPB's spatial distribution in nature is characterized by a high degree of spatial patterning (Thatcher et al. 1980, Turchin et al. 1998); pine beetles occur in very spatially discrete aggregations. This allows for the interesting possibility that the observed spatial patterning may be influenced by the interaction between the SPB and one or more of its natural enemies. Until now, we have had no information on the movement of any of these enemies that could be useful in evaluating theory on spatial pattern formation.

In this study, we quantified the pattern and range of movement of a checkered beetle, *Thanasimus dubius* F.

(Coleoptera: Cleridae), an important predator of the southern pine beetle. We performed a large scale mark-recapture experiment with the checkered beetle that was analogous to the experiment performed previously by Turchin and Thoeny (1993) with the southern pine beetle. Herein, we tested the fit of a simple diffusion model to checkered beetle recapture data and compared it to the fit of a more complicated model that we developed, one that allows for heterogeneous rates of dispersal within the population. The pattern and range of movement of the checkered beetle was then compared with that of its pine beetle prey. We conclude by using these data to evaluate a general model of spatial pattern formation.

Materials and methods

Study organisms

The life cycle of the SPB is well known (e.g., Thatcher et al. 1980) and only a brief description is provided below. Upon attack by the SPB, pines defend themselves by exuding resin (Hodges et al. 1979). When only a single beetle or even a small group of beetles breach the bark surface of a healthy tree, they are usually thwarted by the exudation of copious amounts of resin. However, SPB adults utilize pine terpenoid byproducts (α -pinene) in combination with their own pheromone (frontalin) to elicit congregative behavior toward its host (Kinzer et al. 1969, Renwick and Vité 1969, Payne et al. 1978). This mass attack overwhelms the host's defenses and allows the beetles to successfully gain access to the phloem tissues beneath the bark surface. Consequently, there is a striking Allee effect in the growth rate of the SPB within a tree. As a tree begins to fill with beetles, the SPB in the vicinity usually shift attack to a different host, most frequently an adjacent pine (Payne 1980). This results in a concentrated area of infestation known as a spot. After offspring complete their development within a spot, they either contribute to spot expansion or disperse in search of new or other existing spots (Hain 1989, Turchin and Thoeny 1993, Cronin et al. 1999). As a result of their congregatory behavior, the pine forest landscape resembles a patchwork of spatially discrete SPB aggregations (Turchin et al. 1998).

Adult checkered beetles are attracted to the volatiles released by the SPB and pine tree, and are among the earliest natural enemies to arrive after the pine beetle attack sequence has been initiated (Vité and Williamson 1970, Dixon and Payne 1979a, b, 1980). These predators capture and consume pine beetle prey on the bark surface and then lay eggs within the fissures and underneath bark chips of the tree's trunk (Thatcher and Pickard 1966, Dixon and Payne 1979a, Reeve 1997). After hatching, the larval checkered beetles enter the

pine beetle galleries and feed on the developing SPB (Thatcher and Pickard 1966, Dixon and Payne 1979). Several lines of evidence suggest that the checkered beetles may play an important role in SPB population dynamics: 1) they occur in high abundance on the bark surface of attacked trees (Reeve 1997), 2) mortality inflicted by adult checkered beetles can exceed 60% (Reeve et al. 1995, Reeve 1997), 3) at the scale of a whole Nation, Forest, checkered beetles exhibit a numerical response to their prey and a negative density-dependent relationship between SPB population growth rate and checkered beetle density (Reeve 1997), and 4) development rates of the checkered beetle are asynchronous with that of their prey which may destabilize SPB population dynamics (Reeve et al. 1996). These four factors may contribute to the oscillatory population dynamics (Turchin et al. 1991, 1999) and the formation of spatial patchiness in the distribution of SPB (Turchin et al. 1998).

Mark-recapture study

Checkered beetle mark-recapture experiments were conducted in the Catahoula and Winn Districts of the Kisatchie National Forest, Louisiana, USA. Two sites were chosen from the former (CAT-I and CAT-II) and one from the latter (WINN) district and all three shared the following characteristics: 1) trap transects radiating outward from the checkered beetle release point consisted predominantly of host trees suitable for the prey's development (loblolly [*Pinus taeda*] and shortleaf [*P. echinata*] pine); 2) transects were not divided by unsuitable habitat (except occasionally by gravel service roads); and 3) pine beetle infestations were absent from the area (as determined by ground and aerial surveys). CAT-I and II were separated by a distance of 8.6 km and both were more than 35 km from WINN.

Trap stations were established in four cardinal directions and at fixed distances of 0.1, 0.2, 0.3, 0.4, 0.5 km (for replicate 1) a trap at 0.35 km was used in place of traps at 0.3 km and 0.4 km), and every 0.25 km thereafter to a distance of 2 km from the center of the site (only two stations were used at a distance of 0.1 km to avoid excessive recaptures at the most proximal traps). At each station a single multi-funnel trap (Lindgren 1983) was deployed. Traps were 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 bottle of natural steam-distilled turpentine released using a cotton wick. This trapping method has routinely been used to census both pine beetle and checkered beetle population densities and forms the basis for forecasting population trends (Billings 1988, Turchin et al. 1991).

We initially used the trapping grids to obtain adult checkered beetles for the mark-recapture study. Traps were checked daily and the contents immediately transported to the laboratory where the beetles were stored at 10°C. Most insects for this study were kept in cold storage for ≤ 7 d; all were kept ≤ 14 d. This procedure appears to have no significant detrimental effects on checkered beetle behavior (unpubl.). Once sufficient numbers (500 minimum) had been collected, each beetle was marked with a spot of enamel paint on its pronotum. A minimum of 45 of these marked animals were randomly drawn from the collection and placed in the freezer for later estimation of the sex ratio and measurement of body size (mean elytra length in mm). The remaining marked beetles (only active and apparently healthy insects) were transported to the center of an experimental site and placed in cages, formed around the trunks of two pines. The cages were 1-m long cylindrical enclosures that were constructed of fine polyethylene screening and tied loosely at both ends to the trunk of the tree (see Reeve 1998). Checkered beetles were placed in these cages to give them sufficient time to equilibrate to their new environment and reduce the likelihood of dispersal in response to this trauma. After 30 min, the cages were removed.

Funnel traps were checked daily for the first week and then twice weekly until the recapture rate declined below a few individuals per census date. We added a small piece of No-Pest Strip (Bio-Strip, Reno, NV; active ingredient, 2,2-dichlorovinyl dimethyl phosphate) to each funnel's collecting cup to kill the beetles before they could escape. Trap contents were returned to the laboratory and the number of marked checkered beetles determined for each direction and distance. We further recorded the sex of each recaptured insect and its mean elytra length (in mm). A total of five replicate dispersal experiments were performed among the three sites. Site summaries are provided in Table 1.

Table 1. *Thanasimus dubius* mark-recapture replicates.

Replicate	Location	Date initiated	Number released	% recaptured
1	CAT-I	15 March, 1994	500	38.4
2	CAT-I	19 April, 1994	911	28.5
3	CAT-I	11 November, 1994	647	10.1
4	CAT-II	6 April, 1995	847	40.3
5	WINN	17 May, 1995	402	21.6

Predicting spread with a diffusion model

For each replicate mark-release experiment we computed $C(r)$, the cumulative number of checked beetles recaptured at each distance r from the release point. At traps nearby the release point, $C(r)$ was often high relative to the total number of beetles released, thus depleting the number of insects available for recapture at more distant traps. To correct for this problem, we multiplied $C(r)$ by $N_0/(N_0 - \Sigma C_p)$, where N_0 is the number of marked beetles released and ΣC_p is the sum of all beetles recaptured at distances more proximal to the source than r . This correction factor represented the remaining marked beetles that were available for recapture at more distant traps (r and beyond).

We compared the corrected recapture data with the pattern of spatial spread predicted by a simple diffusion model. Turchin and Thoeny (1993) provided the derivation for the following analytical formula for predicting spatial spread (see also Awerbuch et al. 1979, Okubo 1980):

$$C_r = Ar^{-1/2} e^{-r \cdot B} \quad (1)$$

Here,

$$A = \frac{\alpha N_0}{\sqrt{8\pi \cdot D \cdot \delta}} \quad (2)$$

where α = recapture efficiency of the trap, N_0 = marked beetles released, D = diffusion rate and δ = disappearance rate (death or emigration from the experimental grid). The parameter A is known as the scale parameter and is proportional to the product of the number of beetles released and the recapture efficiency. $B = \sqrt{D \cdot \delta}$ is a measure of the spatial scale of dispersal. An insect population with a large value of B would have a greater dispersal range than one with a smaller B . The 'real value' of this particular model is that it is based on parameters that can be quantified through experimentation. However, we do not attempt in this study to estimate the unknown parameters comprising A and B (α , D and δ). We do note, though, that checked beetle adults are fairly long lived relative to the duration of the mark-recapture experiments (6-8 wk in the laboratory; Turnbow et al. 1978, Lawson and Morgan 1992), suggesting that δ in this case is primarily a measure of emigration loss.

The model above has the linear form,

$$\ln(C_r) + \frac{1}{2} \ln(r) = \ln(A) - r \cdot B \quad (3)$$

and can be fit using least-squares regression (Sokal and Rohlf 1995). Turchin and Thoeny (1993) provide the methodology for converting B into a more intuitive measure of dispersal - the radius of a circle, r_x , encompassing a given percentage of dispersers (x). Here, r_x is determined by numerically solving the equation

$$x = \frac{\int_0^{r_x} r^{1/2} \exp[-r \cdot B] dr}{\int_0^{\infty} r^{1/2} \exp[-r \cdot B] dr} \quad (4)$$

The median dispersal distance (i.e. the radius enclosing 50% of the dispersers) is determined by solving for $x = 0.5$. Similarly, we determine the radii enclosing 66.7% and 95% of the dispersers by solving for $x = 0.667$ and 0.95, respectively. Numerical solutions for these dispersal quantiles were obtained using Gauss 3.0 (Aplice Systems Inc. 1992).

The pattern of recaptures with distance has been known to depart from the distribution predicted by simple diffusion models (Dobzhansky and Wright 1943, 1947, Inoue 1978, Okubo 1980, Kareiva 1983, Turchin 1998, Plant and Cunningham 1991). Among insects, these deviations often take the form of a leptokurtic distribution: i.e. lower-than-expected recaptures near, and greater-than-expected recaptures farther away from the source (Turchin 1998). Leptokurtic distributions may arise when there are heterogeneities in the population, for example, when the population is comprised of two or more subgroups that have different dispersal capabilities. Although the Bessel function subsumed in model (1) causes the distribution of recaptures to be slightly leptokurtic, we can account for stronger leptokurtosis, and hence heterogeneous dispersal abilities, by allowing for two values of A and B . In this case, eq. (1) is re-written as the summation of two diffusion models (the heterogeneous diffusion model):

$$C_r = A_1 r^{-1/2} e^{-r \cdot B_1} + A_2 r^{-1/2} e^{-r \cdot B_2} \quad (5)$$

where A_1 and A_2 and B_1 and B_2 are the scaling parameters and the scale of dispersal, respectively, for the two types of dispersers. This model is one of the first of its kind that allows for both the disappearance of insects (δ) and heterogeneity in dispersal ability (see also Plant and Cunningham 1991). We tested the fit of this heterogeneous diffusion model to the combined data from all Kvc replicates. Here, pooling was necessary to increase the observations upon which the four parameters were to be estimated. We standardized recaptures among replicates by dividing the number of recaptures at each distance within a replicate by the total number of marked checked beetles released in that replicate. The proportion recaptured at each distance was fit to eq. (5) and parameters estimated using nonlinear regression in SYSTAT 8.0 (Wilkinson 1998). Dispersal quantiles were derived by solving for r_x in a similar fashion to eq. (4). Ninety-five percent confidence intervals (CIs) for A_1 , A_2 , B_1 and B_2 were obtained through bootstrapping: for 1000 repetitions (bootstrap samples), five dispersal replicates were drawn at random (with replacement) and used to estimate the four parameters (Efron and Tibshirani 1993, Manly 1997). The range of

values enclosing 95% of the bootstrapped estimates of each parameter represented the 95% CIs.

We note that this is only a phenomenological model in which, a priori, we have no evidence of a heterogeneous population of dispersers. Our intent here was to obtain a robust estimate of dispersal distances from a model that is best supported by our data. However, if the heterogeneous diffusion model represents a more appropriate description of checkered beetle recaptures-with-distance, the two scale-of-dispersal parameters, B_1 and B_2 , are expected to be significantly different (i.e., that there are two different kinds of dispersers in the population). To determine if the difference was significant, we examined whether the asymptotic 95% CI of $B_2 - B_1$ (from the nonlinear procedure in SYSTAT) was significantly different from zero. Below, we explore the possibility that differences between male and female checkered beetles or variations in size may be a source of heterogeneous dispersal abilities within this population.

Net displacement

The models we used assumed that a population's net displacement or directionality in space should be zero. We tested this prediction for our mark-recapture study by determining the net displacement of marked checkered beetles in each experimental replicate (Turchin and Thoeny 1993). To accomplish this, we first designated the checkered beetle release point as the origin of a two-dimensional plane (x and y coordinates equal zero). The east-west and north-south transects corresponded to the x - and y -axis, respectively. Net displacement (ND) of recaptured checkered beetles along the x -axis was $ND = (\sum x C_x) / N$, where x = recapture distance along the east-west transect, C_x = number of recaptures at distance x , and N = total number of recaptures along the transect. A similar procedure was used for calculating displacement along the y -axis. To avoid biasing displacement estimates, when a trap was missing on one arm of a transect (e.g., east), we deleted the trap at the same distance on the opposite arm (west).

Effects of sex and size

Sex-related differences in dispersal were addressed in two ways. First, we assessed whether the sex-specific dispersal data were better fit by the heterogeneous diffusion model (5) than the simple diffusion model (1). Proportions of each sex recaptured-with-distance, for all sites combined, were fit to model (5) and the asymptotic 95% CIs surrounding the difference between the scale-of-dispersal parameter, $B_2 - B_1$, were computed. If the CIs did not overlap zero, this would indicate that heterogeneous dispersal rates occur within each sex and

that the more complex model (5) would provide a better fit to the male and female dispersal data. Second, we performed an analysis of covariance to determine the effect of sex (main effect) and recapture distance (covariate) on the proportion of checkered beetles recaptured. Proportion recaptured was transformed using $\ln(C_x) + \frac{1}{2} \ln(r)$ to comply with the linear dispersal model (3). A quadratic term (r^2) was also added to the model to account for any nonlinear change in recaptures-with-distance.

Because insect size may affect dispersal ability or survivorship (recall that θ is determined by the diffusion and disappearance rate), we examined whether checkered beetle size (mean elytra length) varied with recapture distance. In this analysis, all replicates were combined and distances were divided into six classes: 0 km (the random sample obtained from pre-released beetles), 0.10 km, 0.20 km, 0.30 km, 0.45 km (traps at 0.40 km and 0.50 km combined), and 1.25 km (all traps beyond 0.50 km combined). A two-way completely randomized fixed-factor ANOVA was used to determine the effect of checkered beetle sex (females are generally larger than males) and recapture distance on elytra length. Differences among means were analyzed with Tukey's HSD test (Sokal and Rohlf 1995).

Comparison of prey and predator dispersal

One purpose in quantifying the range of dispersal of the checkered beetle was to enable comparison to the dispersal of its prey, the SPB. Turchin and Thoeny (1993) have previously quantified the movement patterns of the latter species using a design directly comparable to one presented here. Nine dispersal replicates are reported in their study, each providing a close fit to the simple diffusion model (1). We evaluated whether the data were better described by the heterogeneous diffusion model using the criteria outlined above for the checkered beetle. The better of the two models were used to compute 50%, 66.7% and 95% dispersal quantiles and we compared the 95% CIs of the SPB quantiles with those from the checkered beetle.

Results

Predicting spread with a diffusion model

The average number of checkered beetle recaptures (based on traps positioned in four cardinal directions at each distance) declined significantly with increasing distance from the point of release (for all five replicates, $P \leq 0.032$; Fig. 1). The linear model (3) based on a simple diffusion process explained an average of 64% of the variation in the recapture data (based on the coefficient of determination, R^2 ; Table 2), suggesting that as a first approximation, checkered beetle dispersal can be

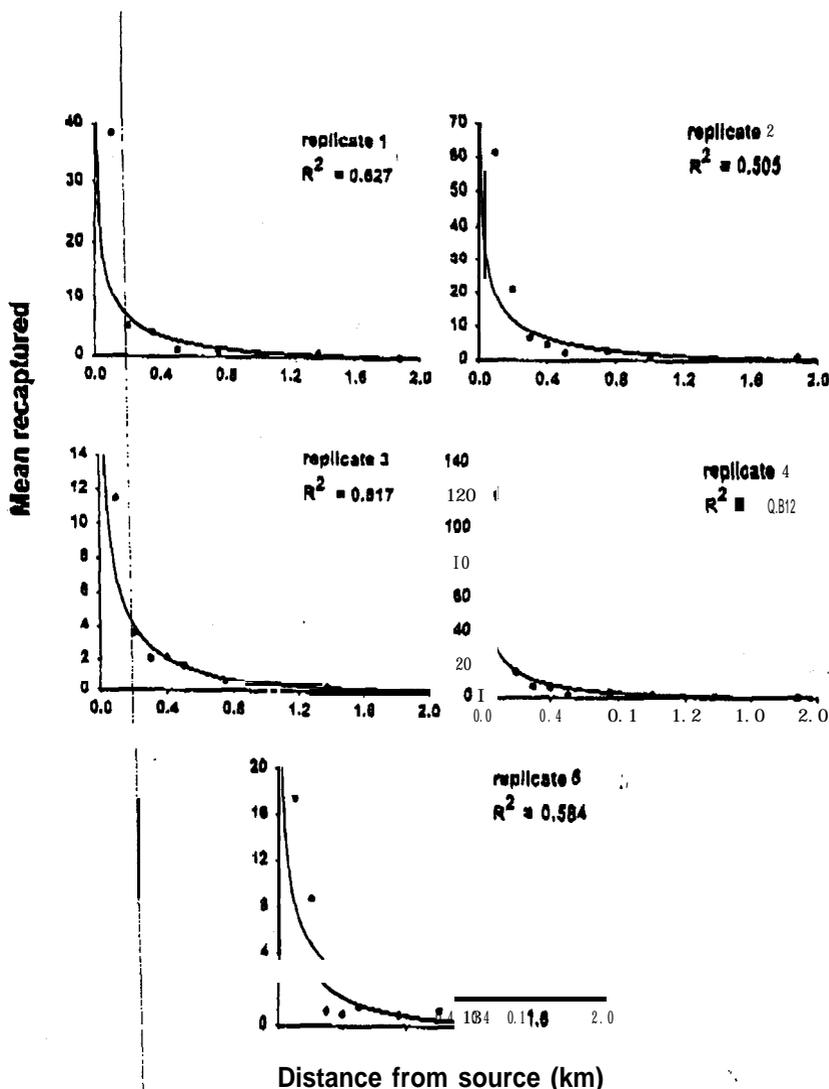


Fig. 1. Checkered beetle recaptures with distance for the five experimental replicates. Curve is based on the simple diffusion model (eq. 1), and coefficient of determination, R^2 , is based on least-squares regression using eq. 3.

adequately characterized by a simple diffusion process. The 50%, 66.7% and 95% dispersal quantiles based on this model are presented in Table 2.

Although the dispersal data are reasonably approximated by model (1), there is a clear pattern of deceleration in the slope of the recaptures. In three of five replicates (2, 3, 4), a significant quadratic term indicated that the relationship was curvilinear, not linear as model (3) would predict. The heterogeneous diffusion model was able to account for this nonlinear pattern of recaptures with distance (Fig. 2A), and provided a better fit to the data ($R^2 = 0.753$). A significant difference between the two scale-of-dispersal parameters, B_1 and B_2 (95% CI's for $B_2 - B_1$ was 0.39, 2.26), suggested that there is important heterogeneity in the dispersal ability of the checkered beetles, and argues in support of the acceptance of this over the simple diffusion model. By allowing for a more leptokurtic (fat-tailed) distribution of recaptures, this model predicted dispersal quantiles that were broader than those from the simple diffusion model (Table 3).

Irrespective of the choice of diffusion model, the net displacement of checkered beetles, on average, did not deviate significantly from the origin (Fig. 3). This supports one of the basic assumptions of both models: beetles should diffuse equally in all directions from the point of origin.

Effects of sex and size

When checkered beetles were divided by sex, we still observed a nonlinear pattern of recaptures-with-distance (Fig. 2B, C). However, our criteria for accepting the heterogeneous model (and nonlinearity in the recaptures-with-distance), that $B_2 - B_1$ is significantly greater than zero, was not met for either the males (95% CI: -2.04, 5.82) or the females (-0.65, 4.31). A reduction in statistical power of our test, resulting from using half as much data as the test for all recaptured beetles (Fig. 2A), may explain the lack of significant curvature in male and female recaptures-with-distance.

The pattern of recaptures-with-distance did not vary significantly between male and female checkered beetles. Based on an ANCOVA, we found a strong effect of the covariate distance ($F_{1,61} = 41.42$, $P < 0.001$) and the quadratic term, distance \times distance ($F_{1,61} = 22.78$, $P < 0.001$; indicative of a nonlinear relationship), but no effect of sex or distance \times sex ($F_{1,61} = 0.02$, $P = 0.882$ and $F_{1,61} = 0.03$, $P = 0.866$, respectively) on the natural log of the proportion recaptured ($+\frac{1}{2} \ln(p)$). Finally, we did find an effect of checkered beetle size on dispersal. In general, there was a significant, but gradual, decline in the size of recaptured beetles with distance (Fig. 4). Most notably, checkered beetles recaptured in funnel traps were significantly smaller than those in the collection of beetles that were originally marked and released ($F_{1,1011} = 37.47$, $P < 0.001$). For females, there was a continual decline in size of recaptured insects, but not for males (Fig. 4).

Comparison of prey and predator dispersal

For each of the southern pine beetle dispersal replicates (see Turchin and Thoeny 1993), as well as for all replicates combined (Fig. 5), we were unable to detect nonlinearity in the dispersal curves. In addition, all attempts to fit the heterogeneous diffusion model to SPB recaptures failed to converge on a unique solution. This probably occurred because the heterogeneous diffusion model has more parameters than are needed to fit these apparently linear data, i.e. the model was overparameterized (Draper and Smith 1981). We therefore accepted the simple diffusion model as the most appropriate for the SPB and used the parameter estimates from Turchin and Thoeny (1993; see Table 4). Based on a comparison between the two species, we found no difference in the radius containing 50% and 66.7% of the dispersing insects (Table 4). However, the radius containing 95% of the insects was significantly greater for the checkered beetle than the SPB. This difference is apparently due to the long tails in the recaptures-with-distance for the checkered beetle: that

is, proportionately more predators are dispersing long distances than their prey. The extreme distances that the checkered beetles are capable of dispersing is demonstrated by two marked beetles that were recaptured more than 8 km away in funnel traps used for other research projects.

Discussion

Despite the widespread acceptance that spatial heterogeneity and movement are of considerable consequence to the population dynamics of predators and their prey (for recent reviews see Hanski and Gilpin 1997, Tilman and Kareiva 1997, Turchin 1998), the southern pine beetle-checkered beetle system represents one of the very few in which we have quantitative data on the pattern and scale of movement of both predator and prey species. What makes this even more unique is that the scale of dispersal spans more than 2 km: few studies of any species have quantified movement patterns exceeding an area this large (Turchin 1998).

The redistribution pattern of checkered beetles following their release was in reasonable accord with the expectations of a simple diffusion model (Okubo 1980, Kareiva 1983, Turchin 1998). This pattern of diffusion, in which recaptures were highest at the point of origin and dropped off at a decelerating rate with distance, has been found for a number of insect species (e.g., Kareiva 1983, Turchin 1998). However, our data deviated significantly from these expectations in that we consistently had higher-than-expected rates of recaptures in the more distant traps. This leptokurtic distribution (having fat tails) is not at all an uncommon source of deviation from simple diffusion models, and is thought to be commonly brought about by heterogeneous diffusion rates within the population (Inoue 1970, Okubo 1980, Kareiva 1983, Plant and Cunningham 1991, Turchin 1998). Dobzhansky and Powell (1974), for example, provided evidence for genetically based differences in diffusion rates within *Drosophila pseudoobscura*: flies carrying the recessive gene for orange eye had lower diffusion rates than wild-type flies.

Table 2. Parameter estimates and dispersal quantiles (radius of a circle, in km, enclosing different proportions of dispersers) for the checkered beetles based on a simple diffusion model (eq. 1, see Methods). Coefficients of determination (R^2), the proportion of the variance in recaptures that was explained by the model, were obtained by least-squares regression.

Replicate	A	B	R^2	Dispersal quantiles		
				50%	66.7%	95%
1	4.096	0.670	0.653	0.793	1.141	2.618
2	6.918	0.798	0.526	0.944	1.359	3.118
3	2.553	0.609	0.851	0.720	1.037	2.379
4	9.853	0.598	0.676	0.707	1.019	2.336
5	3.037	0.553	0.533	0.654	0.942	2.161
Mean	5.291	0.645	0.648	0.764	1.100	2.522
Lower 95% CI	1.491	0.528	0.483	0.624	0.899	2.062
Upper 95% CI	9.091	0.763	0.812	0.903	1.300	2.983

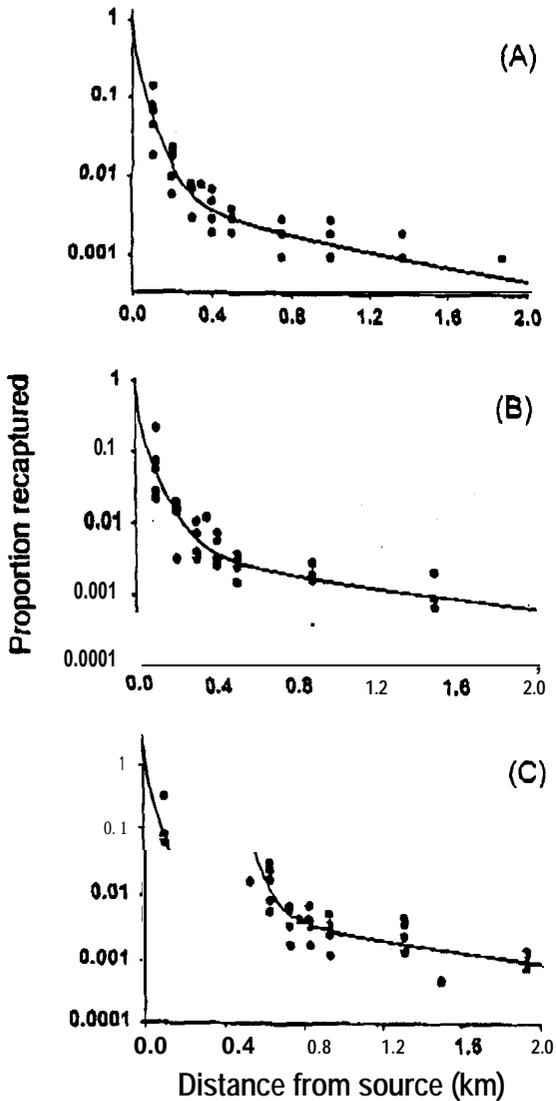


Fig. 2. Proportion of (A) total, (B) male and (C) female marked checkered beetles recaptured for all five replicates combined. Curves are based on the heterogeneous, two-disperser model (eq. 5).

In this paper, we presented a new and simple approach to incorporating heterogeneity in dispersal ability into a diffusion framework (see also Inoue 1978 and Plant and Cunningham 1991). Employing this heteroge-

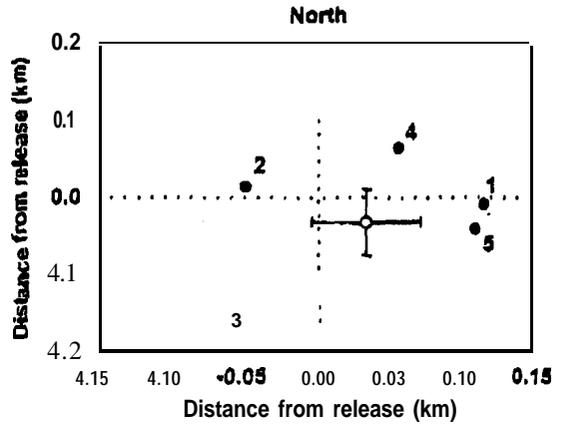


Fig. 3. Net displacement of *Thanastmus dubius* in the five replicate mark-recapture experiments. The open circle represents the mean net displacement ± 1 se.

neous diffusion model, we found a much improved fit to the checkered beetle dispersal data: one that did a particularly good job of accounting for the fat tails in the recapture distributions. Based on this model, checkered beetles were found to have a great capacity, for dispersal. We estimated that an average of 50% of the released beetles dispersed beyond 1.25 km, 33% dispersed beyond 2 km and 5% dispersed beyond 5 km.

In contrast, we could find no evidence for heterogeneity in dispersal ability for the SPB: the recaptures-with-distance were linear, indicating homogeneous rates of dispersal within the population (Fig. 5). Thus, dispersal distances for the SPB were estimated using the simple diffusion model. This model is based on the same framework as the heterogeneous model but allows for only one type of disperser in the population. Using this simple diffusion model, we found the SPB to be slightly less dispersive than their predators. The main difference between the two species was in the tails of their redistributions: as noted by the significantly larger radius necessary to enclose 95% of the dispersing checkered beetles, more checkered beetles were undergoing long-distance dispersal than their pine beetle prey.

Within-population heterogeneity in dispersal ability may have been in part attributable to sex- and size-related differences among adult beetles. While males and females did not differ in the range or pattern of dispersal, the recaptures-with-distance for each sex exhibited

Table 3. Checkered beetle dispersal parameter estimates based on the heterogeneous diffusion model, eq. 5 ($R^2 = 0.753$). 95% confidence intervals were obtained by bootstrapping proportions recaptured from the pooled data sets.

Statistic	Parameters				Dispersal quantiles		
	A_1	B_1	A_2	B_2	50%	66.7%	95%
mean	0.064	0.069	0.0030	1.391	1.243	2.015	5.099
Lower 95% CI	0.018	0.048	0.0015	1.007	0.736	1.297	3.560
Upper 95% CI	0.179	0.130	0.0042	4.170	4.478	6.728	15.391

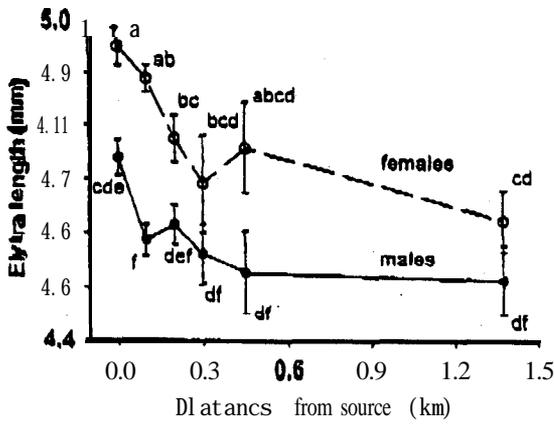


Fig. 4. Checkered beetle size (mean elytra length) in relation to beetle sex and recapture distance. ANOVA indicated a significant effect of sex ($F_{1,1011} = 30.20$, $P < 0.001$) and distance ($F_{5,1011} = 7.77$, $P < 0.001$), but not an interaction between the two ($F_{5,1011} = 1.35$, $P = 0.241$). Means \pm se associated with different letters are significantly different at $P < 0.05$ (based on Tukey's HSD).

a nonlinear trend comparable to the combined data set. This result suggests that sex-specific differences are not the primary source of heterogeneity in the checkered beetle population. However, size, which is related to sex, did influence dispersal ability in this population: smaller checkered beetles were more likely to be recaptured, and for the females, more likely to be recaptured at long distances (Fig. 4). Whether this is due to the smaller insects having a greater propensity to disperse farther or to discover funnel traps, we do not know. However, based on energetic considerations (Roff 1991) and evidence from the literature (i.e., Roff 1977, Dingle and Evans 1987, Kinn et al. 1994, Ellers et al. 1998; but see Hanks et al. 1998) we would have expected larger, not smaller, insects to be more dispersive.

Theoretical ecologists have long emphasized the need for quantitative information on the rate and pattern of dispersal if we hope to fully understand the temporal

Table 4. Estimated dispersal quantiles with 95% CIs (radius of a circle in km enclosing different proportions of dispersers) for the checkered beetle and southern pine beetle based on the best-fit model (heterogeneous and simple diffusion models, respectively). CIs for the radius enclosing 95% of the dispersers do not overlap between the two species, indicating that they are significantly different ($P < 0.05$).

Dispersal quantiles	Checkered beetle	Southern pine beetle
50%	1.24 (0.74, 1.48)	0.63 (0.45, 0.92)
66.7%	3.02 (1.30, 6.73)	0.99 (0.65, 1.34)
95%	5.10 (3.56, 15.89)	2.27 (1.48, 3.05)

dynamics and spatial distributions of predator and prey populations (e.g., Kareiva 1990, Turchin 1998). In many cases, the types of dynamics and spatial patterns that arise hinge upon the differences in movement between the two species (e.g., Mimura and Murray 1978, Reeve 1988, Comins et al. 1992). Now that we have quantified the pattern and range of movement of the checkered beetle relative to its bark beetle prey, how can we use these data to address the cause for the formation of discrete pine beetle infestations in a relatively homogeneous pine-forest landscape? As a first step, we can evaluate existing models of patch formation; in particular, those models that treat the spatial dimension as a continuum (e.g., Mimura and Murray 1978, Wolkind et al. 1991, Turchin et al. 1998). In these models, spatial patterning, or diffusive instabilities, can arise if the following features of the system are present. First, high densities of the prey (activator species), should have a positive effect on both prey and predator populations. This can be satisfied if the prey exhibits an Allee effect and the predator aggregates to elevated prey densities. Second, increased numbers of predators (inhibitor species) should have a negative effect on prey and predator population growth rates. Finally, predators should disperse substantially faster (higher diffusion rates) than their prey. The way this activator-inhibitor system works to create spatial patterning is as follows. A perturbation that elevates prey densities beyond the constraints of the Allee effect would result in accelerated population growth and the development of a prey outbreak. Predators would respond by increasing their density in the vicinity. In the absence of diffusion, the predators would eventually suppress the outbreak. However, with greater rates of diffusion than the prey, the predators would tend to "wander away" from the outbreak. As a consequence, the ratio of predators to prey within the outbreak would be lower than if there was no predator diffusion, and therefore, the predators would be less effective at suppressing the prey. Immediately adjacent to the outbreak, the opposite would be true: a higher predator/prey ratio and greater suppression of the prey. This pattern of "underaggregation" of predators within the

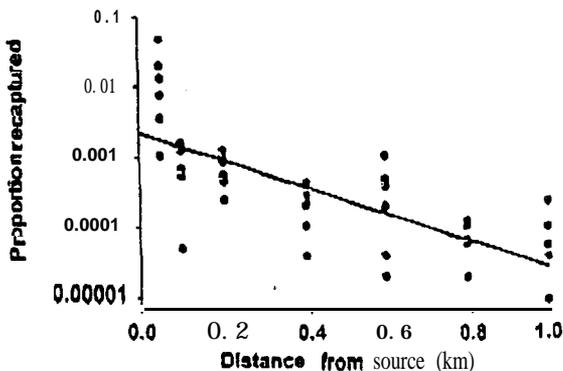


Fig. 5. Proportion of marked southern pine beetles recaptured for all replicates combined in the study by Turchin and Thorny (1993). Line is fit by least-squares regression.

outbreak foci, but "overaggregation" at the periphery can result in the formation of patches of high prey densities with very distinct borders.

Very few experimental studies have addressed the concept of diffusive-driven instability (but see Brodmann et al. 1997, Maron and Harrison 1997). However, the pine beetle-checkered beetle system fits well within this continuous model framework: due to management practices, pine forests in the southeastern United States are quite uniform at scales of several or more kilometers, and the movement of both species within the forest are well described by diffusion-based models. Many of the conditions necessary for diffusive instability are also present in this system. The SPB exhibits a striking Allee effect (see Materials and methods), and the checkered beetles not only aggregate to areas of prey outbreak (Vitè and Williamson 1970, Dixon and Payne 1979a, b, 1980), but also cause a decrease in prey abundance as their density increases (Reeve et al. 1995, Reeve 1997). Additional support for this model comes from the fact that the ratio of checkered beetles to SPB increases away from the center of an infestation; i.e., an underaggregated distribution of predators (Turchin et al. 1998; Fig. 11.4). The one condition for diffusive instability that is not met is that checkered beetle dispersal must be substantially greater than that of its prey. The differences in dispersal outlined in Table 4 would not constitute a substantial difference. Therefore, the creation of spatial patterning through this general model of diffusive instability does not appear to be likely. The basic modeling framework, however, is still well suited to the SPB, and through the addition of more biological realism, we may yet understand the causes of spatial patterning in this system. We are currently conducting experiments to address what we consider to be our most pressing need for these future modeling endeavors: data on the behavior and movement of checkered beetles within and around the boundaries of SPB infestations.

Finally, our result that checkered beetles have a dispersal ability that is equal to or slightly greater than their pine beetle prey lends further support to our earlier prediction that this species is an important predator of the SPB. High dispersal ability, coupled with the checkered beetle's strong reactivity to SPB aggregation pheromones (Vitè and Williamson 1970), would enable it to rapidly track pine beetle infestations in space. This certainly supports what has been observed in nature: pines at very early stages of attack by the SPB often have high densities of checkered beetles (Dixon and Payne 1979a, b, 1980, Reeve 1997). Their effectiveness as a control agent, however, may be tempered by the apparent underaggregated distribution of the checkered beetles relative to the SPB (occurring in higher ratios at the infestation perimeter; Turchin et al. 1998): possibly as a consequence of the higher rates of diffusion of a subset of the checkered beetle population

in comparison to the SPB. Increasing the effectiveness of this predator may therefore be possible through a number of as yet untested approaches: for example, by 1) the augmentative release of checkered beetles in the center of infestations, 2) reducing the checkered beetle's propensity to disperse (possibly by manipulating semiochemical concentrations), or 3) by selecting, through artificial or natural means, the relatively sedentary subset of the checkered beetle population (i.e., the large adult individuals). Information on the pattern and range of movement of the SPB and its natural enemy has revealed new paths to follow which may lead to the improvement of the biological control of this devastating pest.

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