

Influence of Multiple Factors on Insect Colonization of Heterogeneous Landscapes: A Review and Case Study with Periodical Cicadas (Homoptera: Cicadidae)

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Ann. Entomol. Soc. Am. 99(5): 809–820 (2006)

ABSTRACT The literature on herbivorous insects in heterogeneous habitats has addressed insect population responses to patch size, distance from source populations, habitat edges, and variation in host stem density. Studies typically conclude that insect colonists respond positively to the area of host plant patches, but there is little consensus on how insects respond to variation in host density at the patch level. Although observed variation likely results partially from differences in study species and focal habitats, deviations from expectations also may reflect the importance of unmeasured habitat parameters. In this study of colonization by cicada *Magicicada cassinii* (Fisher) in an experimentally fragmented old field, we simultaneously examined landscape variation in patch size, distance from the sources of colonization, and local host plant stem density (at a within-patch scale) and also considered edge effects. Per stem colonization was positively related to proximity to the population source and habitat patch size but negatively related to local host stem density. The effect of edge was nonsignificant. When coarser scale estimates of local stem density (calculated by averaging the figures for all quadrats within patches) were used in analyses, fewer significant main effects were found and sometimes interactions occurred. Our study highlights the importance of including all potential explanatory variables in analyses, with what we feel is a novel observation that the explicit consideration of fine-scale, within-patch variation in local stem density can be important to the interpretation of insect dispersal and colonization.

KEY WORDS cicadas, colonization, heterogeneous habitats, rough-leaved dogwood, host plant density

IN THE PAST 20 YEARS, many studies have analyzed the patterns and mechanisms of insect movement and dispersal. This topic is key to several areas in insect ecology, including metapopulation dynamics (Hanski et al. 1994, Halley and Dempster 1996, Hill et al. 1996, Kindvall 1999), habitat fragmentation (Cappuccino and Martin 1997, Golden and Crist 1999, Summerville and Crist 2001), optimal search strategies (Cain 1985, Withers and Harris 1996), diffusion models (Kareiva 1983, Marsh 1995, Schneider 1999), and the role of density dependence in dispersal (Stein et al. 1994, Herzog 1995). Although the specific question varies among these studies, each addresses the role of spatial factors as determinants of insect movements in heterogeneous habitats, including factors such as patch size, patch quality (e.g., the density of food plants, species composition within the patch, or the host's phenological state), distance from the source point of dispersal, and amount of patch edge. Most studies vary

one or two of these factors experimentally while keeping the others constant and then measure response variables such as probability of colonization into different habitat patches, population densities, or local persistence.

Although the experimental isolation of single factors is an essential starting point, it is also important to understand the effects of different factors when they operate jointly in a multivariate world. In this study, we first briefly review the literature on spatial patterns of colonization by herbivorous insects. (We restrict the discussion to this functional group, because the relevant literature is very large and other well-studied taxa such as parasitoids face different spatial challenges.) We address the four factors that occur most frequently in the literature: patch size, distance from a source, edge effects, and density of host plants. Because of heterogeneity in spatial scale and target variables in the studies of this brief review, which also includes articles focusing on population abundance and dispersion (not just movements per se), we do not attempt a formal meta-analysis. We then describe the results of a field study of cicada *Magicicada cassinii* (Fisher) (Homoptera: Cicadidae), which examines

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the joint effects of patch size, host plant density, distance, and edge on colonization in a heterogeneous landscape. Finally, we suggest an explanation for the apparent discrepancies in prior literature regarding the role of host plant density in explaining distributions of insects, namely, the influence of fine-scale (within-patch) spatial heterogeneity in host densities.

Role of Patch Size. A recent review of the literature concludes that an increase in patch size increases the population size of insect herbivores (Connor et al. 2000). These findings fit the theoretical expectation that patch size increases both the probability of colonization and the likelihood of herbivore persistence after colonization (MacArthur and Wilson 1967, Wilson and Simberloff 1969). Larger patch size has been documented to increase the likelihood of colonization for a diverse array of insect taxa, including grasshoppers (Kindvall 1999), butterflies (Harrison 1989, Hanski et al. 1994, Summerville and Crist 2001), leaf beetles (Bach 1986, Lawrence and Bach 1989), and flies (Eber and Brandl 1994, Eber and Brandl 1996). These studies also have concluded that patch size increases herbivore population numbers (as was also shown for a guild of sap-feeding bugs; Raupp and Denno 1979). By contrast, in some studies isolated host plants (i.e., very small habitat patches) were more likely to be selected for oviposition (a form of colonization) by butterflies (MacKay and Singer 1982, Shapiro 1984, Zalucki and Suzuki 1987). However, these authors indicate that their observations are explained by the species' preferences for edge habitats, a related but distinct phenomenon that is discussed below. High populations of herbivores also can build up on small patches if the capacity to disperse is very limited (Doak 2000a). There are also examples reported of a null relationship between patch size and abundance of herbivorous insects (Grez and González 1995); this may occur if the range of spatial scales in the study is too small to see the expected effects.

Role of Distance from Source Population. Distance from the source habitat is negatively associated with the frequency of colonization or patch occupation in many insect taxa, including beetles (Matter 1996, Grevstad and Herzig 1997), sawflies (Stein et al. 1994), butterflies (Harrison 1989, Hanski et al. 1994), and grasshoppers (Kindvall and Ahlén 1992), as is predicted by theory (MacArthur and Wilson 1967, Wilson and Simberloff 1969). In contrast, distance from source to patch was found to be unimportant in flies (Eber and Brandl 1996) and moths (Förare and Solbreck 1997). This type of variation does not necessarily contradict theory, however, because species may be able to colonize any patch within a range of short distances (Grevstad and Herzig 1997), especially if they are strong-flying species (Dempster et al. 1995). In addition, in some studies colonization probability is increased at a distance for mobile species, if far patches are followed by a hard dispersal barrier (a "fence effect"); this effect has been found in some springtail species dispersing between tussocks (Hertzberg et al. 1994, Hertzberg 1997).

Edge Effects. Some taxa seem to be attracted to isolated hosts or those on the edges of habitat patches (e.g., tingid bugs, Cappuccino and Root 1992; locust-boring beetles, McCann and Harman 1990), particularly for mating assemblages (Rodenhouse et al. 1997) or for oviposition. This edge effect has been especially noted in the Lepidoptera (Courtney and Courtney 1982, MacKay and Singer 1982, Shapiro 1984, Cappuccino and Martin 1997). Because different insect taxa have distinct preferences for the center or edges of habitat patches, responses to edges can lead to induced patch size effects. Given the geometrical relationship of perimeter to area, with relatively more edge in small patches, a species that is attracted to edges may treat a very small patch (or single host plant) as "all-edge" (Shapiro 1984, Courtney and Forsberg 1988). Conversely, other species may avoid edges and concentrate on the patch interior; this may lead to small patches being avoided (Matter 1996) or traversed without stopping (Kindvall 1999). It is important to distinguish edge effects from patch size effects, per se, to develop a mechanistic underpinning for landscape effects on behavior and population dynamics.

Role of Host Plant Density. Although there is reasonable consensus in the literature over the role of patch size and isolation in determining the probability and frequency of insect colonization, there have been many conflicting reports about the effects of host plant density. This topic has been the subject of an old debate; see Stanton (1983) for a historical review. More recently, Capman et al. (1990) wrote that the "lack of agreement with theoretical predictions and the conflicting results of many studies, suggest that much remains to be learned about the relationships between dispersion patterns of herbivorous insects and their host plants." Many results conclude that an increase in host plant density leads to an increase in herbivore populations, for example, in butterflies (Cromartie 1975, Hanski et al. 1994), lygaeid bugs (McLain and Shore 1990), and beetles (Bach 1980, Turchin 1987). A simulation model (Cain 1985) predicted an increase in colonization success with host density. An interesting variation on this idea is that a positive relationship could saturate; the colonization rate may increase with host density but eventually level off (Rauscher 1983). However, there are also many studies that conclude that although host abundance (total host population size) increases herbivore density, host density (numbers per area) is inversely related to herbivore density. This largely unresolved conflict has been stressed by Capman et al. (1990). An inverse relationship between host and herbivore density is seen in some of the same broad taxonomic groups that provide examples of positive relationships; examples have been noted in butterflies (Hayes 1981, Courtney and Forsberg 1988, Capman et al. 1990), bugs (A'Brook 1973, Smith and Linderman 1974), beetles (Pimentel 1961a, b; Bach 1988b), and flies (Delobel 1982, Eber and Brandl 1994).

In a series of articles in the 1980s, C. E. Bach (Bach 1980, 1986, 1988a, b) explored the relationships be-

tween patch size, host density, and herbivore population movements. One of the principal conclusions of these studies was that the lack of general patterns in the literature on the effects of plant spatial patterns on herbivore density was due to confounding effects; the abundance of nonhost plants and their increasing diversity with patch size can affect the arrangement and abundance of host plants and thus indirectly influence the ability of herbivores to find and use their hosts. The role of nonhost plants has been recognized by Ellingson and Andersen (2002), and studies have found positive effects of plant diversity on colonization (Morrow et al. 1989), negative effects (Kareiva 1985, Lawrence and Bach 1989), or instead observed that dispersers simply ignore nonhost plants and quickly move on (Withers et al. 1997).

These articles recognize that the distribution of host plants can be affected by the distribution of other plant species within a patch, which may influence the spatial arrangement of host plants by consuming space or resources, which then may affect the distribution of specialist insect herbivores. Nonhost plants are only one of many factors that can lead to such indirect effects on the spatial dynamics of herbivores; the important issue for this study is that the local distribution of host plants, whatever its derivation, is critical to the understanding of population dynamics in the system (Capman et al. 1990). However, some studies explicitly assumed that the arrangement of host plants within the patches was uniform (Matter 1996, Kindvall 1999). This is not always unreasonable, but if host densities vary widely within patches this assumption could lead to incorrect conclusions. In a study of butterfly dispersal in a heterogeneous landscape by Summerville and Crist (2001), the inclusion of a measure of habitat quality (total cover of flowering forbs) for each habitat patch led the authors to the conclusion that habitat quantity (area) and habitat quality are not necessarily correlated. For example, they suggest that moderately sized patches of high quality may be equally as enticing to butterflies as large patches of lower quality, a pattern that would be misinterpreted without inclusion of a measure of host plant density.

In this article, we reanalyze data from our recent study of *M. cassinii* in a fragmented landscape (Cook et al. 2001, Cook and Holt 2002) to illustrate the interplay of spatial factors in insect dispersal. We document dispersal by cicadas into an experimentally fragmented and previously uninhabited old field site, in which suitable habitat for oviposition varied in patch size, distance from the neighboring forest, and local host stem density (both within and between patches). This project adds an additional spatial factor to those commonly cited in studies of insect dispersal in heterogeneous landscapes: variation in host densities at the within-patch scale. In general, we expected that the inclusion of fine-scale variation in local stem density in a study design accounting for other commonly studied factors would help to provide a clearer understanding of cicada responses to other landscape variables. We expected statistical results to change with this addition if there are any spatial correlations

between any stem density and the other variables, and in particular if within-patch variation in stem density varies with patch size. These patterns seemed visually apparent at the study site. We suggest that our results highlight the importance of jointly assessing the impacts of host density, patch area, edge, and distance in studies of insect dispersal.

Materials and Methods

Data were collected during and after the cicada emergence of May–June 1998 at the University of Kansas Field Station and Ecological Reserves located in northeastern Kansas (Cook et al. 2001, Cook and Holt 2002). Cicadas emerged from the woods adjacent to the study site, within which there was essentially no prior cicada population (Cook et al. 2001). At the time of the study, the site exhibited abundant stands of woody plants, necessary for colonization by cicadas. The insects opportunistically use a variety of trees, shrubs, and woody vines (Williams and Simon 1995), although a few species are avoided (White et al. 1982, Cook et al. 2001). Our studies document the patterns and implications of insect colonization into a “new” habitat.

The study site contains a mosaic of habitat patches (arranged to represent different degrees of habitat fragmentation) arrayed within a closely mown interstitial matrix (Fig. 1). The patches occur in three sizes: large (50×100 m), medium (12×24 m), and small (4×8 m). The smaller patches are clustered into groups, with an aggregate area spanned by the cluster similar to a large patch (Fig. 1). Woody plant densities vary tremendously over short spatial scales, leading to high within-patch heterogeneity in all patch types (Cook et al. 2005). The adjacent forest was determined to be the principal source of dispersing cicadas (Cook et al. 2001). Multiple cicada species were active in the region, as is typically the case, but only the single species *M. cassinii* was observed in the study site. [Note that although most recent references, including those in this article, refer to the species as “*M. cassini*,” the spelling in the original description is *M. cassinii* (Fisher 1851), which we use in this article.]

Woody plant censuses were conducted at 452 permanent 4 by 4-m quadrats, with two sampling locations per small patch and 30 per large patch, in which each tree >2 m is individually tagged and measured (Holt et al. 1995, Yao et al. 1999). This level of sampling provides the opportunity to look at plant abundances at a fine spatial scale and allows us to examine intrapatch heterogeneity. In the late 1990s, large portions of the site had a canopy of up to 2.5–3.0 m in height, whereas other areas remained dominated by grasses and perennial forbs, creating a complex array of microhabitats from which invading periodical cicadas could select. The dominant tree species in our mid-successional community is rough-leaved dogwood, *Cornus drummondii* C.A. Mey., comprising 93% of all individuals taller than 2 m in 1998. Given the dominance of dogwoods, it is reasonable for our purposes

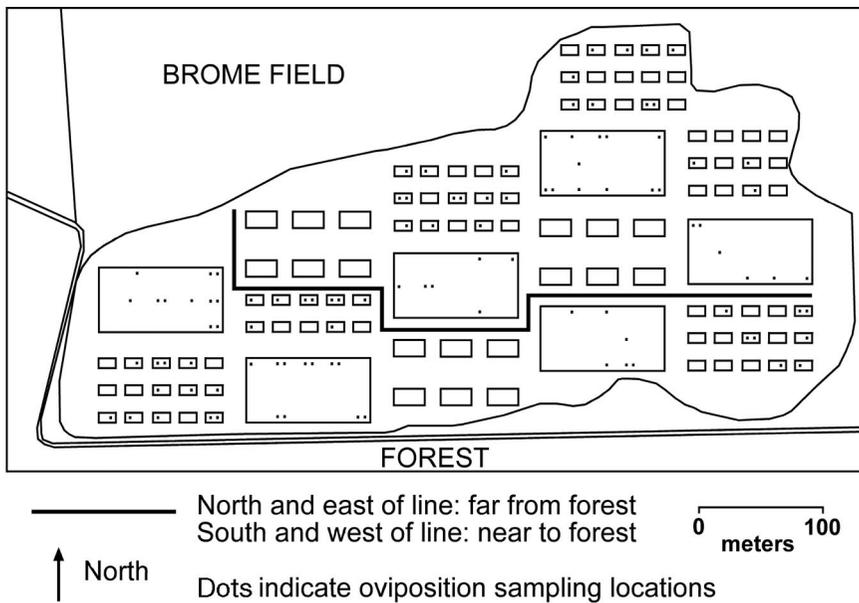


Fig. 1. Diagrammatic map of Kansas Fragmentation Study, Nelson Environmental Study Area, Kansas Field Station and Ecological Reserves, Jefferson County, Kansas.

to consider the site to consist of a monoculture of this woody species, at least in areas where woody plants exist.

A set of woody individuals were selected as potential colonization "targets" for cicadas. Dogwoods were randomly selected from the 1997 data set of tagged trees based on distance to the forest (near or far, Fig. 1), size of patch (large or small; medium patches were omitted from this study), and tree density within the local 4 by 4-m area (density classes of 1–2, 3–5, 6–10, 11–15, and >15 stems per 16 m², summed across all tree species). We selected 10 individuals for each combination of distance, patch size, and density, forming a sample of 200 dogwoods in a three-way factorial design (Cook et al. 2001). Because we did not have an a priori hypothesis about how far into a patch cicadas would perceive the "edge" to extend, we considered two possible definitions of edge, within 2 m and within 4 m of the patch boundary, and classified all study trees according to these criteria. We were thus able to test for an edge effect in large patches (we could not investigate any such effects on small patches because all trees occurred within 2 m of the edge). Unfortunately, because the distribution of trees is not even throughout the site, and because the decision to study edge effects occurred after the trees were selected, sample sizes were not equal for this variable: when edge was defined as within 2 m of the boundary, there were 36 trees on the edge and 64 in the interior, and when edge was defined as being within 4 m of the boundary there were 81 on the edge and only 19 in the interior.

Whereas the movement of individual cicadas is difficult to quantify directly, egg nests are very easy to identify and count. Moreover, for colonization, what matters initially is egg placement not just adult move-

ment because egg placement indicates the establishment of a multigenerational population within the site. Thus, for purposes of this study we define colonization as immigration followed by oviposition, and our index of colonization is the frequency of egg masses. After mating, females lay eggs in the underside of small tree branches, by using their ovipositors to make a linear series of slits, almost always near the tips of branches where the diameter is 3–11 mm (White 1980). A given female can make multiple slits per stem and oviposit on more than one stem. For each tree examined, we selected the longest branch in each of the four cardinal directions, determined the length of any slit series within 50 cm of each end, and calculated the mean of these four measurements. This average is used as the dependent variable throughout this article.

Statistical Analyses. To explore the importance of spatial factors in female cicada oviposition (colonization) decisions, we ran a series of general linear models (GLMs) on our cicada oviposition measure, mean slit damage per woody stem. Although our objectives were to investigate the interplay between four spatial factors (patch size, distance, stem density, and edge), we were not able to consider all four in the same analysis, because small patches were "all edge," and analyses of edge effects were possible when considering large patches only. We thus performed statistical analyses including data from all patches with patch size, distance, and stem density as predictor variables and later performed analyses on data from large patches only with edge, distance, and stem density as predictors.

First, we ran a GLM with patch size, distance to the nearby forest, local stem density, and all possible interactions as predictor variables. In this and all subsequent GLMs, patch size and distance are categorical

variables and local stem density is a continuous variable, thus creating mixed model analyses where stem density occurs with one of the other variables. [This first three-way GLM is similar to that reported in Cook et al. (2001), excepting that stem density is treated as a categorical variable there.]

Although this GLM represented the best possible method of evaluating the statistical importance of (and the interplay between) patch size, distance, and stem density, in our literature review we discovered that most comparable studies of insect populations considered fewer than three variables simultaneously. We thus explored whether the inclusion or exclusion of each variable affected conclusions regarding the statistical significance of the others. We also ran all possible GLMs with two of the above-mentioned variables and their interaction as predictors, and additional GLMs with each spatial measure as a single predictor, and compared the various analyses to see which factors were found to be significant in different combinations.

Next, because most studies we reviewed used less detailed stem density data than we had available, most often as an estimate of stem density per patch, we twice recalculated each of the above-mentioned GLMs that included stem density class as a predictor to compare our results from those in other studies. In the first such reanalysis, we aggregated our stem density data such that our measure of stem density was average density over all quadrats within each patch, rather than density per 4 by 4-m quadrat, and reran the GLMs. In the second reanalysis, we further aggregated the stem density data such that our measure of stem density was average stem density of the entire 50 by 100-m cluster of patches (15 small patches or one large patch; Fig. 1) and reran the GLMs. This allowed us to determine whether our conclusions would change if we had less fine-scale data available on host plant stem density.

To test for edge effects on oviposition, we performed two analyses (in each, only woody stems in large patches are considered because small patches lack both interior and exterior). 1) We ran a GLM on cicada slit damage (colonization) on trees in large patches, by using stem density (fine scale and a continuous variable, as above), distance to the forest (near or far), and whether the tree is at the edge of a patch (within 2 m or not) as predictor variables. 2) We recategorized trees according to whether they were within 4 m of the edge and reran the previous GLM.

Results

The three-way GLM testing effects of patch size, distance from the forest, and (fine-scale) stem density found that the magnitude of cicada oviposition (colonization) per stem depended statistically on all three variables (Table 1). Cicadas were most likely to oviposit on dogwoods when they were near to the forest, on large patches, and in low-density stands (Fig. 2; Cook et al. 2001). All three primary variables thus had

statistically significant effects, and none of the interaction terms were significant (Table 1).

Importance of Resolution in Stem Density Data. The results of most statistical models, including host stem density, changed with resolution in stem density data (Table 1). When stem density alone was used as a predictor, the GLM became nonsignificant when we used the lowest resolution stem density data. All two factor models found both variables to be significant, with no interaction, by using fine-scale stem density. Both two-factor models including stem density lost a significant main term effect and gained a significant interaction when patch-scale stem density was used, and had even fewer significant terms when cluster-scale stem density was used (Table 1). When we reran the three-way GLM using lower resolution host density data, two predictor variables lost statistical significance when using patch-scale stem density, and none were significant under cluster-scale stem density (Table 1).

Edge Effects. In the GLM analyses that included edge as a predictor variable, distance to the forest and stem density generally had significant effects (distance was marginally nonsignificant when edge was defined as <4 m from the patch boundary). Edge categorization did not have a significant main effect in either GLM, and no interactions were found to be significant at the 0.05 level (Table 2).

Discussion

This study shows that dispersing cicadas responded to a suite of spatial variables (patch size, distance from source, and stem density, but possibly not edge). Qualitatively, cicadas were more attracted to near and large than small and far habitat patches and also to host plants in thinner rather than denser stands. In our system, the three primary variables (patch size, distance, and stem density) had statistically independent effects (there were no interaction terms; Table 1). As an example, this means cicadas comparatively preferred a large over a small patch when both are near to the forest, but also when the pair was far from the forest. Similarly, cicadas preferred trees in less dense stands both within large patches and within clusters of small patches, and preferred near to far patches to some degree both when stem densities are greater in large patches, or greater in small patches. Generally, this statistical result indicates that all three preferences were always evident to some degree under all circumstances, and no preference for one variable trumped a preference for any of the others.

Although we consider the original three-factor GLM to be the correct model for interpretation within our system, the relative importance ascribed to these factors in explanatory statistical models changed when we reduced the measured spatial resolution in host plant stem density by aggregating quadrats. Our reason for this exercise was to make the results from our study comparable with data used in other studies; we believe this justifies the risk of type I statistical errors due to the performance of nonindependent analyses.

Table 1. Changes in slit damage GLM results with resolution in stem density data

Model	df	Seq. SS	Adj. SS	Adj. MS	F	P	Seq. SS	Adj. SS	Adj. MS	F	P	Seq. SS	Adj. SS	Adj. MS	F	P
Size	1	1097.5	1097.5	1097.5	10.91	0.001										
Error	198	19922.5	19922.5	100.6												
Total	199	21020.0														
Distance	1	1178.6	1178.6	1178.6	11.76	0.001										
Error	198	19841.4	19841.4	100.2												
Total	199	21020.0														
Density	1	2925.5	2925.5	2925.5	32.01	<0.001	645.8	645.8	645.8	6.28	0.013	145.0	145.0	145.0	1.38	0.242
Error	198	18094.5	18094.5	91.4			20374.2	20374.2	102.9			20875.0	20875.0	105.4		
Total	199	21020.0					21020.0					21020.0				
Size	1	1097.46	1097.46	1097.46	11.49	0.001										
Distance	1	1178.55	1178.55	1178.55	12.34	0.001										
Interaction	1	17.40	17.40	17.40	0.18	0.670										
Error	196	18726.58	18726.58	95.54												
Total	199	21020.00														
Distance	1	1178.55	433.8	433.8	5.19	0.024	1178.6	4.6	4.6	0.05	0.822	1178.6	609.6	609.6	6.08	0.015
Density	1	3400.0	3042.9	3042.9	36.38	<0.001	1493.5	2121.6	2121.6	23.49	<0.001	27.2	32.9	32.9	0.33	0.567
Interaction	1	47.9	47.9	47.9	0.57	0.450	647.1	647.1	647.1	7.17	0.008	147.2	147.2	147.2	1.47	0.227
Error	196	16393.6	16393.6	83.6			17700.8	17700.8	90.3			19667.0	19667.0	100.3		
Total	199	21020.0					21020.0					21020.0				
Size	1	1097.5	407.8	407.8	4.72	0.031	1097.46	69.40	69.40	0.73	0.394	1097.46	97.5	97.5	0.96	0.328
Density	1	2970.4	2977.6	2977.6	34.45	<0.001	564.48	172.06	172.06	1.81	0.180	33.9	37.8	37.8	0.37	0.542
Interaction	1	10.2	10.2	10.2	0.12	0.732	730.95	730.95	730.95	7.69	0.006	38.3	38.3	38.3	0.38	0.539
Error	196	16942.0	16942.0	86.4			18627.11	18627.11	95.04			19850.3	19850.3	101.3		
Total	199	21020.0					21020.00					21020.0				
Size	1	1097.46	401.18	401.18	5.05	0.026	1097.46	15.47	15.47	0.18	0.671	1097.46	1097.46	124.68	1.31	0.253
Distance	1	1178.55	463.18	463.18	5.83	0.017	1178.55	18.72	18.72	0.22	0.640	1178.55	1178.55	0.38	0.01	0.950
Density	1	3448.71	2992.21	2992.21	37.68	<0.001	1362.98	483.84	493.84	5.78	0.017	162.48	162.48	228.90	2.41	0.122
Interaction ^a	1		None significant at P = 0.05					None significant at P = 0.05					None significant at P = 0.05			
Error	192	15247.38	15247.38	79.41			16406.72	16406.72	85.45			18231.37	18231.37	94.96		
Total	199	21020.00					21021.00					21021.00				

Bold values indicate $P < 0.05$. Fine-scale host density is stem density per 4 by 4-m plot. Patch-scale stem density is stem density per 4 by 8-m small patch and by 50 by 100-m large patch. Cluster-scale host density is stem density per 50 by 100-m cluster of patches (15 small patches or the large patch).

^a All possible two-way interactions and a three-way interaction were considered. None were found to be statistically significant.

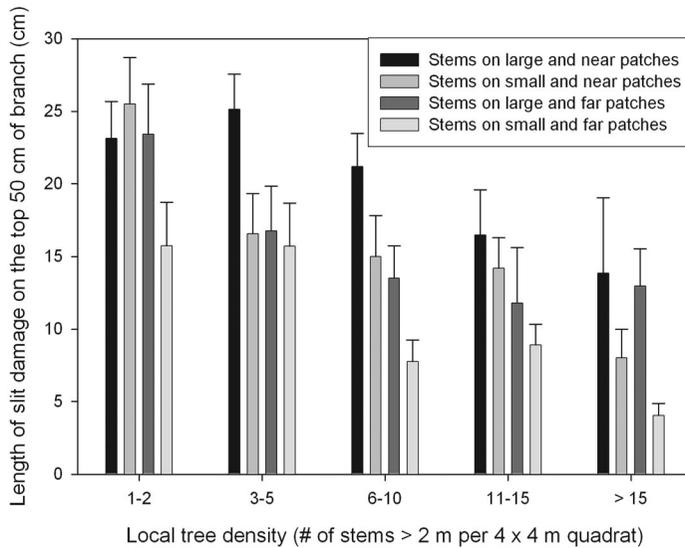


Fig. 2. Effects of patch size, distance to the nearby forest, and local tree stem density on cicada slit damage on *C. drummondii*. Mean slit length per outer 50 cm of branches \pm 1 SE are shown. Stem density is treated as a continuous variable in statistical analyses but is used as a categorical variable here for purposes of clarity and because the study stems were originally selected categorically.

The effect of this shift in resolution was to lose statistically significant variables, and sometimes to gain interaction terms.

When resolution was decreased from the 4 by 4-m level to the coarser patch level, stem density frequently ceased to be a statistically significant factor, although sometimes occurred instead in interaction terms. Thus, it seemed qualitatively (and artificially) that the preference for lower stem density was trumped by the preference for patch size or distance, or possibly that cicadas only preferred less dense host stands when choosing among small or among large patches only, or among near or far patches only. At neither of the coarser scales of resolution in host stem density would we have clearly recognized that the three variables (patch size, distance to the forest, and stem density) each had important and largely independent effects on cicada oviposition, and we would have assumed a greater degree of situational dependence than was necessary. Not surprisingly, when we considered fewer variables, fewer were found to be important. More importantly, and confusingly, with only partial information we might have concluded that a preference for large patches trumped any preference for distance, but with another set of partial information we could have concluded the converse.

Statistically, although it has been suggested that the loss of significant factors in the GLMs with changes in stem density resolution is an effect of decreased sample size, we do not believe this explains our observations. Degrees of freedom used in the GLMs remain unchanged between analyses with different resolution in stem density, and in at least some combinations of variables interaction terms come and go, which would not occur if only changes in sample size were important. A better interpretation of these patterns is that

the loss of stem density detail in the later GLMs moves components of variation from main term effects to interaction and error terms, changing statistical significance. Thus, explicit recognition of within-patch variation in stem density facilitates a more accurate analysis, and helps to optimize the amount of variation explained by model terms. If we had fewer spatial variables available or coarser scale stem density information, we would likely have concluded that each factor might matter, but depending on the exact analysis we could have arrived at conflicting criteria for their impact on dispersing cicadas. Such differences in the scale of spatial resolution among studies could account in part for divergent patterns reported in the literature.

Given the statistically significant and independent effects of the three primary variables included in our study (in the appropriate three-factor model; Table 1), we can now look at each spatial characteristic of the landscape separately and suggest mechanisms to explain the patterns observed. The simultaneous inclusion of all three spatial parameters, especially fine-scale spatial variation in host plant density, provides useful insight into determinants of insect movements in heterogeneous landscapes.

Patch Size and Distance Effects. Our results are consistent with the considerable number of studies that conclude that large habitat patches and those near a source are more likely to be colonized by herbivorous insects (Kindvall and Ahlén 1992, Hanski et al. 1994, Hanski and Thomas 1994, Hill et al. 1996, Matter 1996, Withers and Harris 1996, Summerville and Crist 2001), as is predicted by theory (Gustafson and Gardner 1996). Large patches are probably selected due to the greater abundance of oviposition sites (in our case, tree biomass) there. Patches near the forest are likely

Table 2. GLMs testing effects of distance to forest (near or far), local stem density (continuous or fine scale), and edge (at edge or not) on cicada stem damage (oviposition) in large patches

Source	df	Seq. SS	Adj. SS	Adj. MS	F	P
Edge defined as within 2 m of patch edge						
Distance	1	454.76	365.73	365.73	4.03	0.048
Density	1	1610.86	986.56	986.56	10.88	0.001
Edge	1	496.35	2.05	2.05	0.02	0.881
Distance*density	1	4.55	11.99	11.99	0.13	0.717
Distance*edge	1	116.18	330.03	330.03	3.64	0.060
Edge*density	1	94.84	288.49	288.49	3.18	0.078
Distance*edge*density	1	264.47	264.47	264.47	2.92	0.091
Error	92	8342.22	8342.22	90.68		
Total	99	11384.23				
Edge defined as within 4 m of edge						
Distance	1	454.76	261.46	261.46	2.77	0.099
Density	1	1610.86	1209.06	1209.06	12.82	0.001
Edge	1	185.86	20.42	20.42	0.22	0.643
Distance*density	1	27.59	77.18	77.18	0.82	0.368
Distance*edge	1	1.75	82.08	82.08	0.87	0.353
Edge*density	1	287.11	289.36	289.36	3.07	0.083
Distance*edge*density	1	139.32	139.32	139.32	1.48	0.277
Error	92	8676.98	8676.98	94.31		
Total	99	11384.23				

preferentially selected because they are encountered first. Periodical cicadas can fly 100–200 m or more (Karban 1981, White et al. 1983), but dispersal gradients have been observed over distances <150 m, similar to our results (Karban 1981, Lloyd et al. 1982). (The likelihood of dispersal also decreases even at these short distances for small mammals and woody plants at our site (Diffendorfer et al. 1995a, b; Schweiger et al. 1999; Yao et al. 1999).)

Edge Effects. A variety of published studies reveal a preference for edges for oviposition (Courtney and Courtney 1982, MacKay and Singer 1982, Shapiro 1984, Zalucki and Suzuki 1987, Cappuccino and Martin 1997). An increase in herbivore numbers at edges has been variously explained by an ovipositional response to a shortage of hosts (Courtney and Forsberg 1988), a statistical artifact (MacKay and Singer 1982), a behavioral response to the eggs of other females (Shapiro 1984), higher incidence of sunlight at edges (Bowers and Stamp 1987), or other reasons (Cappuccino and Root 1992). In Cook et al. (2001), we hypothesized that periodical cicada oviposition damage would be greater on small patches, because prior cicada studies found the greatest density of egg nests on saplings at woodland edges (White 1980), which are also the site of mating aggregations (Rodenhous et al. 1997). We did not find that to be the case, and we also found no direct evidence that cicadas behaved differently within 2 or 4 m of a patch edge than in the interior. However, it is conceivable that cicadas may still preferentially colonize patch edges, based on two lines of reasoning: 1) Given that most trees on the site are <3.5 m, the cicadas may perceive the entire site as essentially “all-edge” (Simon et al. 1981; C. Simon, personal communication), and edge effects could develop later in time. 2) Cicadas may view edges at a scale other than 2 or 4 m, and thus we could overlook edge effects because of constraints in our study design. These possibilities remain speculative, and we must

conclude here that edge effects are probably not important in our system.

Variation in Host Density. The results of our study shed light on discrepant results in the literature over the role of host plant density in explaining the distribution of insect herbivores in a heterogeneous environment. Our results are consistent both with studies that found that herbivore numbers increase with numbers of host plants (Cromartie 1975, Bach 1980, Turchin 1987, McLain and Shore 1990, Hanski et al. 1994) and also with those that found that there is a decrease in herbivore density with increasing host density (Delobel 1982, Bach 1988b, Courtney and Forsberg 1988, Capman et al. 1990, Eber and Brandl 1994). Controlling for density, the number of host plants scales directly with habitat area. The apparent conflict in causality of the two spatial factors is not a conflict in our study; they each have independent effects that are both detectable given the appropriate study design. In this sense, our results are consistent with those of Summerville and Crist (2001). The broad, analytical, cross-taxon agreements between our results and those of many other similar studies indicate that this idea could be useful in explaining local distributions of herbivorous insects.

This decrease in oviposition per tree with an increase in host density could be explained by the cicadas' perception of the habitat as available biomass rather than numbers of individual trees, because the density, size, and shape of dogwoods vary considerably both within and between patches (W.M.C., personal observation). Other studies also link insect dispersal decisions to measures of plant size or quality: sheer size of the plant and its contrast against the background (Antolin and Addicott 1991), and how “lush” a patch is, which is not necessarily dependent on the number of stems (Herzig and Root 1996). Other sensory cues have been suggested to be important: chemical cues (Ralph 1977, Morrow et al. 1989)

and the spectral patterns of appropriate foliage (Prokopy and Owens 1983). In their review of visual detection of plants by herbivorous insects, Prokopy and Owens (1983) strongly stressed the differences in perception by insects at a distance from a habitat patch (gross spectral contrasts and movement are important due to the lack of clarity in images from compound eyes) and at short distances from a patch (individual trees may be detected rather than a clump). It seems unlikely that periodical cicadas can distinguish the number of trees from simple gross biomass from outside a patch. Also, isolated trees or those at the edge of stands, which tend to have more axial foliage and spreading branches, may take more damage than do clumped trees with sparser lower branches, because periodical cicadas strongly prefer to oviposit near the ends of thin branches (White 1980, Williams and Simon 1995). Our results are logically consistent with any of these ideas. Observed lower oviposition in dense stands is likely not due to behavioral responses to nearby eggs laid by other females (as it can be in the Lepidoptera; Shapiro 1984), because Simon et al. (1981) found cicada egg nests to be aggregated at small spatial scales.

Our results may seem to be contrary to that of the resource concentration hypothesis (Root 1973), which predicts greater density (number per plant) of specialist herbivores where their host plants are abundant. This issue continually arises when density of herbivores and their hosts is investigated (Bach 1986, 1988a; Capman et al. 1990; McLain and Shore 1990), but a simultaneous preference for large habitat patches (i.e., ones high in resources) and a decrease of herbivores with host density is possible in any patch within which the host density varies. Indeed, in landscapes where the smallest patches can be considered to be all-edge (Shapiro 1984, Capman et al. 1990) such patches are likely to be too small to have any within-patch variation and may even consist of only a single plant (MacKay and Singer 1982). These situations are highly likely to create an apparent conflict in the data between preferences for large patches and for isolated hosts, especially when host densities within large patches are highly variable but low on average. However, if large habitat patches truly have both greater abundances of host plants and uniformly higher host densities than small patches, this will probably result in a positive relationship of herbivore density with both variables.

Analytically, it is critical to attempt to determine at which spatial scales the study organism operates, and whether behavior seems to vary from small to larger scales. For example, Simon et al. (1981) found cicada oviposition to be patchy at the scale of meters, but not at the scale of tens of meters. Dispersing herbivores may possibly perceive a heterogeneous "large patch" as an aggregation of closely associated small patches, and there the host biomass over the whole large patch may not be important. The experimental design of our site allows an investigation of this issue, because clusters of small patches occupy a total area (including gaps between neighbors) equal to that of a nearby

large patch (Robinson et al. 1992, Holt et al. 1995, Yao et al. 1999). Capman et al. (1990) took an experimental approach to investigate the importance of spatial scale, when they found the now familiar pattern of simultaneous preference for large patches and less dense stands. Dispersed patches were brought closer together experimentally, and the patch size effect in oviposition per stem disappeared. Their insects probably no longer recognized the patches as distinct at close distances, but instead responded to the distribution of small clusters of plants no matter whether they were in large or small "patches." Our system probably represents for cicadas a comparable spatial scale to that of two studies of butterflies in patchy landscapes (Capman et al. 1990, Schultz and Crone 2001): too far apart for animals to move between patches with no effects of distance, but too close to be a true metapopulation (Harrison 1991, 1994; Hanski et al. 1995; Eber and Brandl 1996; Förlare and Solbreck 1997).

Movement within Patches. Although we have concentrated on the selection criteria used by individuals approaching habitat patches, we also suggest that within-patch movements contributed to the simultaneous patterns of greater colonization in large patches and in less dense tree stands. Several authors have discussed mechanisms that could lead to our observed patterns. Cappuccino and Root (1992) discuss a mechanism where tingid bugs ran randomly into a patch but then redistribute themselves within the patch by a series of purposeful movements (also see Holt 1992). Large patches could receive more cicada oviposition per stem if the insects moved through habitat patches more slowly when they contained greater numbers of the host plant (Ralph 1977, Shapiro 1984, Turchin 1986, Withers et al. 1997) or if emigration was negatively related to patch size (Matter 1996, Kindvall 1999). Cicadas might have responded mechanistically to simple gradients in host density (Ralph 1977), but this is probably not the key explanation at our site because it had a very patchy and complex tree distribution. Alternatively, cicadas searching for oviposition sites could have dispersed via several short flights between neighboring plants followed by a single longer flight, and then more short flights (Withers et al. 1997). Large patches contain more trees than do small patches, and tree stands can be more continuous and closer together in large patches. Cicadas dispersing from a stand in a large patch might have been more attracted to nearby stands in the same patch, rather than stands in adjacent small patches, which were at a distance ≈ 10 m away. However, this distance between patches is small compared with dispersal distances observed by other studies (Karban 1981, White et al. 1983), so simple distance might not be much of an impediment at this scale. Although the exact behavioral mechanism may not be certain, female cicadas make many short flights and sometimes multiple egg nests, sometimes on completely different stems, so the decisions that lead to a series of movements can affect the pattern of oviposition (and thus colonization).

Synthesis. Overall, we can summarize our characterization of the selection criteria used by dispersing and ovipositing cicadas in a heterogeneous landscape. Proximity to the source was an important criterion. Because trees were more common on large patches as measured both by absolute number and by average density (Yao et al. 1999), cicadas were apparently attracted to the greater amount of available woody habitat found on large patches. Cicadas also were attracted to isolated trees, but this is not necessarily contradictory with the patch size preference. Our interpretation is that cicada site selection operated at multiple scales: at the coarse scale, the insects first selected a larger area (i.e., patch) with greater available tree biomass on which to oviposit and then possibly used different criteria while moving at a finer scale within the patches. Because local host density varied greatly within large patches, damage from cicadas was either concentrated or diluted by the number of trees in a particular area. At the smaller scale, the insects seemed to prefer trees in sparser stands, so their overall pattern of movements involved the superposition of patch size effects (gross abundance) onto within-patch heterogeneity (fine-scale data on local stem density).

Comparing our results to those of other studies of insect herbivores in heterogeneous landscapes, we suggest that our approach of simultaneously accounting for variation in patch size, distance to source areas, and fine-scale variation in host stem density is broadly useful in understanding insect movements. Suggesting the simultaneous inclusion of additional explanatory variables, as we do here, is not new but critically important to the analysis of observed patterns. More interestingly, fine-scale variation in host plant occurrence has been suggested as a critical factor explaining the distribution of strongly dispersal-limited species (Doak 2000b), but we think our interpretation of cicada movement is novel for species that have freedom of movement within the scale defined by our study. Apparently contradictory responses to patch size and interpatch host stem density may be reconciled by recognizing the scale at which focal individuals perceive stem density or choose to aggregate (Simon et al. 1981), because behavioral mechanisms may thus operate differently within habitat patches than between them. The literature on insect distributions in heterogeneous landscapes includes many trends that seem to apply across taxonomic groups, and recognition of the impacts of fine-scale heterogeneity in host density may help to clarify seemingly disparate results among other studies.

Acknowledgment

We thank J. Yao, our collaborator in the larger study of cicadas at the study site, and the assistance of field crews through the years at the Kansas Fragmentation Study. We also thank G. Pittman and B. Johanning for overseeing the maintenance of the study site. N. Slade, J. S. Ashe, H. Alexander, B. Foster, K. Price, C. Simon, and two anonymous reviewers made helpful suggestions regarding the manu-

script. This study was supported in part by the General Research Fund of the University of Kansas, REU supplements, the Kansas Field Station and Ecological Reserves, and National Science Foundation Grants DEB-9308065 and DEB-0076064. W.M.C. and R.D.H. thank the Global Institute of Sustainability at Arizona State University and the University of Florida Foundation, respectively, for support.

References Cited

- A'Brook, J. 1973. The effect of plant spacing on the number of aphids trapped over cocksfoot and kale crops. *Ann. Appl. Biol.* 74: 279–285.
- Antolin, M. F., and J. F. Addicott. 1991. Colonization, among shoot movement, and local population neighborhoods of two aphid species. *Oikos* 61: 45–53.
- Bach, C. E. 1980. Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata* (Fab.). *Ecology* 61: 1515–1530.
- Bach, C. E. 1986. A comparison of the responses of two tropical specialist herbivores to host plant patch size. *Oecologia* (Berl.) 68: 580–584.
- Bach, C. E. 1988a. Effects of host plant patch size on herbivore density: underlying mechanisms. *Ecology* 69: 1103–1117.
- Bach, C. E. 1988b. Effects of host plant patch size on herbivore density: patterns. *Ecology* 69: 1090–1102.
- Bowers, M. D., and N. E. Stamp. 1987. Patterns of oviposition in *Hemileuca lucina* (Saturniidae). *J. Lep. Soc.* 41: 131–140.
- Cain, M. L. 1985. Random search by herbivorous insects: a simulation model. *Ecology* 66: 876–888.
- Capman, W. C., G. O. Batzli, and L. E. Simms. 1990. Responses of the common sooty wing skipper to patches of host plants. *Ecology* 71: 1430–1440.
- Cappuccino, N., and R. B. Root. 1992. The significance of host patch edges to the colonization and development of *Corythucha marmorata* (Hemiptera: Tingidae). *Ecol. Entomol.* 17: 109–113.
- Cappuccino, N., and M.-A. Martin. 1997. The birch tube-maker *Acrobasis betullella* in a fragmented habitat: the importance of patch isolation and edges. *Oecologia* (Berl.) 110: 69–76.
- Connor, E. F., A. C. Courtney, and J. M. Yoder. 2000. Individuals-area relationships: the relationships between animal population density and area. *Ecology* 81: 734–748.
- Cook, W. M., and R. D. Holt. 2002. Periodical cicada oviposition damage: visually impressive, yet dynamically irrelevant. *Am. Midl. Nat.* 147: 214–224.
- Cook, W. M., J. Yao, and R. D. Holt. 2001. Spatial variability in oviposition damage by periodical cicadas in a fragmented landscape. *Oecologia* (Berl.) 127: 51–61.
- Cook, W. M., J. Yao, B. L. Foster, R. D. Holt, and L. B. Patrick. 2005. Secondary succession in an experimentally fragmented landscape: community patterns across space and time. *Ecology* 86(5): 1267–1279.
- Courtney, S. P., and S. Courtney. 1982. The 'edge effect' in butterfly oviposition: causality in *Anthocharis cardamines* and related species. *Ecol. Entomol.* 7: 131–137.
- Courtney, S. P., and J. Forsberg. 1988. Host use by two pierid butterflies varies with host density. *Funct. Ecol.* 2: 67–75.
- Cromartie, W. J. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *J. Appl. Ecol.* 12: 517–533.

- Delobel, A.G.L. 1982. Effects of sorghum density on oviposition and survival of the sorghum shoot fly, *Atherigonia soccata*. *Entomol. Exp. Appl.* 31: 170–174.
- Dempster, J. P., D. A. Atkinson, and M. C. French. 1995. The spatial population dynamics of insects exploiting a patchy food resource. *Oecologia (Berl.)* 104: 354–362.
- Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1995a. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus* and *Peromyscus*). *Ecology* 76: 827–829.
- Diffendorfer, J. E., N. A. Slade, M. S. Gaines, and R. D. Holt. 1995b. Population dynamics of small mammals in fragmented and continuous old-field habitat, pp. 175–199. In W. Z. Lidicker [ed.], *Landscape approaches in mammalian ecology and conservation*. University of Minnesota, Minneapolis.
- Doak, P. 2000a. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. *Ecology* 81: 1828–1841.
- Doak, P. 2000b. Habitat patchiness and the distribution, abundance, and population dynamics of an insect herbivore. *Ecology* 81: 1942–1857.
- Eber, S., and R. Brandl. 1994. Ecological and genetic spatial patterns of *Urophora cardui* (Diptera: Tephritidae) as evidence for population structure and biogeographical processes. *J. Anim. Ecol.* 63: 187–199.
- Eber, S., and R. Brandl. 1996. Metapopulation dynamics of the tephritid fly *Urophora cardui*: an evaluation of incidence-function model assumptions with field data. *J. Anim. Ecol.* 65: 621–630.
- Ellingson, A. R., and D. C. Andersen. 2002. Spatial correlations of *Diceroprocta apache* and its host plants: evidence for a negative impact from *Tamarix* invasion. *Ecol. Entomol.* 27: 16–24.
- Fisher, J. C. 1851. On a new species of cicada. *Proc. Acad. Nat. Sci. Phila.* 5: 272–275.
- Förare, J., and C. Solbreck. 1997. Population structure of a monophagous moth in a patchy landscape. *Ecol. Entomol.* 22: 256–263.
- Golden, D. M., and T. O. Crist. 1999. Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. *Oecologia (Berl.)* 118: 371–380.
- Grevstad, F. S., and A. L. Herzog. 1997. Quantifying the effects of distance and conspecifics on colonization: experiments and models using the loostribe leaf beetle, *Galerucella californiensis*. *Oecologia (Berl.)* 110: 60–68.
- Greig, A. A., and R. H. González. 1995. Resource concentration hypothesis: effect of host plant patch size on density of herbivorous insects. *Oecologia (Berl.)* 103: 471–474.
- Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77: 94–107.
- Halley, J. M., and J. P. Dempster. 1996. The spatial population dynamics of insects exploiting a patchy food resource: a model study of local persistence. *J. Appl. Ecol.* 33: 439–454.
- Hanski, I., and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biol. Conserv.* 68: 167–180.
- Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75: 747–762.
- Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* 72: 21–28.
- Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* 70: 1236–1243.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biol. J. Linn. Soc.* 42: 73–88.
- Harrison, S. 1994. Metapopulation and conservation, pp. 111–128. In P. J. Edwards, R. M. May and N. R. Webb [eds.], *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, Oxford.
- Hayes, J. L. 1981. The population ecology of a natural population of the pierid butterfly *Colias alexandria*. *Oecologia (Berl.)* 49: 188–200.
- Hertzberg, K. 1997. Migration of Collembola in a patchy environment. *Pedobiologia* 41: 494–505.
- Hertzberg, K., H. P. Leinaas, and R. A. Ims. 1994. Patterns of abundance and demography: Collembola in a habitat patch gradient. *Ecography* 17: 349–359.
- Herzig, A. L. 1995. Effects of population density on long-distance dispersal in the goldenrod beetle *Triphaba virgata*. *Ecology* 76: 2044–2054.
- Herzig, A. L., and R. B. Root. 1996. Colonization of host patches following long-distance dispersal by a goldenrod beetle, *Triphaba virgata*. *Ecol. Entomol.* 21: 344–351.
- Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J. Anim. Ecol.* 65: 725–735.
- Holt, R. D. 1992. A neglected facet of island biogeography: the role of internal spatial dynamics in area effects. *Theor. Popul. Biol.* 41: 354–371.
- Holt, R. D., G. R. Robinson, and M. S. Gaines. 1995. Vegetation dynamics in an experimentally fragmented landscape. *Ecology* 76: 1610–1624.
- Karban, R. 1981. Flight and dispersal of periodical cicadas. *Oecologia (Berl.)* 49: 385–390.
- Kareiva, P. 1985. Finding and losing host plants by *Phyllotreta*: patch size and surrounding habitat. *Ecology* 66: 1809–1816.
- Kareiva, P. M. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia (Berl.)* 57: 322–327.
- Kindvall, O. 1999. Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *J. Anim. Ecol.* 68: 172–185.
- Kindvall, O., and I. Ahlén. 1992. Geometrical factors and metapopulation dynamics of the bush cricket, *Metrioptera bicolor* Philippi (Orthoptera: Tettigoniidae). *Conserv. Biol.* 6: 520–529.
- Lawrence, W. S., and C. E. Bach. 1989. Chrysomelid beetle movements in relation to host-plant size and surrounding non-host vegetation. *Ecology* 70: 1679–1690.
- Lloyd, M., J. A. White, and N. Stanton. 1982. Dispersal of fungus-infected periodical cicadas to new habitat. *Environ. Entomol.* 11: 852–858.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- MacKay, D. A., and M. C. Singer. 1982. The basis of an apparent preference for isolated host plant by ovipositing *Euptychia libye* butterflies. *Ecol. Entomol.* 7: 299–303.
- Marsh, D. M. 1995. Patch boundary flight behavior of the Mexican bean beetle (Coleoptera: Coccinellidae). *Environ. Entomol.* 24: 1515–1519.
- Matter, S. F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. *Oecologia (Berl.)* 105: 447–453.

- McCann, J. M., and D. M. Harman. 1990. Influence of the intrastand position of black locust trees on attack rates of the locust borer (Coleoptera: Cerambycidae). *Ann. Entomol. Soc. Am.* 83: 705–711.
- McLain, D. K., and D. J. Shore. 1990. Spatial and temporal density dependence of host plant patch use by the ragwort seed bug, *Neocoryphus bicrucis* (Hemiptera: Lygaeidae). *Oikos* 58: 306–312.
- Morrow, P. A., D. W. Tonkyn, and R. J. Goldberg. 1989. Patch colonization by *Trirhabda canadensis* (Coleoptera: Chrysomelidae): effects of plant species composition and wind. *Oecologia* (Berl.) 81: 42–50.
- Pimentel, S. 1961a. The influence of plant spatial patterns on insect populations. *Ann. Entomol. Soc. Am.* 54: 61–69.
- Pimentel, S. 1961b. Species diversity and insect population outbreaks. *Ann. Entomol. Soc. Am.* 54: 76–86.
- Prokopy, R. J., and E. D. Owens. 1983. Visual detection of plants by herbivorous insects. *Annu. Rev. Entomol.* 28: 337–364.
- Ralph, C. P. 1977. Search behavior of the large milkweed bug, *Oncopeltus fasciatus* (Hemiptera: Lygaeidae). *Ann. Entomol. Soc. Am.* 70: 337–342.
- Raupp, M. J., and R. F. Denno. 1979. The influence of patch size on a guild of sap-feeding insects that inhabit the salt marsh grass *Spartina patens*. *Environ. Entomol.* 8: 412–417.
- Rausher, M. D. 1983. Alteration of oviposition behavior by *Battus philenor* butterflies in response to variation in host-plant density. *Ecology* 64: 1028–1034.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* (Wash. DC) 257: 524–526.
- Rodenhouse, N. L., P. J. Bohlen, and G. W. Barrett. 1997. Effects of woodland shape on the spatial distribution and density of 17-year periodical cicadas (Homoptera: Cicadidae). *Am. Midl. Nat.* 137: 124–135.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecol. Monogr.* 43: 95–124.
- Schneider, J. C. 1999. Dispersal of a highly vagile insect in a heterogeneous environment. *Ecology* 80: 2740–2749.
- Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82: 1879–1892.
- Schweiger, E. W., J. E. Diffendorfer, R. Pierotti, and R. D. Holt. 1999. The relative importance of small-scale and landscape-level heterogeneity in structuring small mammal distributions, pp. 175–207. *In* G. W. Barrett and J. D. Peles [eds.], *Landscape ecology of small mammals*. Springer, New York.
- Shapiro, A. M. 1984. "Edge effect" in oviposition behavior: a natural experiment with *Euchloe ausonides* (Pieridae). *J. Lep. Soc.* 38: 242–245.
- Simon, C., R. Karban, and M. Lloyd. 1981. Patchiness, density and aggregative behavior in sympatric allochronic populations of 17-year cicadas. *Ecology* 62: 1525–1535.
- Smith, F. F., and R. G. Linderman. 1974. Damage to ornamental trees and shrubs resulting from oviposition by periodical cicadas. *Environ. Entomol.* 3: 725–732.
- Stanton, M. L. 1983. Spatial patterns in the plant community and their effects upon insect search, pp. 125–157. *In* S. Ahmad [ed.], *Herbivorous insects: host-seeking behavior and mechanisms*. Academic, New York.
- Stein, S. J., P. W. Price, T. P. Craig, and J. K. Itami. 1994. Dispersal of a galling sawfly: implications for studies of insect population dynamics. *J. Anim. Ecol.* 63: 666–676.
- Summerville, K. S., and T. O. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82: 1360–1370.
- Turchin, P. 1987. The role of aggregation in the response of Mexican bean beetles to host-plant density. *Oecologia* (Berl.) 71: 577–582.
- Turchin, P. B. 1986. Modelling the effect of host plant patch size on Mexican bean beetle emigration. *Ecology* 67: 124–132.
- White, J. 1980. Resource partitioning by ovipositing cicadas. *Am. Nat.* 115: 1–28.
- White, J., M. Lloyd, and R. Karban. 1982. Why don't periodical cicadas normally live in coniferous forests? *Environ. Entomol.* 11: 475–482.
- White, J., P. Ganter, R. McFarland, N. Stanton, and M. Lloyd. 1983. Spontaneous, field tested and tethered flight in healthy and infected *Magacidada septendecim* L. *Oecologia* (Berl.) 57: 281–286.
- Williams, K. S., and C. Simon. 1995. The ecology, behavior and evolution of periodical cicadas. *Annu. Rev. Entomol.* 40: 269–295.
- Wilson, E. O., and D. S. Simberloff. 1969. Experimental zoogeography of islands: defaunation and monitoring techniques. *Ecology* 50: 267–278.
- Withers, T. M., and M. O. Harris. 1996. Foraging for oviposition sites in the Hessian fly: random and non-random aspects of movement. *Ecol. Entomol.* 21: 382–395.
- Withers, T. M., M. O. Harris, and C. Madie. 1997. Dispersal of mated female Hessian flies (Diptera: Cecidomyiidae) in field arrays of host and nonhost plants. *Environ. Entomol.* 26: 1247–1257.
- Yao, J., R. D. Holt, P. M. Rich, and W. S. Marshall. 1999. Woody plant colonization in an experimentally fragmented landscape. *Ecography* 22: 715–728.
- Zalucki, M. P., and Y. Suzuki. 1987. Milkweed patch quality, adult population structure, and egg laying in the monarch butterfly. *J. Lep. Soc.* 41: 13–22.

Received 15 April 2004; accepted 30 November 2004.