DISSERTATION

SPATIAL ECOLOGY OF CACTUS BUGS: INTERACTIONS AMONG SUITABLE HABITAT, CONNECTIVITY, AND MOVEMENTS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY ROBERT LEE SCHOOLEY ENTITLED SPATIAL ECOLOGY OF CACTUS BUGS: INTERACTIONS AMONG SUITABLE HABITAT, CONNECTIVITY, AND MOVEMENTS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

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A key issue in spatial ecology and conservation biology is how individuals and populations respond to habitat patchiness. It is critical that we develop some guidelines regarding how much of the complexity of landscape structure and movement behavior must be considered to understand how animals live in fragmented landscapes. I address this and related topics with a system of cactus bugs (*Chelinidea vittiger*) and their host plant, *Opuntia polyacantha*, in the short-grass steppe of Colorado. Within two patchy landscapes that differed in matrix structure, I examined how landscape structure influenced the inter-patch movements and the distribution and abundance patterns of *C. vittiger*. Movement rates of adults were strongly affected by the nature of the matrix. Hence, dispersal is not a fixed value for *C. vittiger*; it depends on the resistance of matrix elements. Patch area set an upper constraint to the number of individuals within patches, and density was negatively related to patch area. Models of the occupancy and abundance of *C. vittiger* among patches that included a measure of patch connectivity that ignored matrix structure performed well for a landscape with a fairly homogeneous matrix. A more complex model that adjusted connectivity based on matrix structure was

needed to explain patterns on a landscape with a heterogeneous matrix. Experimental releases of individuals within the matrix demonstrated that the ability of *C. vittiger* to detect habitat patches depended on environmental conditions. In particular, their movement behavior and perceptual range was strongly influenced by wind direction. These results suggest that *C. vittiger* uses olfaction to find habitat patches. For some species, perceptual range may be anisotropic and patch connectivity may be temporally dynamic and directional. We need to broaden our view of connectivity so that it explicitly considers the natural history of the focal species. Developing useful generalizations about the degree of complexity that must be incorporated when investigating patchy systems should be possible, but only after a more complete empirical foundation is established of how different species respond to environmental heterogeneity.

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CHAPTER I

OVERVIEW

Habitat fragmentation due to human land use remains one of the key issues in conservation biology. Moreover, suitable habitat for most animals is naturally patchy. This patchiness is especially evident for habitat specialists, such as insect species with only one or a few host plant species, which inhabit 'fragmented' landscapes because their suitable habitat has a restricted distribution. Hence, insect-host plant systems should be useful systems for asking questions about how animals deal with life in patchy environments. These systems have the potential to provide insights of general importance to both basic and applied ecology. Here, I explore a system that includes cactus bugs (*Chelinidea vittiger*) and their single host plant, plains prickly pear cactus (*Opuntia polyacantha*), in the short-grass steppe of Colorado.

Historically, the central focus in research on animal responses to habitat patchiness has been on the area and isolation of suitable habitat patches. This view of landscapes partly resulted from the basic ideas of island biogeography theory (MacArthur and Wilson 1967) being applied to terrestrial systems. The matrix between suitable habitat patches was treated as homogeneous and neutral (Wiens 1995). As the dominant conceptual framework in spatial ecology and conservation biology has shifted from island biogeography theory to metapopulation ecology (Hanski and Simberloff 1997), the range

of spatial population structures that are considered metapopulations has broadened to include 'patchy populations' (Harrison and Taylor 1997). Nevertheless, the 'neutral-matrix' view remains the standard in most metapopulation research (Hanski 1994, 1998, Wiens 1997). Only recently has there been progress in meshing the approaches of metapopulation ecology and landscape ecology to consider potential matrix effects explicitly (e.g., Pither and Taylor 1998, Roland et al. 2000, Joly et al. 2000, Ricketts 2001). This 'matrix-matters' view has required that additional attention be given to movement behavior and inter-patch transfers of animals. This emphasis is overdue because movement is the key element for all systems with spatial population structure (Ims 1995, Wiens et al. 1993, Wiens 1997). A realistic picture of how animals live in fragmented landscapes necessitates that movement behavior be treated in some detail. Exactly how much detail is needed to understand the dynamics of patchy systems remains an open question.

In Chapter 2, I focus on the movements, distribution, and abundance of *C. vittiger* in two landscapes that differ in matrix structure. A mark-recapture study of inter-patch movements indicates that cactus bugs exhibit a patchy population structure (Harrison and Taylor 1997). The observed difference in movement rates between the landscapes is partly explained by an experiment on the effect of matrix structure on movement behavior. I next evaluate several theoretical predictions regarding how animal density should be related to patch area. My results indicate that patch area mainly sets an upper constraint on the number of individuals (Thompson et al. 1996) and that limited knowledge and undermatching of resources relative to an ideal free distribution (Ranta et al. 1999) may contribute to the observed patterns. I then evaluate the relative roles of

patch-level traits and landscape variables in explaining patterns of incidence and abundance for *C. vittiger*. Furthermore, I compare the performance of models that include a measure of patch connectivity representing either a 'neutral-matrix' or a 'matrix-matters' view of landscapes. My overall approach blends aspects that are typical of metapopulation ecology with those of landscape ecology, and my results provide some general insights into how habitat specialists respond to landscape structure.

In Chapter 3, I examine the movements of cactus bugs in the matrix in more detail. Specifically, I attempt to determine (1) whether the pathways of individuals are nearly directional as predicted by simulation models (Zollner and Lima 1999), and (2) what the perceptual range (Lima and Zollner 1996) is for *C. vittiger*. The results indicate that cactus bugs probably use olfaction to find patches of suitable habitat, and this outcome complicates any attempt to evaluate movement behavior and perceptual range. Importantly, these insights also suggest that we need to broaden our views of patch and landscape connectivity so that they explicitly consider the dominant senses that animals use to navigate around their patchy landscapes. Connectivity can be temporally dynamic and directional.

In Chapter 4, I shift my approach a bit by forgoing the patch-matrix view that I employed in the previous chapters. Instead, I take more of a pure statistical approach for examining the relationships between *C. vittiger* and its host plant in which I do not define habitat 'patches' *a priori*. I also increase the spatial extent of the study compared to my previous work so that a broader range of habitat variability is included. I explore how the grain size of measurement influences the association between *C. vittiger* and *Opuntia* along a 700-m transect. My results indicate that multi-scale studies must be carefully

interpreted because the degree of spatial autocorrelation in errors from regression models can change with grain size. That is, the degree of bias in traditional statistical approaches, due to spatial dependency of ecological data, depends on the spatial grain of observation.

In spatial ecology, we are currently struggling with trying to understand how much of the complexity of real landscapes and of animal behavior must we incorporate into our views of patchy systems. My study provides useful insights about when fairly simple approaches that focus solely on suitable habitat will suffice, and when more complex approaches that explicitly consider matrix effects and movement behavior are required. Such empirical studies are critical if we are to develop a general understanding of how species interact with their patchy landscapes.

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CHAPTER II

CACTUS BUGS IN PATCHY LANDSCAPES: MOVEMENTS, CONSTRAINTS, AND CONNECTIVITY

Introduction

Habitat is naturally patchy and many landscapes are being fragmented even further due to human land use. Therefore, an understanding of how individuals and populations respond to habitat patchiness is a central pursuit in both spatial ecology and conservation biology. Recent emphasis in spatial ecology has been on metapopulations (Hanski and Simberloff 1997). Most fragmented systems may not fit classical models of metapopulations, however, and they are better viewed as patchy populations or as systems with mixed structures and intermediate characteristics (Harrison and Taylor 1997). Although it is difficult to make clear distinctions regarding spatial population structure, the main factor defining such structure is the dispersal distance of organisms relative to interpatch distances. Patchy populations have substantially more interpatch transfer than do classical metapopulations. Hence, for animals in subdivided habitat, data on movements are required to determine the scale at which they respond to environmental patchiness and to describe spatial population structure (Addicott et al.

1987, Wiens 1989, 1997, Amarasekare 1994, Harrison and Taylor 1997, Tilman and Kareiva 1997, Doak 2000).

A main research focus for all patchy systems has been the effect of patch area on the density of organisms within patches because this relationship has important implications for the dynamics of populations and communities and for issues in conservation (Matter 2000). Several hypotheses make explicit predictions about whether density should increase, remain constant, or decrease with increasing size of habitat patches (see Connor et al. 2000). For instance, Root (1973) proposed the resource concentration hypothesis, which states that specialized herbivores are more likely to find and remain on host plants that are concentrated in pure, large, or dense patches. In this case, density should be positively correlated with patch size; movement behavior (immigration and emigration) is the key mechanism (Root 1973, Kareiva 1983). In contrast, a constant relationship between density and patch area is predicted by the sampling colonization hypothesis (Haila et al. 1993), in which patch area 'randomly samples' individuals from an available pool. The sampling colonization hypothesis is thus a null model for density-area relationships. Finally, a realistic modification of the ideal free distribution proposes that individuals have limited knowledge of the resources in their surroundings. This constraint produces 'undermatching' (Kennedy and Gray 1993, Ranta et al. 1999), in which low-resource patches have more individuals, and high-resource patches have fewer individuals, than expected. With undermatching, density is negatively correlated with patch area.

Reviews and meta-analyses of empirical density-patch area relationships have documented a diversity of responses (Kareiva 1983, Stanton 1983, Bowers and Matter

1997, Bender et al. 1998, Connor et al. 2000). Overall, Connor et al. (2000) concluded that animal densities were positively correlated with patch area, with insects and birds having large or moderate positive correlations and mammals having near zero correlations. Bowers and Matter (1997) restricted their analysis to mammals and suggested that density-area patterns may be scale-dependent: landscapes with smaller, less isolated patches tend to have negative-density area relationships and landscapes with larger, more isolated patches tend to have positive relationships (see also Grez and González 1995). Responses to fine-scale heterogeneity may primarily reflect individual-level processes, whereas responses to broad-scale heterogeneity are more likely to reflect extinction-colonization dynamics (Haila et al. 1993, Hanski 1994*a*, Bowers and Matters 1997).

I hypothesize that patch area sets the upper limit to the abundance of individuals within patches. Many ecological variables exhibit a limiting-factor relationship (Blackburn et al. 1992, Kaiser et al. 1994, Brown 1995, Thompson et al. 1996, Cade et al. 1999). Numerous factors potentially can limit the value of an ecological variable at any given place or time, but one of these factors sets an upper limit reached only when it is the active limiting factor (Kaiser et al. 1994). Hence, bivariate scattergrams often display a triangular shape in which data points are widely distributed below an upper bound. The variation below this upper bound is due to the actions of other variables that can drag data points below the upper constraint line (Thompson et al. 1996). There is visual evidence of triangular distributions of abundance versus patch area for some specialist insects (see Figures 2 in Connor et al. 1997, Midtgaard et al. 1998), but previous analyses have not modeled patch area-abundance associations as limiting-factor relationships.

Of course, terrestrial habitat patches are not islands but instead are elements of a broader landscape (Wiens 1995). The incidence and abundance of animals in patches of suitable habitat may be strongly influenced by patch context and connectivity. Patch context refers to the location of a patch relative to the structure of the surrounding mosaic (Wiens et al. 1993*a*, Wiens 1997). Connectivity refers to the degree that the landscape facilitates or hinders the movement of organisms among patches (Taylor et al. 1993, Tischendorf and Fahrig 2000). The distinction between patch context and connectivity can be somewhat blurry, especially for patchy populations. Processes such as context-dependent patch selection and matrix-dependent movement can act in tandem to influence the distribution of individuals.

Connectivity has been viewed and measured in different ways between two branches of spatial ecology. In metapopulation ecology, connectivity is measured at the patch scale (Moilanen and Hanski 2001, Tischendorf and Fahrig 2001) and the matrix is often portrayed as featureless, unsuitable habitat (Hanski 1998, Wiens 1997). Therefore, patch connectivity is the inverse of patch isolation and depends only on the linear distances to other patches of suitable habitat and their areas (Hanski 1994*b*, 1998). In landscape ecology, connectivity is measured at the 'landscape scale' across multiple patches (Moilanen and Hanski 2001, Tischendorf and Fahrig 2001) and there is a strong focus on how the texture of the landscape affects movements (Crist et al. 1992, Taylor et al. 1993, Wiens et al. 1993*a*, Wiens et al. 1997). Different matrix elements may differ in resistance to movement and thus represent unequal costs and benefits to individuals. In reality, connectivity can be evaluated logically at either the patch or landscape scale depending on the questions being asked, and matrix effects can be included into

connectivity measures even when systems operate at relatively broad spatial scales (Åberg 1995, Petit and Burel 1998, Moilanen and Hanski 1998, Pither and Taylor 1998, Hokit et al. 1999, Roland et al. 2000, Joly et al. 2001). Approaches within fields of spatial ecology need not be distinct. Developing generalizations as to when the matrix matters remains a critical challenge to both branches.

Here, I examine the influence of landscape structure on the movements, distribution, and abundance of cactus bugs (*Chelinidea vittiger* Uhler, Hemiptera: Coreidae). *C. vittiger* is a habitat specialist with suitable habitat that is naturally patchy. My investigation blends approaches characteristic of landscape ecology and metapopulation ecology. First, I examine the effects of matrix habitat on movement behavior and distances. I combine results on inter-patch transfers of individuals with those on inter-patch distances to demonstrate that *C. vittiger* operates toward the patchy population end of the population structure spectrum (Harrison and Taylor 1997). Second, I examine the dispersion pattern of individuals among patches and ask whether they are aggregated even after controlling for the patchiness of suitable habitat. Third, I examine the effects of patch area on the incidence and abundance of *C. vittiger* and test predictions from the resource concentration, sampling colonization, and undermatching hypotheses. Fourth, I compare the potential of two measures of connectivity to improve the performance of statistical models in explaining the occupancy and abundance of *C. vittiger* among patches. One connectivity measure ignores the nature of the matrix (neutral-matrix model), whereas the other measure modifies linear distances between patches by the structure of the matrix (matrix-matters model).

Many studies of patchy systems have focused on a single life stage of a species in one type of landscape. Moreover, for systems that operate on broad spatial scales, surveys of animals within patches often are limited to presence-absence data. Throughout this study, I compare responses of three life stages of *C. vittiger* in two landscapes that differ in matrix structure and ask whether models of occupancy and of abundance provide similar conclusions.

Natural History of Cactus Bugs

Chelinidea vittiger is an ectophagous insect that is closely tied to its host plant, *Opuntia* cactus. The geographic range of this cactus bug essentially corresponds with the distribution of flat-jointed *Opuntia* spp. (platyopuntias) in the United States, Canada, and northern Mexico (Mann 1969, Herring 1980). Adults of *C. vittiger* feed on mature pads of *Opuntia*, whereas nymphs are more likely to feed on immature pads and fruits (De Vol and Goeden 1973).

C. vittiger is univoltine in my study area and in southern California (De Vol and Goeden 1973), but it may be bivoltine in other areas (Mann 1969). The adult sex ratio is approximately 1:1 (De Vol and Goeden 1973, Schooley unpublished data). Most mating occurs from April to mid June. Males and females are polygamous and no courtship behavior occurs (De Vol and Goeden 1973). Females attach eggs to the underside of cactus spines or to grass stems and twigs close to the host plant (Mann 1969). Eggs hatch in ca. 13 days and then *C. vittiger* develops through five nymphal stages that take a total of ca. 73 days (De Vol and Goeden 1973). The new adults are active for several months

in the fall, but they do not mate during this time. Cactus bugs overwinter in the adult stage (Mann 1969, De Vol and Goeden 1973). The lifespan for adults is ca. 9-12 months (De Vol and Goeden 1973).

Adult *C. vittiger* are capable of flight, but they rarely fly (Hamlin 1924, Dodd 1940, Mann 1969, De Vol and Goeden 1973). Instead, cactus bugs typically walk between host-plant patches through a matrix of unsuitable habitat. The nature of the matrix may influence the movements and distribution of *C. vittiger*. Burger and Louda (1994, 1995) provided evidence from fine-scale experiments that *C. vittiger* occurred most often on those pads of *Opuntia fragilis* in mixed- grass prairie where the nearby vegetation had been reduced or removed.

C. vittiger was among the first cactus insects released into Australia during the 1920s as part of the biological control program against *Opuntia* (Dodd 1940). Its limited effectiveness as a control agent in Australia, and in another release in California (Goeden et al. 1967), was likely due to its restricted movements (De Vol and Goeden 1973). However, there are no quantitative data on the movement rates of *C. vittiger*.

Methods

Study area and suitable habitat

I conducted my studies at the Central Plains Experimental Range (CPER) in north-central Colorado ($40^0$49'N, $104^0$46'W), 61 km northeast of Fort Collins, at 1650 m elevation. The climate is semiarid, with an average of 321 mm of annual precipitation (Lauenroth and Sala 1992), which is mainly delivered in brief spring and summer

thunderstorms. The CPER is located in the short-grass steppe and has vegetation dominated by two bunchgrasses, *Bouteloua gracilis* and *Buchlöe dactyloides* (Lauenroth and Milchunas 1991). My main plots were located on upland habitats that also included *Aristida longiseta*, *Artemisia frigida*, and *Eriogonum effusum*. The area received moderate grazing from cattle.

Suitable habitat for *C. vittiger* consisted of patches of a single species of low-growing platyopuntia, plains prickly pear (*Opuntia polyacantha*). Cover of *O. polyacantha* is 1 – 5% on shortgrass steppe (Hart and Ashby 1998), but this succulent may contribute 14 – 56% of the above-ground biomass (Sims et al. 1978). *O. polyacantha* is more common on uplands than in swales (Hyder et al. 1966, Milchunas et al. 1989, Chapter 4), and it is patchy at multiple spatial scales.

I established two 0.5-ha plots (100 x 50 m) in July 1998. *Opuntia* occurred just outside of the plot boundaries, so the plots were not isolated patch networks, such as is typical for metapopulation studies. The two plots were separated by 240 m and considered independent landscapes because I detected no movement of marked cactus bugs between them (see *Inter-patch movements*). I intentionally selected the two landscapes so that one had a relatively homogeneous matrix of low vegetation structure (low-matrix landscape), whereas the other had a more heterogeneous matrix and overall higher structure (high-matrix landscape). Hence, the landscapes differed in the degree of matrix heterogeneity and in the average structure of the matrix. Both of these landscape attributes are relevant to different comparisons that I will make. The landscapes were not replicated because I could not find other areas where the cover and spatial distribution of *Opuntia* and the matrix structure were similar enough to be considered replicates unless I

reduced the size of the plots considerably. I chose to maintain an appropriate spatial extent for the questions of interest rather than employing a smaller, inappropriate scale to allow for replication of plots (Hargrove and Pickering 1992, Schindler 1998, Oksanen 2001). Moreover, most of the statistical evaluations are conducted within the two landscapes in which patches were the sampling units, and they were highly replicated.

Patch definition and distribution

Whenever possible, delineation of patches should be guided by the behavior of the study animal, so that landscapes are described from an organism-based perspective (Wiens 1995, Pearson et al. 1996). I based my patch criterion on preliminary observations of the movement behavior of *C. vittiger* at the edges of cactus clumps. Adults would sometimes move short distances (<0.25 m) into the matrix and then immediately return to the same clump. I interpreted this type of movement as exploratory behavior from a given patch. In contrast, if adults moved longer distances into the matrix, then typically they would continue moving away from the original cactus clump and not return right away. I interpreted this behavior as an inter-patch transfer. Therefore, I defined individual patches of suitable habitat as clumps of *O. polyacantha* in which each pad was within 0.25 m of another pad.

A preliminary survey (8-13 July 1998) indicated that patches with a long axis <10 cm rarely were occupied by *C. vittiger* nymphs (patch occupancy = 0.016, $n = 61$), so I disregarded these patches in my surveys. I marked all other cactus patches with a uniquely numbered metal tag. Using an electronic distance-measuring instrument (EDM,

Pentax PTS-II05), I mapped the locations of all patch centers. The accuracy of the EDM is ca. ±5 mm (Wiens et al. 1993*b*).

The template of suitable habitat for cactus bugs depends not only on the number and size of *Opuntia* patches, but also on their spatial arrangement. Dispersion patterns can be scale-dependent (Crist and Wiens 1996, Schooley and Wiens 2001). Therefore, I quantified the distribution of patches across multiple scales by comparing the observed mean 1^{st}-10^{th} nearest-neighbor distances (NND) with those expected under the null hypothesis of complete spatial randomness. For each landscape, I generated the expected random patterns with computer simulations in which patches (same numbers as observed) were randomly placed within a 100 x 50 m plot. The expected NND were the grand means of the mean NND from 999 simulations. Significant deviation from randomness was tested by comparing the observed NND with 95% confidence intervals for the expected values, which were constructed with the 25^{th} lowest and highest mean NND from the 999 simulations (Crist and Wiens 1996). I express results graphically as the ratio of the observed to expected NND. A ratio >1 indicates a regular pattern, <1 is aggregated, and ratios near 1 are random (Crist and Wiens 1996). I examined the multi-scale dispersion of all patches and of only large patches ($>10^3 cm^2$) that were most likely to be occupied by *C. vittiger* (see Results).

Patch-level variables

I quantified the area, shape, and quality of each patch. Patch area was calculated as an ellipse using the length of the (major) long axis of the patch and that of the (minor) axis

perpendicular to the long one. As an index for patch shape, I used the ratio of the length of the minor axis to that of the major axis. This shape index was maximized at 1.0 for a circle and assumed smaller values for more linear patches. I used the horizontal coverage of the host plant, *O. polyacantha*, as a measure of patch quality. The coverage was visually scored by two observers and assigned to one of three categories: class 1 (0 – 33%), class 2 (34 – 66%), and class 3 (67 – 100%). The two observers were consistent in classifying the quality of 82% of a random subset of the patches (n = 56), and the discrepancies were always minimal (i.e., never class 1 vs. class 3).

Patch connectivity

I measured connectivity at the patch level, which is more typical of a 'metapopulation approach' than a 'landscape ecology approach' (Moilanen and Hanski 2001, Tischendorf and Fahrig 2000, 2001), but I also present summary statistics for each plot to contrast the overall structural connectivity of the two landscapes. Moilanen and Nieminen (2002) concluded that the connectivity measures that perform best are those based on circular buffers around patches and those typical of the incidence function model (IFM) approach, in which the distances to other patches are explicitly considered. My connectivity measures are hybrids of the buffer and the IFM types.

I included not just occupied patches (e.g., Hjermann and Ims 1996, Moilanen and Hanski 1998, Hokit et al. 1999, Moilanen and Nieminen 2002), but all patches in my estimation of patch connectivity, for several reasons. First, the formulae that I used for connectivity are weighted by patch area so that smaller patches, which may be occupied

less often than are larger ones, already contribute less to connectivity. Second, unoccupied patches may function as 'stepping stones' and still be important to movement and patch connectivity. Third, if a system behaves like a patchy population, then unoccupied patches could influence the perceived habitat quality of a focal patch. For instance, an adult female might choose to oviposit in a patch that has unoccupied but suitable habitat patches nearby.

Initially, I measured patch connectivity following a 'neutral-matrix' model in which I measured the distances to other patches of suitable habitat and their areas. In this approach, the nature of the matrix between patches was ignored. The neutral-matrix connectivity (*Cn*) of patch *i* was defined as

$$Cn_i = \sum \frac{A_j}{d_{ij}^2} \qquad j \neq i$$

where A_j is the area of patch $_j$ and d_{ij} is the linear distance between the centers of patches *i* and *j*. Originally, I calculated *Cn* for three buffer sizes that included all surrounding patches within 3, 5, or 7 m of patch *i*. I removed any focal patches from analyses that were closer to a plot boundary than the specified distance to eliminate any edge effects (i.e., artificially reduced connectivity). The measures of *Cn* for the three buffer sizes were highly correlated (all $r \geq 0.98$), however, so I used only the measure of *Cn* based on a 5-m buffer (78.5-m^2 circular area). Therefore, all subsequent multiple regression models were built with a subset of the focal patches that were >5 m from a plot boundary, whether the model included connectivity as an explanatory variable or not.

I next developed a 'matrix-matters' model of connectivity (*Cm*) in which the distance between patches is replaced with an effective distance, which is a distance weighted by the structure of the matrix (Moilanen and Hanski 1998, Petit and Burel 1998, Hokit et al.

1999). High vegetation structure between two patches increases the effective distance between them (and decreases the connectivity) more so than does low vegetation structure. *Cm* of patch *i* was defined as

$$Cm_i = \sum \frac{A_j}{\left(\sum_h m_h d_{hij}\right)^2} \qquad j \neq i$$

where m_h is a measure of the vegetation height for matrix type h and d_{hij} is the straight-line distance between patches i and j that crosses matrix type h. As with *Cn*, I calculated *Cm* using all patches within a 5-m buffer of patch *i*.

To calculate m_h, I combined field sampling with geostatistics and GIS analysis. From 8-23 September 1998, I used point-intercept sampling to measure the maximum height of vegetation within the matrix. On each plot, I established a grid of 2626 points (101 x 26). Points were spaced at 1-m intervals along the long axis of each plot and at 2-m intervals across the short axis. At each point, I measured maximum vegetation height in 5-cm intervals (class 0 = bare ground, class 1 = 1-5 cm, class 2 = 6-10 cm, and so on). Next, I used kriging to generate a contour map of vegetation structure based on the grid of sampled points. Kriging is an interpolation technique in which estimated values at points not sampled are based on values at nearby sample locations and the degree of autocorrelation across those distances (Bailey and Gatrell 1995, Robertson 2000). In essence, weights are applied to neighboring sample points based on their distances and the spatial structure of the data, which is summarized by a variogram model (Rossi et al. 1992, Bailey and Gatrell 1995). I used GS$^+$ software (Robertson 2000) to develop variogram models separately for each plot and then to create kriged maps (with underlying grids of kriged values) using punctual kriging. Finally, I imported the kriged

values of vegetation structure into ArcView GIS and created polygons for 10 structure classes (h = 1-10 matrix types), which I then used to compute Cm.

I expected that the models of occupancy and abundance with Cm and Cn would perform about the same for the Low-Matrix landscape. In contrast, I expected that the Cm models would outperform the Cn models for the High-Matrix landscape.

Inter-patch movements

Empirical data.—Field observations indicated that inter-patch movements by nymphs were uncommon. I conducted a mark-resight study to determine the general movement rates of adults among patches. I wanted to establish the time period when most movement occurred, to compare movements between the sexes, and to contrast movement rates between the low-matrix and high-matrix landscapes.

I performed mark-resight surveys during the non-mating season (2–16 September 1998) and the following mating season (19–29 May 1999). In each landscape, I applied unique marks to individuals (with dot combinations of Testors model paint on the pronotum) within patches in two core areas (30 x 30 m each) centered in the north and south halves of the plot. This design produced a buffer of ≥10 m around the marking zone. I marked 1 –13 individuals (usually ≤5) per patch from a representative sample of patches. These source patches were spread throughout the marking zones and included a range of patch sizes. During the non-mating season, I marked 247–251 individuals per landscape from 57–73 source patches; during the mating season, I marked 96–147 individuals per landscape from 22–32 patches. I then surveyed all patches within the entire plot (core marking areas plus the buffer) 6–11 days after marking. These

differences in resighting intervals did not affect the comparisons of interest (see *Results*). I measured movement distance as net displacement, which was simply the distance between the center of the patch where an individual was marked and the center of the patch were it was resighted.

Correction via simulation.—In mark-resight studies, movement distances are often underestimated due to the restricted size of the study area (Baker et al. 1995, Koenig et al. 2000). For instance, if a *C. vittiger* adult was marked in a patch on the edge of the marking zone and moved >10 m in a certain direction across the buffer, then it would leave the plot and not be accessible for resighting. The downward bias in estimates of movement rates will depend on actual movement distances and the size and shape of the study area. One solution to this problem is to correct the observed distribution of moves for detection probabilities within the maximum detection distance (Baker et al. 1995, Koenig et al. 2000). The probability of detecting a movement of a given distance is estimated via simulation in which a large number of individuals move a given distance in random directions from random starting points within the plot. The detection probability equals the proportion of simulated moves that fall within the plot. One can then correct the observed movement distribution by dividing the number of moves for a given distance by the detection probability for that distance. For my plots, I assumed that all movements ≤10 m had a detection probability of 1 because of the buffer, so I estimated detection probabilities in 2-m intervals from 12 to 52 m (the maximum observed move). All simulated moves originated in random locations within the marking zones of the plot. For each distance, I simulated 10,000 movements. I compare corrected distributions of movements with the Smirnov test (Conover 1980), which is based on the maximum

separation between two empirical distribution functions and is sensitive to differences in central tendency and in variance.

Movement experiment: matrix and edge effects

I conducted a field experiment to examine the effects of vegetation structure of the matrix on movement behavior of adult *C. vittiger*. I contrasted movements between two matrix types that bracketed the natural range of vegetation structure on my main plots. Because the movement behavior of animals at habitat boundaries may be crucial to landscape connectivity (Wiens et al. 1985, 1993a, Stamps et al. 1987, Hansen and di Castri 1992, Lidicker 1999), I also evaluated whether the edge between low and high-matrix areas influenced the movement patterns of *C. vittiger*. Most past work on edge-related movements of habitat specialists has focused on edges between suitable habitat patches and the matrix (e.g., Kuussaari et al. 1996, Haddad 1999, Ries and Debinski 2001, Schultz and Crone 2001) instead of on edges between different matrix elements.

The experimental area was located several km from the main study plots in grassland with high vegetation structure. No *Opuntia* occurred within the area or nearby (ca. 100 m). I created three plots (10 x 10 m each) of low structure by mowing the existing vegetation. These plots were surrounded on all sides by naturally high vegetation. This manipulation created a sharp, high-contrast edge.

From 9-22 June 2000, I collected individuals ≤3 h prior to their release from an area several km from the experimental plots and then released the bugs (n = 14) singly into one of the low-matrix plots (200-403 cm from an edge of the high matrix) and monitored

their movement pathways. Individuals were always released into a low-matrix plot because I was interested in whether they exhibited any deflection behavior when encountering the edge of the high matrix. I provide evidence from another movement study (Chapter 3) that this protocol of not alternating releases between the two matrix types did not bias the main movement metric that is compared (Appendix 2.1). I conducted trials between 910 and 1240 when soil surface temperatures measured in the low-matrix area ranged from 27.9 to 39.5 °C and windspeeds at 5 cm above ground level ranged from 0.5 to 6.0 km/h.

Using standard techniques for measuring insect movements (Wiens et al. 1993*b*, Turchin 1998, Schooley and Bestelmeyer 2000), I recorded the pathways by placing sequentially numbered flags at the bug's location at 1-min time steps. To avoid disturbing the bugs, I waited ≥1 time step before placing the flag. I mapped the flag locations for each pathway by triangulation with a measuring tape (Turchin 1998). At each flag, I also measured the maximum vegetation height in 5-cm intervals (i.e., the same sampling technique used to measure matrix structure on the main plots).

I used a within-subject design to compare movements between matrix elements, which should control for variation among individuals in movement behavior or variation among trials in environmental conditions. Using signed ranks tests, I compared three movement metrics between low and high vegetation structure: mean step length, mean vector length (MVL) and net displacement rate (Wiens et al. 1993*b*). Mean step length is the average distance moved during 1 min. MVL is a measure of directionality that is a unit vector measure of the dispersion of turning angles (Batschelet 1981). MVL varies from 0 (uniform) to 1 (perfectly directional). Values for MVL can depend on the number of

steps used in their calculations (Batschelet 1981). Therefore, I truncated the portion of each pathway in either the low or high matrix that had the most steps so that the MVL was based on an equal number of steps for the two matrix types. Net displacement is the straight-line distance between the initial and final locations. Because pathways differed in the total number of steps, I report net displacement rate (cm/s).

I estimated edge permeability (Wiens et al. 1985, Stamps et al. 1987, Ries and Debinski 2001) as the proportion of individuals approaching the edge (<50 cm) between matrix types that subsequently crossed it. Because animals may not choose to stay in a landscape element until they sample the habitat across an edge (Ries and Debinski 2001), I also estimated the proportion of individuals that returned to the low-matrix habitat after moving >50 cm into the high-matrix habitat. Finally, I asked whether the general direction of the path was maintained after crossing the edge. For each individual, I measured the difference between the angle from the start location (within the low matrix) to the edge and the angle from the edge to last location. I then calculated a mean and a 95% CI (Batschelet 1981) for these angular differences. If the 95% CI includes zero, then there is no evidence that the edge caused a change in the overall direction of the path.

Surveys of C. vittiger

I counted the number of individuals of *C. vittiger* in each patch during three time periods to examine the dynamics of occupancy and abundance among life stages. Nymphs were counted from 5-8 August 1998. Several nymphal stages may occur

simultaneously (De Vol and Goeden 1973). During my surveys, most nymphs were 3rd or 4th instars. I tallied non-mating adults from 10-17 September 1998. I counted adults during the mating season from 27-29 May 1999 and refer to these individuals as 'mating adults' although not all individuals were mating during the surveys. I attempted to count all individuals within a patch by carefully examining each *Opuntia* pad and the vegetation and bare ground within the patch. I did not determine the sex of individuals. All surveys were conducted on days without measurable precipitation between 830 and 1730, with most counts completed by 1330.

Spatial independence of samples

The presence of spatial autocorrelation in ecological data can bias tests of association and produce misleading results from multiple regression analyses (Thomson et al. 1996, Lennon 2000). One of my explanatory variables, patch connectivity, exhibited positive spatial autocorrelation at short distances (<10 m). However, simulations conducted by Lennon (2000) demonstrate that when the response variable is not autocorrelated then the non-spatial regression methods remain valid (Lennon 2000). The abundances of the three life stages of *C. vittiger* were not spatially correlated on either landscape (Appendix 2.2).

Dispersion of individuals among patches

Many previous tests of the dispersion patterns of insects have overestimated the degree of aggregation (Connor et al. 1997). This bias arose from the inappropriate use of a Poisson distribution as a null model, which assumes that the size of the 'sample units'

(e.g., patch area, leaf size) is constant. Because the variance of the Poisson distribution equals its mean, an index of dispersion can be calculated from the ratio of the variance of counts of individuals per sample unit and the mean number of individuals per sample unit. A variance/mean ratio >1 indicates aggregation and a ratio <1 indicates regularity. When the sample units vary in size, however, random distribution of individuals will lead to a variance/mean ratio >1, so naïve use of a simple Poisson model often will lead to the incorrect inference that individuals are aggregated (Connor et al. 1997).

In this study, patch area varied over several orders of magnitude, so I followed the approach advocated by Connor et al. (1997). I fit a generalized linear model that related the counts of individuals to log(patch area) using a Poisson response probability distribution together with a log link function (Proc GENMOD, SAS Institute 1996). The dispersion parameter in the generalized linear model (ϕ_1) provides an estimate of the degree of aggregation that is adjusted for the variation in size of sample units because the number per sample unit is directly modeled as a function of sample unit size (Connor et al. 1997). The estimate of ϕ_1 should be near 1 if the counts are Poisson random. Additional covariates can be included in the generalized linear model, so I constructed a second model that included log(patch area) and patch quality as explanatory variables, because these two variables collectively index the amount of *Opuntia* in a patch, and then estimated the dispersion parameter (ϕ_2). For the three life stages of *C. vittiger* in both landscapes, I estimated ϕ_1 and ϕ_2 and tested whether they differed from 1 with χ^2 tests (Connor et al. 1997).

Patch area and occupancy

I was interested in whether the relationship between patch area and occupancy was consistent among the three life stages. Conversely, a certain life stage might express a stronger threshold response in which the probability of occupancy rises abruptly once a critical patch size is reached. I used logistic regression models (Proc LOGISTIC, SAS Institute 1996) to examine the effects of patch area on the probability of patch occupancy by *C. vittiger*. These models used a binomial response probability distribution together with a logit link function. For each life stage and landscape, I present incidence functions based on predicted probabilities of occupancy. I also used logistic regression models to examine whether patch area affected the probability that patches occupied by nymphs in early August remained occupied by adults in mid September. These patch 'transition-incidence' functions have been used for metapopulation studies in which the disappearance of individuals from a patch represents a local extinction (Sjögren-Gulve and Ray 1996). For all logistic regression models, I calculated R^2 as 1 – (deviance of model of interest / deviance of intercept-only model).

Patch area and abundance: constraint lines

I used quantile regression (Terrell et al. 1996, Scharf et al. 1998, Cade et al. 1999) to estimate the upper bound for the relationship between patch area and abundance. Regression quantiles are an application of the univariate concept of quantiles to linear models (Cade et al. 1999). Quantile regression is based on least absolute deviation

(LAD) regression, which models the conditional median (50^{th} quantile) so that ca. 50% of the observations are above (and below) the estimated regression line. This approach can be extended to any quantile (Cade et al. 1999). I modeled the upper constraint line as the 95^{th} regression quantile (i.e., ca. 95% of the observations are below the fitted line). LAD regression models are fit by minimizing the sum of the absolute values of the residuals instead of the sum of the squares of the residuals, as in typical least squares regression (Scharf et al. 1998, Cade et al. 1999). Likewise, quantile regression models minimize the sum of weighted absolute deviations, where the weights equal the quantile (e.g., 0.95) for positive residuals and 1 minus the quantile for zero and negative residuals. Estimates of regression quantiles are insensitive to extreme values of the dependent variable (outliers) because the fit is unaffected by changes in magnitude of the values as long as the values remain above or below the estimated regression quantile (i.e., the signs of the residuals are maintained). Moreover, regression quantiles are equivariant to nonlinear monotonic transformations, such as logarithmic transformations (Cade et al. 1999). I evaluated the relationship between patch area and *C. vittiger* abundance with $\log_{10}$-transformed data.

Triangular-shaped scattergrams, in which both the central tendency and the variation of the dependent variable increase as a function of the independent variable, provide strong evidence for a limiting-factor relationship. Additional support is provided by a direct comparison of the 95^{th} and the 50^{th} regression quantile slopes (Terrell et al. 1996). A greater rate of change near the extreme of the distribution ($95^{th} > 50^{th}$) indicates an upper-limit relationship between the two variables. Therefore, I present parameter estimates for models relating *C. vittiger* abundance to patch area for both the 95^{th} and 50^{th} regression quantiles.

I tested for non-zero slopes using a quantile rank-score test statistic that is appropriate for heterogeneous error distributions (Cade et al. 1999). The *P*-values were calculated using a permutation approximation based on 10,000 permutations. I constructed 95% confidence intervals for parameter estimates by inverting the hypothesis-testing process in an iterative fashion, which provides confidence intervals that may be asymmetric. Estimates of quantile parameters near the extremes of distributions are inherently less precise than estimates of central tendency (Cade et al. 1999). For quantile regression models, I followed Koenker and Machado (1999) and calculated a coefficient of determination (R) as 1 – (sum of the weighted absolute deviations of the model of interest / sum of the weighted absolute deviations of the intercept-only model). To convert R to units of measure comparable to R^2 based on squared units of measure, I report R^2 for quantile regressions as $1 - (1 - R)^2$ (McKean and Sievers 1987). All quantile regression analyses were conducted with BLOSSOM Statistical Software (Cade and Richards 1999).

Density-area hypotheses

One approach to testing the relationship between density and patch area (Connor et al. 1997) is to regress log(number of individuals) against log(patch area). Under the sampling colonization hypothesis, the slope of such a regression should equal 1. A slope >1 would indicate that density increases with increasing patch size, which would be consistent with the resource concentration hypothesis (Root 1973), whereas a slope <1 would be consistent with the undermatching hypothesis. Ordinary least squares regression assumes homogeneous error distributions and thus it is usually not appropriate

for analyzing count data in which the variance typically increases with the mean (Connor et al. 1997). In contrast, quantile regression can accommodate heteroscedastic errors (Cade et al. 1999). Therefore, I tested predictions from the density-area hypotheses by examining the slope coefficients from the quantile regression models of the abundance of *C. vittiger* versus patch area.

Multiple regression models: selection and inferences

To evaluate the importance of patch-level traits and landscape connectivity to occupancy and abundance of *C. vittiger* among *Opuntia* patches, I used an approach to model selection based on information theory (Burnham and Anderson 1998). The key initial step in this procedure is to develop a set of *a priori* candidate models that are biologically reasonable. One then uses Akaike Information Criterion (AIC), which is based on the Kullback-Leibler distance between models, to select the 'best' model from the candidate set and to rank the remaining models. This AIC-based approach to model selection considers both model fit and the number of model parameters (Burnham and Anderson 1998).

I developed a set of 20 candidate models (Table 2.1). All models contained patch area as an explanatory variable because any model excluding it seemed to be biologically unjustified. First, I constructed a subset of models that included only patch-level variables (Models 1 – 4). Next, I added either neutral landscape connectivity (Models 5 – 8) or matrix-matters connectivity (Models 9 – 12) to these base models. Finally, I added an interaction term (patch area*connectivity) to the neutral-matrix models (Models 13 –

16) and to the matrix-matters models (Models 17 – 20). An interaction between patch area and connectivity might happen if larger patches were less influenced by patch isolation than were smaller patches. Alternately, if there is a critical patch size, then small patches might be unoccupied even if they are highly connected. Although an interaction between patch area and connectivity could be an essential characteristic of patchy landscapes, it is rarely evaluated explicitly in explanatory landscape models (but see Quintana-Ascencio and Menges 1996, Kehler and Bondrup-Nielsen 1999).

For models of patch occupancy, I used logistic multiple regression (Proc GENMOD, SAS Institute 1996) and calculated AIC for each model as

$$AIC = -2(\text{log-likelihood}) + 2K$$

where the log-likelihood for the models is computed at the maximum likelihood parameter estimates under that model, and K = number of estimable parameters (Burnham and Anderson 1998). The value of K equals the number of explanatory variables plus 2 (for the intercept and the residual variance). I was able to use this form of AIC (instead of AIC_c) because the ratio of sample size to K was large (>40) for my models (Burnham and Anderson 1998). Likewise, I did not use QAIC because my data for these logistic models were not overdispersed based on the variance inflation factor (Burnham and Anderson 1998) for my global models (Models 16 and 20).

For models of abundance, I used 95th quantile multiple regression models and calculated an AIC for each model as

$$AIC = n(\log \hat{\sigma}^2) + 2K$$

where $\hat{\sigma}$ is the sum of weighted absolute deviations (Hurvich and Tsai 1990). Note that this form of AIC also includes one term for model fit and a second term that is a penalty for the number of parameters in the model.

The model with the lowest AIC value is considered the best model. Because AIC is on a relative scale, it is useful to report results as AIC differences defined as

$$\Delta_i = AIC_i - \text{minimum AIC}$$

across all candidate models (Burnham and Anderson 1998). The best model has $\Delta_i = 0$. Often one model does not stand out as a clearly superior model, however, and several competing models may approximate the data equally well. As a rule of thumb, models for which $\Delta_i \leq 2$ have substantial support and should receive consideration when making inferences (Burnham and Anderson 1998).

It is also helpful to calculate a set of 'Akaike weights', w_i, defined as

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_r)}.$$

Each w_i provides the weight of evidence that model i is the best model. Akaike weights are normalized relative likelihoods that sum to 1 (Burnham and Anderson 1998). I also defined a 90% confidence set for the best model by summing the Akaike weights (largest to smallest) until the total was just ≥ 0.90. I present results only for those models within the 90% confidence set. Finally, to compare the importance of individual variables, one can sum the Akaike weights for the variables across all models in which they occur (Burnham and Anderson 1998). This approach is especially useful in situations in which one model does not obviously stand out as the best model. I compared the importance of patch quality versus patch shape by summing their Akaike weights. Each of these patch-

level traits occurred in 10 candidate models in a balanced fashion. I also evaluated the relative support for the five categories of models (Table 2.1) by summing their Akaike weights. Each model category had four models and the base, patch-level variables were common to all categories.

Results

Landscape patterns

Both plots represented highly fragmented landscapes in which the suitable habitat of *Opuntia* occurred in discrete patches that covered <5% of the landscape (Fig. 2.1, Table 2.2). The density of patches was somewhat higher on the low-matrix landscape than on the high-matrix landscape. Patch area was variable on both plots, with the range covering several orders of magnitude (Table 2.2). Frequency distributions of patch area were strongly skewed with long right tails.

The dispersion pattern of all *Opuntia* patches was aggregated at most scales examined (Fig. 2.2). The exceptions were that patches were regularly spaced at the finest scale (1^{st} NND) on the low-matrix landscape, and patches tended toward random at intermediate scales (3^{rd}-5^{th} NND) on the high-matrix landscape. For the analysis constrained to only large patches, the dispersion patterns differed between the two landscapes (Fig. 2.2). On the low-matrix landscape, large patches were regularly spaced at the finest scale (1^{st} NND), aggregated at intermediate scales (2^{nd}-5^{th} NND), and random at the largest scales

(6^{th}-10^{th} NND). On the high-matrix landscape, large patches were randomly distributed at all scales.

The density and multi-scale dispersion of *Opuntia* patches determines the mean distances between patches of suitable habitat for *C. vittiger*. If one considers patches of all sizes and only the nearest neighbor, then the mean distance between patches is ≤1.6 m on both plots (see mean NND given on *X*-axes in Fig. 2.2). If one considers only large patches that have a reasonable chance of being occupied, however, and assumes that an individual may not always move to the closest patch so that distances to all patches in local neighborhood (e.g., 1^{st}-7^{th} NND) are important, then the relevant inter-patch distances are ≤12.9 m (Fig. 2.2).

Under the neutral-matrix model, the median of patch connectivity was 1.5 times higher on the low-matrix landscape than on the high-matrix landscape (Table 2.2) due to the difference in patch density between the two plots. The kriged maps of matrix structure (Fig. 2.3) clearly reflected the differences between the plots; the high-matrix landscape had more heterogeneous vegetation structure that was higher overall. The patch connectivity of both landscapes was reduced when using the matrix-matters measure instead of the neutral-matrix measure (Table 2.2), but more so for the high-matrix landscape. Hence, the median of patch connectivity was 3.0 times higher on the low-matrix landscape than on the high-matrix landscape under the matrix-matters model. That is, the disparity between the two landscapes in overall structural connectivity was doubled if the nature of the matrix was considered.

Inter-patch movements

Based on the simulated movements, the probability of detecting an actual movement decreased steeply and linearly from 12 to 40 m and then leveled off somewhat until 52 m (Fig. 2.4). The distributions of corrected movement distances (Fig. 2.5) indicated that most inter-patch movement by adult *C. vittiger* occurs during the mating season. This inference is valid even with the slight differences in resighting intervals between the two seasons (Fig. 2.5), given that the median net displacement during the non-mating season was zero on both plots (most individuals were resighted in the same *Opuntia* patch where they were marked 6-11 days earlier). During the mating season, there were no differences in the distributions of movements between the sexes on the low-matrix landscape (Smirnov Test, $T = 0.215$, $P > 0.20$) or on the high-matrix landscape ($T = 0.243$, $P > 0.20$). However, individuals moved over twice as far on the low-matrix landscape than on the high-matrix landscape ($T = 0.41$, $P < 0.01$) during the mating season.

Movement experiment: matrix and edge effects

All 14 pathways included segments in both the low- and high-matrix areas (Fig. 2.6a). Individual paths included a total of 12-48 steps ($\bar{x} = 25$) with a total path length of 258-848 cm ($\bar{x} = 520$). The score for vegetation height along the paths ranged from 0.9-1.4 ($\bar{x} = 1.22$) for the low-matrix areas and from 2.4-4.9 ($\bar{x} = 3.67$) for the high-matrix areas.

Thus, the height of vegetation was generally 0-5 cm in the low-matrix area, whereas it was typically 11-20 cm in the high-matrix area.

The vegetation structure of the matrix strongly affected the mean step length of moves by *C. vittiger* ($S = 52.5$, $P = 0.0001$, $n = 14$). The mean step length was more than twice as long in the low-matrix area ($\bar{x} = 37.4$ cm, SE = 3.7) compared to the high-matrix area ($\bar{x} = 15.6$ cm, SE = 2.1). Likewise, matrix structure influenced the degree of directionality of the paths ($S = 37.5$, $P = 0.0166$, $n = 14$). Based on the mean vector length, paths were straighter in the low-matrix area ($\bar{x} = 0.93$ cm, SE = 0.02) compared to the high-matrix area ($\bar{x} = 0.85$ cm, SE = 0.03). The combined effects of matrix structure on these two components of movement behavior (step length and path tortuosity) produced a net displacement rate for the high-matrix habitat that was only 33% of that for the low-matrix habitat (Fig. 2.6b).

The edge between the two matrix elements was completely permeable; all individuals encountered the edge and continued to move into the high-matrix element. Likewise, none of the individuals returned to the low-matrix area after crossing into the high-matrix area. This lack of an edge effect on the movements of *C. vittiger* was further supported by my comparison of the angle of the pathways from the release location to the edge with the angle from the edge to last location. The mean difference in these angles was only 14.4° with a 95% CI [-5.6, 34.4] that included zero. The general bearing of the trails was maintained after encountering and crossing a high-contrast edge between matrix elements.

Dispersion of individuals among patches

During the surveys of *C. vittiger* on the low-matrix landscape, I counted a total of 2932 nymphs, 1878 adults, and 462 mating adults. On the high-matrix landscape, I counted 1611 nymphs, 1282 adults, and 341 mating adults. All life stages on both landscapes were aggregated among patches of *Opuntia*, even after accounting for the considerable variation in patch sizes (Table 2.3). The degree of aggregation was greater for nymphs than for the two adult stages.

Patch area and occupancy

On the low-matrix landscape, overall patch occupancy was 60% for nymphs, 47% for adults, and 26% for mating adults. On the high-matrix landscape, occupancy was 68% for nymphs, 48% for adults, and 32% for mating adults. As expected, the probability that a patch was occupied was positively related to patch area. However, the shape of the incidence curves differed among the life stages (Fig. 2.7). The sigmoidal curves for adults rose relatively abruptly after a minimum patch size was reached, whereas the relationships between occupancy and patch area were more gradual for nymphs and mating adults. Accordingly, patch area explained more variation in occupancy for adults ($R^2 = 0.44$ for low-matrix; $R^2 = 0.47$ for high-matrix) than it did for other life stages (all $R^2 \leq 0.23$).

Temporal dynamics in patch area and incidence are evident in the curves for the three life stages of *C. vittiger* (Fig. 2.7). The downward shift in curves from nymphs compared

to adults was primarily across small patches; both of these life stages had a high probability of occupying large patches. The direct comparison with transition-incidence functions supported this pattern. The probability that a patch was occupied by nymphs but unoccupied by adults was negatively related to patch area on the low-matrix landscape (coefficient = -2.98, SE = 0.28, $R^2 = 0.37$, $n = 448$) and the high-matrix landscape (coefficient = -3.36, SE = 0.37, $R^2 = 0.48$, $n = 321$). The downward shift in incidence curves from adults compared to mating adults was mainly across large patches (Fig. 2.7); both adult stages had low incidences on small patches.

Patch area and abundance

The relationship between the abundance of *C. vittiger* and patch area had a triangular shape for all life stages on both landscapes (Fig. 2.8). The 95th regression quantiles seemed to estimate effectively the ceilings of the relationships. The slopes of the estimated regression lines and the amount of explained variance differed among the life stages (Fig.2.8). The strongest relationship was for the adult stage, which mirrors the results from the logistic regressions of patch area and occupancy. The estimated slopes for the 95th regression quantiles were steeper than those for the 50th regression quantiles (Table 2.4), except for the nymphal stage on the high-matrix landscape. Overall, these results provide strong evidence that patch area sets the upper constraint to the abundance of *C. vittiger*.

All point estimates of the slope coefficients for abundance versus patch area were <1 (0.239-0.527) for the 95th regression quantile models, and the 95% CIs for these slopes

did not include 1 (Table 2.4). The density of *C. vittiger* decreased with increasing patch size. The same conclusion is reached for the 50^{th} regression quantiles (Table 2.4), which measure central tendency and may represent better the intended predictions of the area-abundance hypotheses. One caveat is necessary, however, because Connor et al. (1997) suggest that the expected slope under a constant density hypothesis may be <1 when there are many patches with no individuals. Therefore, I reanalyzed the relationship between abundance and patch area for only the subset of patches that were occupied. Again, all estimates of the slope coefficients for abundance versus patch area were substantially <1 (Appendix 2.3).

Multiple regression models: patch traits and connectivity

Evaluation of models and variables.—The AIC-based approach to model selection did not identify one specific model for a particular life stage and landscape that was clearly the best model to use in making inferences regarding patterns of occupancy (Table 2.5) and abundance (Table 2.6). Instead, several models had similar support ($\Delta_i \leq 2$) as the best approximating model, which indicates that the evaluation of the importance of individual variables should be based mainly on across-model inferences. However, the added information contained in the abundance data (versus presence-absence) provided better resolution in the selection of models. There were only 2-3 models of abundance with $\Delta_i \leq 2$ for any life stage-landscape combination, whereas there were 4-5 models of occupancy with $\Delta_i \leq 2$. Moreover, the Akaike weights for the best models ranged from .341-.659 for the abundance models but only .206-.330 for the occupancy models.

The patch quality and patch shape variables frequently were included in the models with strong support ($\Delta_i \leq 2$; Tables 2.5, 2.6), but patch quality was a relatively more important explanatory variable (Fig.2.9). Often the summed Akaike weights for patch quality were near 1.0, especially in the low-matrix landscape, which indicates that there was virtually no support for the models without patch quality. Five of the six best models of occupancy included patch quality (Table 2.5), and all six best models of abundance included it (Table 2.6). Patch shape was a more important variable for explaining abundance than for explaining occupancy (Fig. 2.9). Four of the six best models of abundance included patch shape (Table 2.6), but only one of the best models of occupancy included it (Table 2.5).

The models that included only patch traits (area, quality, shape) and ignored patch connectivity performed relatively well (Fig. 2.10) only for two occupancy models in the low-matrix landscape (adults and mating adults) and one in the high-matrix landscape (mating adults). Some measure of connectivity was required for all other situations. As expected, the neutral-matrix measure of connectivity performed as well or better than the matrix-matters measure for models of occupancy and abundance for the low-matrix landscape (Fig. 2.10). In contrast, the models with the matrix-matters measure of connectivity received large Akaike weights for the high-matrix landscape (Fig. 2.10). For the analysis of abundance, the best models for the three life stages on the low-matrix landscape included the neutral-matrix connectivity variable, whereas the three best models for the high-matrix landscape included the matrix-matters measure of connectivity (Table 2.6). Whether or not an interaction between patch area and connectivity was needed in a model depended on the response variable; the interaction

seemed unnecessary for models of occupancy, but it received relatively strong support in most models of abundance (Fig.2.10).

Interpretation of effects.—To understand the relationships between the explanatory variables and the occupancy and abundance of *C. vittiger*, I examined the signs of the coefficients for the variables in all models with strong support ($\Delta_i \leq 2$). The signs were consistent among these competing models, so I present parameter estimates only for the best models in each life stage-landscape combination (Tables 2.7, 2.8). As expected, both occupancy and abundance were positively related to patch area and to patch quality. In contrast, there was a negative relationship between both response variables and patch shape. However, recall that patch shape was most important in the quantile regression models of abundance (Table 2.8). Hence, after controlling for the coverage of the host plant, patches that were more linear (and had relatively more edge) had a greater maximum number of individuals.

The relationship between connectivity and the distribution and abundance of *C. vittiger* depended on life stage. I will focus on those life stage-landscape combinations where a connectivity measure had strong support (Fig. 2.10). For nymphs on both landscapes, connectivity was negatively related to occupancy (Table 2.7); more isolated patches were more likely to be occupied. For adults on the high-matrix landscape, connectivity was positively related to occupancy (Table 2.7).

There was generally strong support for the inclusion of a patch area*connectivity interaction term for the models of abundance (Fig. 2.10). Hence, the coefficient for connectivity depended on the value of patch area. One can calculate a 'total slope' for connectivity, which includes the interaction effect, as

$b_{conn} + b_{int}X_{area}$

where b_{conn} is the estimated coefficient for connectivity, b_{int} is the estimated coefficient of the interaction between patch area and connectivity, and X_{area} is the value of patch area (Neter and Wasserman, 1974). To interpret the effects of connectivity, I plotted these 'total slopes' using *Cn* for the low-matrix landscape and *Cm* for the high-matrix landscape (Fig. 2.11). Despite the interaction, nymphs on both landscapes once again had a negative coefficient for connectivity across all patch sizes. For adults on the low-matrix landscape, the coefficient was negative for all but the largest patches. In contrast, for adults on the high-matrix landscape there was no area*connectivity interaction and connectivity had a positive coefficient. Finally, the pattern of interaction for mating adults was similar on both landscapes; the coefficient was negative for patches $\leq 10^2$ cm^2 but increasingly positive for larger patches. That is, more connected patches had higher abundances and this effect increased with patch size.

Discussion

Spatial population structure

The estimates of movement distances of adults during the mating season, combined with inter-patch distances on the two landscapes, indicate that the spatial population structure of *C. vittiger* represents more of a patchy population than a system with classical metapopulation structure (Harrison and Taylor 1997). Processes such as inter-patch movements and habitat selection by ovipositing females, rather than extinction-

colonization events among subpopulations (Haila et al. 1993, Hanski 1994*a*), influenced the distribution of individuals within a population. There was relatively high connectivity at the landscape scale, despite there being only 3-4% cover of suitable habitat, because *Opuntia* patches occurred in a high density with few large gaps of unsuitable habitat between them. The details of habitat patchiness must be considered when defining structural connectivity, not just the percent of suitable habitat in a landscape (e.g., Andrén 1994).

Although *C. vittiger* functioned like a patchy population at the spatial scale of this study, most individuals were not 'diffusing' great distances across the landscape. Nymphs and non-mating adults were relatively sedentary for ca. 9 months of the year, and median displacement rates for mating adults were only 1-2.5 m/day. Spatial dynamics more akin to a classical metapopulation might occur at broader spatial scales given that gaps in *Opuntia* cover can be >120 m due to topography (see Chapter 4). Habitat patchiness and resultant population structure may be hierarchical across spatial scales (Kotliar and Wiens 1990, Amarasekare 1994).

Landscape structure and movements

Understanding how the composition and spatial organization of landscapes affects animal movements is one of the central concerns in spatial ecology (Crist et al. 1992, Wiens et al. 1993*a*, 1997, Ims and Yoccoz 1997, Turchin 1998). Both of my landscapes were highly fragmented and had similar coverage of suitable habitat. Nevertheless, the mark-resight study indicated that net displacement by *C. vittiger* on the high-matrix

landscape was only 40% of that on the low-matrix landscape. This difference in movement distances might partly reflect dissimilarities in the patch density and inter-patch distances between the two landscapes. I contend that this disparity in the distribution of suitable habitat is unlikely to have produced the pronounced difference in movements by itself. The difference between landscapes in mean nearest neighbor distances of *Opuntia* patches was not great (Fig. 2.2). Instead, the structure of the matrix probably had a strong influence on the displacement rates of *C. vittiger*. This conclusion is supported by the experimental evaluation of matrix structure on movement pathways (Fig. 2.6); the high-matrix element was ca. three times more resistant to movement than was the low-matrix element. Combining a mechanistic approach involving detailed movement pathways with mark-resight studies on general movement distances (Ims and Yoccoz 1997) provided insights into how landscape structure affected movements of cactus bugs. Individuals living in the high-matrix landscape had smaller ecological neighborhoods (Addicott et al. 1987) during the mating season, when dispersal occurred, even though the template of suitable habitat was fairly similar between the two landscapes.

These results for *C. vittiger* add to the growing empirical evidence, much of which comes from studies of relatively vagile, flying insect species (e.g., Pither and Taylor 1998, Roland et al. 2000, Jonsen et al. 2001, Ricketts 2001), that matrix structure can affect movements and inter-patch transfers. Such evidence suggests that simulation models of habitat fragmentation that ignore potential matrix effects and incorporate a single, species-specific parameter for dispersal are unlikely to capture all relevant scenarios in their predictions. For instance, what single displacement parameter would

one use in a model for *C. vittiger*? The distribution of movement distances for animal species in patchy environments will depend on the motivation and behavior of individuals, the amount and distribution of suitable habitat patches, *and* the nature of the intervening matrix.

There were no edge effects on movements of individuals between two matrix elements that formed a sharp, high-contrast edge, so edge permeability (Wiens et al. 1985, Stamps et al. 1987) probably was equally high for more subtle boundaries within the matrix. Although not investigated here, edge effects between patches of suitable habitat and the matrix (Haddad 1999, Ries and Debinski 2001) could have influenced patch emigration probabilities and the observed net displacement rates. Individuals may have been less likely to leave patches surrounded by high vegetation, given the greater resistance to movement that they would encounter in these situations. Finally, higher matrix structure also makes it more difficult for cactus bugs to find patches of suitable habitat (Chapter 3) and thus increases their time in the matrix and any associated costs. For instance, the matrix had no food resources, no observed matings, and less vegetation structure capable of providing cool microclimates during midday (when individuals within patches often are in the shade created by *Opuntia* pads). Unfortunately, there are no data on predation risk for *C. vittiger* in patches or in the matrix. Spiders have been reported as predators of both nymphs and adults of *C. vittiger* elsewhere (Hamlin 1924, De Vol and Goeden 1973), and the few predation events that I observed involved spiders and adult cactus bugs.

Dispersion of individuals among patches

The aggregation of individuals within populations has significant consequences for intraspecific behavioral interactions, predator-prey and herbivore-plant relations, and the stability of single-species and multi-species dynamics (Hanski 1994*a*). For example, independent aggregation of competing species among patches may facilitate coexistence because interspecific interactions are reduced relative to intraspecific interactions (Atkinson and Shorrocks 1981, Ives 1991, Hanski 1994*a*, Sevenster 1996). Many earlier tests of aggregation of insect species have inflated the degree of aggregation, however, because they did not explicitly recognize variation in patch sizes (Connors et al. 1997, see also Sevenster 1996).

C. vittiger was aggregated among patches of *Opuntia* at all life stages examined. This pattern held true when I analyzed the data at nested, finer spatial scales (unpublished data). The dispersion pattern for each life stage represented a different set of processes. For nymphs, the distribution reflected behavior of ovipositing females (movements, patch choice, clutch size) and mortality from the egg stage to the 3^{rd}-4^{th} nymphal stages. For non-mating adults, the spatial distribution mainly echoed the aggregated patterns for nymphs and any changes resulting from mortality from the nymphal stages to the adult stage. For mating adults, the pattern of dispersion was a snapshot taken during a period when most movement among patches occurred. I suspect that obtaining mating opportunities, rather than food resources, was the prime motivation behind movement because mating was a main activity at this time (ca. 45% of individuals were copulating during the surveys). Importantly, the distribution of mating adults does not necessarily

reflect that of ovipositing females who might select distinct patches for egg laying. Few of the females were actually ovipositing during the surveys as it takes only ca. 15 min to deposit a clutch, whereas copulation bouts typically last >5 h and as long as 17 h (De Vol and Goeden 1973, personal observation). It would also be extremely difficult to obtain accurate counts of the distribution of eggs in the field given their small size (length of 1.35 mm, De Vol and Goeden 1973) and concealed placement underneath cactus spines and grass blades.

Optimal foraging models typically do not predict aggregated spatial distributions of individuals relative to distributions of resources (Hanski 1994*a*). Aggregated distributions may reflect limited knowledge regarding resources (Hanski 1994*a*, Ranta and et al. 1999) that restricts individuals from distributing themselves more evenly and 'optimally'. Both ovipositing females and mating adults of *C. vittiger* may have limited knowledge of resources (food and mates) in the patchy landscapes that they inhabit. Alternately, aggregated distributions of individuals among patches may result from movement behavior and conspecific attraction driven by the reduced risk of predation to individuals in clumps (e.g., Turchin and Kareiva 1989).

Patch area and occupancy

Overlaying the incidence curves for the three life stages (Fig.2.7) provided an informative visual representation of the area-dependent filtering that occurs over time. The shift in incidence curves from nymphs to adults partly reflects the patch area-abundance relationships for nymphs (Fig.2.8). Small patches contain fewer nymphs than

do large patches, and thus it is less likely that at least one individual is still alive on these small patches by the adult stage. Patches $<10^2$ cm^2 may represent a sort of sink habitat in that there is virtually no chance of either adult stage occurring on these small patches. The strongest patch area-occupancy relationship was for non-mating adults. In this stage, the smallest patches had a near-zero probability of occupancy, the largest patches were almost always occupied, and there was an intermediate zone where the probability of occupancy increased sharply with patch area. It is in this intermediate zone of patch sizes where factors other than patch area contribute most to incidence. For mating adults, the relatively low plot-level densities, together with their aggregated distribution, resulted in even the largest patches having some chance of being unoccupied.

The minimum patch size where the probability of occupancy is ≥ 0.50 has been considered a useful metric for fragmented systems (e.g., Helzer and Jelinski 1999). Because of differences in overall occupancy rates and shapes of the area-incidence functions, the patch size corresponding to 50% incidence differed by more than one order of magnitude between nymphs and mating adults (Fig. 2.7). Clearly, notions regarding critical patch sizes may depend greatly on which life stage of an animal is surveyed.

Patch area and abundance

Ecological factors often impose upper constraints on response variables. Such limiting-factor relationships may occur in many areas of ecology, including macroecology, physiological ecology, competitive interactions, predator-prey dynamics, and animal-habitat relations (Blackburn et al. 1992, Brown 1995, Thompson et al. 1996,

Scharf et al. 1998, Cade et al. 1999). The limiting-factor approach is a novel way to view patch area-abundance relationships and it provides a fundamentally different way of framing hypotheses. It is uncertain whether the triangular distributions that occur for *C. vittiger* are typical for most systems with subdivided habitat, however, or if they mainly emerge from patchy populations of specialist insects. Triangular distributions are evident for leaf area and the abundance of leaf-mining moths (Connor et al. 1997) and for basidiocarp size and the abundance of fungivorous beetles (Midtgaard et al. 1998). I expect that many patch area-abundance associations may represent limiting factor situations because it seems logical that area (space) would set an upper limit to the number of individuals, but that other factors (measured and unmeasured) could reduce numbers below this upper bound.

A characteristic of classical metapopulations (i.e., not mainland-island ones) is that all subpopulations have some chance of going extinct and of being recolonized (Hanski 1998). These key processes of metapopulations could contribute to triangular area-abundance patterns, in that population size will follow a trajectory during population recovery from zero toward the upper ceiling set by patch area. Hence, part of the space filling below the upper constraint would reflect the temporal dynamics of subpopulations that typify metapopulations. Patch area is a key variable in metapopulation models because it is assumed that larger patches have more individuals, which in turn affects extinction and colonization probabilities (Hanski 1994*b*). Larger patches also would be expected to have greater variance in the number of individuals. This variance structure is not generally included in metapopulation models.

In the area-abundance models for *C. vittiger*, the coefficient for patch area was <1 for all life stages on both landscapes. This result held true for the 95th quantile, the 50th quantile, and the 95th quantile when the analyses were restricted to occupied patches. Moreover, the coefficient for patch area was <1 in the multiple regression models that included other path-level traits and connectivity (Table 2.8), even after the area coefficient was adjusted for the area-connectivity interaction (unpublished data). Therefore, population density was negatively correlated with patch size. This outcome provides no support for the resource concentration hypothesis (Root 1973) or for the sampling colonization hypothesis (Haila et al. 1993). Instead, the negative relationship agrees with predictions from the undermatching hypothesis (Kennedy and Gray 1993, Ranta et al. 1999) and it suggests that imperfect knowledge of resources may be one determinant of the pattern of abundance of *C. vittiger* among patches. Intriguingly, Ranta et al.'s (1999) cellular automata model that incorporated limited knowledge not only predicts undermatching, but also produces a triangular, upper-constraint relationship between the number of individuals and resource levels in patches (see their Fig. 2*b*).

There are other, non-exclusive possibilities for the negative relationship between density and patch area. Certain attributes of patch quality, such as succulence or chemical composition of *Opuntia*, could covary with patch area and thus influence habitat selection. Higher predation rates in larger patches compared to smaller ones could also contribute to the observed relationship. Finally, smaller patches have relatively more edge than do larger patches, and edge effects might influence density-area associations (Bowers and Matter 1997). This last explanation is consistent with my

results that the abundance of *C. vittiger* is negatively correlated with patch shape (Table 2.8) and thus positively correlated with the amount of edge.

Multiple regression models: patch traits and connectivity

For classical metapopulations, Hanski and colleagues (Hanski 1994*b*, 1998, Moilanen and Hanski 1998) have championed the fundamental area-isolation model, which is equivalent to my Model 5 that included only patch area and neutral-matrix connectivity. Model 5 performed poorly in my patchy population system. It was included in only one of the 90% confidence sets of models, for occupancy of mating adults on the low-matrix landscape (Table 2.5), where it received little support as the best model ($w_i = 0.076$). One reason for this weak performance is that there was strong support for the inclusion of patch quality into models for most life stage-landscape combinations. While it is not surprising that the cover of the host plant within patches would be important to a specialist such as *C. vittiger*, Moilanen and Hanski (1998) concluded that adding variables describing the cover of larval host plants did not improve the performance of a basic incidence function model for the Glanville fritillary butterfly (*Melitaea cinxia*). Spatial variation in habitat quality of patches may be more important in patchy populations, where habitat selection by individuals should be an important process, than in less-connected metapopulations. However, the degree of variation in patch quality within the system may be the most important factor; habitat patches of the Glanville fritillary butterfly were "rather uniform in quality" (Moilanen and Hanski 1998).

Patch shape can affect animal abundances by influencing the flux of individuals between patches and the surrounding landscape mosaic (Wiens et al. 1985, 1993a, Stamps et al. 1987). Relatively linear patches contain more edge and may have higher transfer rates because animals will encounter patch boundaries more often. The net effect on abundance will depend on the relative role of patch shape on emigration and immigration. For *C. vittiger*, the patch shape variable received solid support for most of the models of abundance. Consistently, linear patches with more edge (after controlling for patch area) had a greater maximum number of individuals (see also Hamazaki 1996). Therefore, patch shape and the degree of edge may be stronger determinants of immigration than of emigration in cactus bugs. All else being equal, this sort of outcome should be likely for many habitat specialists because of fundamental differences in the processes of emigration and immigration. When an individual within a host plant patch encounters a boundary with the matrix, it *chooses* whether it wants to leave a patch or not. An increase in perimeter:area ratio simply increases how often an individual makes a choice, but not necessarily the probability of emigration. If an animal decides to stay in a patch, it can, no matter how often it bumps into a boundary. This view contrasts sharply with one put forth by Kareiva (1985) that suggests that flea beetles (*Phyllotreta* spp.) wander away from patches and 'lose' their host plants. This sort of maladaptive behavior seems unlikely for most habitat specialists that should recognize boundaries between patches and the matrix and that could incorporate simple movement rules to avoid leaving patches unintentionally (i.e., turn around after x number of steps without encountering the host plant). Moreover, Kareiva concluded that the documented increase in emigration by beetles from smaller patches was because such patches had a higher

perimeter:area ratio than did larger patches and thus were easier to lose. However, patch size and the relative degree of edge were confounded in the experiments so that beetles may have chosen to leave smaller patches simply because they were below a critical size in terms of resources. Additional experimental studies are needed in which patch shape is varied while patch area is held constant (e.g., Hamazaki 1996, Grez and Prado 2000) to determine which view of patch shape and emigration is closest to reality.

The overall results from the AIC-based approach to model evaluation provided insights regarding several key questions in spatial ecology. What are the relative roles of patch traits and the surrounding habitat in determining the distribution and abundance of animals (Mazerolle and Villard 1999)? For *C. vittiger*, the models with solely patch traits performed reasonably well only for a few models of occupancy. Some metric of connectivity seemed necessary for all the models of abundance. Therefore, we might have concluded that landscape effects were relatively minor if we had collected only presence-absence data. Do the effects of patch area and connectivity interact to influence the distribution of individuals in fragmented habitat? An area-connectivity interaction was evident from most models of abundance for *C. vittiger*, but not for the occupancy models. An interaction between patch area and connectivity provides another solid reason for not treating terrestrial habitat patches as isolated islands (Wiens 1995). Does the matrix matter when measuring patch connectivity? The answer depends on the characteristics of the landscape. The neutral-matrix model of connectivity performed at least as well as the matrix-matters model on the landscape with a relatively homogeneous matrix. Likewise, Moilanen and Hanski (1998) concluded that a measurement of isolation that ignored matrix texture was adequate for modeling the incidence of the

Glanville fritillary butterfly in a study area that was "fairly homogeneous". In contrast, there was strong support for the matrix-matters model for *C. vittiger* on the landscape with the heterogeneous matrix. The structure of the matrix influences the occupancy and abundance patterns of various other species in environments where the matrix was described as relatively heterogeneous (e.g., Lawrence and Bach 1989, Åberg et al. 1995, Petit and Burel 1998, Hokit et al. 1999, Joly et al. 2001, Vandermeer et al. 2001). Hence, if 'heterogeneity' can be assessed from an organism-based perspective, then a bit of common sense may go a long ways toward determining when one needs to consider potential matrix effects.

The consistent negative relationship between connectivity and the incidence and abundance of *C. vittiger* nymphs was somewhat surprising. Ovipositing females of some other specialist insects, however, lay more eggs on plants that are more isolated or occur in lower densities (Jones 1977, Courtney and Courtney 1982, Mackay and Singer 1982, Root and Kareiva 1984). Such patterns can result from several processes involving the movement behavior and patch selection of ovipositing females. For instance, when a female spends a relatively long time moving in the matrix before finding a host patch, she may lower her selectivity or lay more eggs because the probability of locating alternate patches may be low (Courtney and Courtney 1982). Egg distribution might also reflect active selection of more isolated patches if these were of higher nutritional quality or had reduced predation risk (Courtney and Courtney 1982). Sorting out these possibilities, and many others, will require detailed data on movement behavior and habitat selection of ovipositing females. Regardless of the exact mechanisms for nymph patterns, the results imply that isolation-dependent movement was not the sole process, and that my measure

of patch connectivity probably also reflected patch context. Again, these two aspects of landscapes may often interact when the spatial population structure represents a patchy population.

Connectivity had different influences on non-mating adults in the two areas. In the low-matrix landscape, the pattern for adults mirrored that for nymphs so that abundance was negatively related to connectivity, except for the largest patches. In the high-matrix landscape, both occupancy and abundance were positively related to connectivity. This shift in 'connectivity effects' between the nymph and adult life stages may represent reduced survival of nymphs in the patches that were more isolated or those surrounded by higher vegetation (a context effect).

The role of connectivity was most consistent with typical isolation effects on movements for mating adults. This outcome is sensible given that mating adults make most of the inter-patch movements. For all but the smallest patches, which were often unoccupied, connectivity was positively related to abundances. That is, more connected patches were more likely to be near the ceiling on abundances set by patch area.

Conclusions

Metapopulation ecology and landscape ecology have seemed to follow somewhat independent trajectories (Wiens 1997, Moilanen and Hanski 2001, Tischendorf and Fahrig 2001). Their courses should be more parallel because individual movement is the key unifying element in both branches (Wiens 1997). In fact, recent studies of broad-scale systems have started to incorporate landscape complexity by examining the effects of matrix structure on movements and distribution patterns. The continued success of

such approaches may signal a merging of metapopulation and landscape ecology. The degree of heterogeneity of the matrix will determine when a mosaic view is warranted, and not whether a system behaves more like a classical metapopulation or a patchy population. Defining the type of spatial population structure (Harrison and Taylor 1997) remains a crucial step, however, because it determines the set of potential processes that might underlie the spatial distribution of animals among patches of suitable habitat. It will only slow progress in spatial ecology if processes characteristic of classical metapopulations are vaguely implied to patchy populations simply because 'metapopulations' currently are in vogue. It is perfectly reasonable to ask questions about patch context and connectivity for patchy populations, but the resulting inferences are about the distribution of individuals within populations, not extinction-colonization dynamics.

My study of *C. vittiger* also demonstrates that patch area can act as an upper constraint to the number of individuals per patch, that different life stages may respond to landscape structure and connectivity in distinct ways, and that information on animal abundances (versus incidence) is more likely to reveal interesting landscape effects such as interactions between patch area and connectivity. These insights have important implications for all patchy systems.

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Table 2.1. Description of *a priori* candidate models used with AIC selection procedures to analyze the influence of patch traits and landscape variables on the distribution and abundance of *C. vittiger*. The main effects were patch area (Area), patch quality (Quality), patch shape (Shape), neutral-matrix connectivity (Cn), and matrix-matters connectivity (Cm).

Model no.	*Model category* Explanatory variables
	Patch traits only
1	Area
2	Area, Quality
3	Area, Shape
4	Area, Quality, Shape
	Patch traits + neutral-matrix connectivity
5	Area, Cn
6	Area, Quality, Cn
7	Area, Shape, Cn
8	Area, Quality, Shape, Cn
	Patch traits + matrix-matters connectivity
9	Area, Cm
10	Area, Quality, Cm
11	Area, Shape, Cm
12	Area, Quality, Shape, Cm
	*Patch traits + neutral-matrix connectivity + area*connectivity interaction*
13	Area, Cn, Area*Cn
14	Area, Quality, Cn, Area*Cn
15	Area, Shape, Cn, Area*Cn
16	Area, Quality, Shape, Cn, Area*Cn
	*Patch traits + matrix-matters connectivity + area*connectivity interaction*
17	Area, Cm, Area*Cm
18	Area, Quality, Cm, Area*Cm
19	Area, Shape, Cm, Area*Cm
20	Area, Quality, Shape, Cm, Area*Cm

Table 2.2. Descriptive statistics for the cover of suitable habitat and landscape connectivity for two naturally patchy landscapes. The 25th and 75th quantiles of the distributions are given in addition to the medians. The sample size (n) is the number of patches used to compute connectivity.

			Patch area (cm^2)		Neutral-matrix connectivity			Matrix-matters connectivity	
Landscape	No. patches	*Opuntia* cover (%)	Median	25-75%	n	Median	25-75%	Median	25-75%
Low matrix	746	4.1	1021	171-3292	532	6.01	3.79-9.07	3.88	2.52-6.19
High matrix	470	3.1	1048	164-4266	313	3.97	2.07-7.17	1.27	0.64-2.38

Table 2.3. Analysis of dispersion patterns of *C. vittiger* among *Opuntia* patches. The dispersion parameters (ϕ_1, ϕ_2) were estimated from generalized linear models with Poisson distributions and log link functions. Models for ϕ_1 include only patch area as an explanatory variable, whereas models for ϕ_2 include path area and patch quality. The dispersion parameters should be ca. 1 if the counts are Poisson random; estimates >1 indicate aggregation. All life stages in both landscapes are aggregated (χ^2 tests, all $P < 0.0001$). The sample size (n) is the number of patches.

Landscape	Life stage	No. of *C. vittiger* per patch				Estimates of dispersion	
		n	Mean	Variance	Var./mean	ϕ_1	ϕ_2
Low matrix	Nymph	740	3.96	43.16	10.89	4.84	4.51
	Adult	744	2.52	24.58	9.74	2.41	2.01
	Mating adult	743	0.62	1.79	2.88	2.07	1.96
High matrix	Nymph	455	3.54	24.12	6.81	3.01	3.00
	Adult	470	2.73	21.92	8.03	2.06	1.85
	Mating adult	470	0.72	2.02	2.78	1.92	1.92

Table 2.4. Estimates of the intercepts (b_0), slopes (b_1), and 95% confidence intervals for β_1 for quantile regression models relating the abundance of *C. vittiger* to patch area ($\log_{10}$-$\log_{10}$ scale). Parameters are reported for the 95th and the 50th regression quantiles. *P*-values are for the null hypothesis that $\beta_1 = 0$ based on rank-score tests. The sample size (n) is the number of patches.

Landscape	Life stage	Quantile	n	b_0	b_1	95% CI for β_1	P
Low matrix	Nymph	95th	740	-0.304	0.444	0.381-0.501	0.001
		50th		-0.755	0.408	0.385-0.440	0.001
	Adult	95th	744	-0.788	0.527	0.496-0.552	0.001
		50th		-0.737	0.359	0.327-0.388	0.001
	Mating adult	95th	743	-0.178	0.239	0.197-0.294	0.001
		50th		0.000	0.000		
High matrix	Nymph	95th	455	-0.194	0.383	0.294-0.425	0.001
		50th		-0.682	0.386	0.352-0.416	0.001
	Adult	95th	470	-0.711	0.490	0.446-0.517	0.001
		50th		-0.752	0.373	0.340-0.405	0.001
	Mating adult	95th	470	-0.229	0.258	0.213-0.327	0.001
		50th		0.000	0.000		

Table 2.5. Summary of AIC selection of logistic regression models for the occupancy of *C. vittiger* among *Opuntia* patches. For each landscape and life stage combination, the listed models are a 90% confidence set on the best model. Each model summary includes the number of estimable parameters (K), $\Delta_i = AIC_i$ – minimum AIC, and Akaike weights (w_i).

				AIC		
Landscape	Life stage	Model†	K	Δ_i	w_i	R^2
Low matrix	Nymphs	6) A,Q,Cn	5	0.000	0.230	0.251
		8) A,Q,S,Cn	6	0.808	0.153	
		2) A,Q	4	1.073	0.134	
		10) A,Q,Cm	5	1.479	0.110	
		14) A,Q,Cn,A*Cn	6	1.997	0.085	
		4) A,Q,S	5	2.170	0.078	
		12) A,Q,S,Cm	6	2.417	0.069	
		16) A,Q,S,Cn,A*Cn	7	2.806	0.056	
	Adults	2) A,Q	4	0.000	0.304	0.490
		10) A,Q,Cm	5	1.390	0.151	
		6) A,Q,Cn	5	1.578	0.138	
		4) A,Q,S	5	1.759	0.126	
		12) A,Q,S,Cm	6	3.101	0.064	
		8) A,Q,S,Cn	6	3.284	0.059	
		18) A,Q,Cm,A*Cm	6	3.316	0.058	
	Mating Adults	4) A,Q,S	5	0.000	0.267	0.188
		8) A,Q,S,Cn	6	0.174	0.245	
		2) A,Q	4	1.939	0.101	
		12) A,Q,S,Cm	6	1.996	0.098	
		16) A,Q,S,Cn,A*Cn	7	2.095	0.094	
		6) A,Q,Cn	5	2.456	0.078	
		10) A,Q,Cm	5	3.939	0.037	
High matrix	Nymphs	10) A,Q,Cm	5	0.000	0.242	0.232
		12) A,Q,S,Cm	6	0.454	0.193	
		9) A,Cm	4	0.845	0.159	
		18) A,Q,Cm,A*Cm	6	1.971	0.090	
		11) A,S,Cm	5	2.273	0.078	
		20) A,Q,S,Cm,A*Cm	7	2.428	0.072	
		17) A,Cm,A*Cm	5	2.843	0.058	
		19) A,S,Cm,A*Cm	6	4.273	0.029	
	Adults	10) A,Q,Cm	5	0.000	0.330	0.509
		12) A,Q,S,Cm	6	1.507	0.155	
		2) A,Q	4	1.776	0.136	
		18) A,Q,Cm,A*Cm	6	1.925	0.126	
		4) A,Q,S	5	2.898	0.077	
		20) A,Q,S,Cm,A*Cm	7	3.449	0.059	
		6) A,Q,Cn	5	3.699	0.052	
		8) A,Q,S,Cn	6	4.869	0.029	
	Mating Adults	1) A	3	0.000	0.206	0.179
		3) A,S	4	1.353	0.105	
		2) A,Q	4	1.487	0.098	

Table 2.5. Continued.

9) A,Cm	4	1.844	0.082
5) A,Cn	4	1.981	0.076
17) A,Cm,A*Cm	5	2.395	0.062
4) A,Q,S	5	3.043	0.045
11) A,S,Cm	5	3.252	0.041
7) A,S,Cn	5	3.302	0.040
10) A,Q,Cm	5	3.392	0.038
6) A,Q,Cn	5	3.426	0.037
19) A,S,Cm,A*Cm	6	3.813	0.031
18) A,Q,Cm,A*Cm	6	3.887	0.029
13) A,Cn, A*Cn	5	3.966	0.028

†See Table 2.1 for full description of all candidate models. Main effects include patch area (A), patch quality (Q), patch shape (S), neutral-matrix connectivity (Cn), matrix-matters connectivity (Cm).

Table 2.6. Summary of AIC selection of 95th quantile regression models for the abundance of *C. vittiger* among *Opuntia* patches. For each landscape and life stage combination, the listed models are a 90% confidence set on the best model. Each model summary includes the number of estimable parameters (K), Δ_i = AIC_i – minimum AIC, and Akaike weights (w_i).

				AIC		
Landscape	Life stage	Model†	K	Δ_i	w_i	R^2
Low matrix	Nymphs	8) A,Q,S,Cn	6	0.000	0.620	0.561
		16) A,Q,S,Cn,A*Cn	7	1.324	0.320	
	Adults	14) A,Q,Cn,A*Cn	6	0.000	0.341	0.767
		18) A,Q,Cm,A*Cm	6	0.993	0.207	
		16) A,Q,S,Cn,A*Cn	7	1.917	0.131	
		10) A,Q,Cm	5	2.463	0.099	
		20) A,Q,S,Cm,A*Cm	7	2.828	0.083	
		6) A,Q,Cn	5	3.205	0.069	
	Mating Adults	16) A,Q,S,Cn,A*Cn	7	0.000	0.486	0.369
		20) A,Q,S,Cm,A*Cm	7	1.959	0.182	
		12) A,Q,S,Cm	6	3.553	0.082	
		4) A,Q,S	5	3.813	0.072	
		8) A,Q,S,Cn	6	4.099	0.063	
		2) A,Q	4	5.311	0.034	
High matrix	Nymphs	18) A,Q,Cm,A*Cm	6	0.000	0.347	0.536
		10) A,Q,Cm	5	1.526	0.162	
		20) A,Q,S,Cm,A*Cm	7	1.788	0.142	
		17) A,Cm,A*Cm	5	2.088	0.122	
		9) A,Cm	4	3.241	0.069	
		12) A,Q,S,Cm	6	3.456	0.062	
	Adults	12) A,Q,S,Cm	6	0.000	0.659	0.764
		20) A,Q,S,Cm,A*Cm	7	1.907	0.254	
	Mating Adults	20) A,Q,S,Cm,A*Cm	7	0.000	0.513	0.454
		17) A,Cm,A*Cm	5	1.963	0.192	
		18) A,Q,Cm,A*Cm	6	2.302	0.162	
		19) A,S,Cm,A*Cm	6	2.827	0.125	

†See Table 2.1 for full description of all candidate models. Main effects include patch area (A), patch quality (Q), patch shape (S), neutral-matrix connectivity (Cn), matrix-matters connectivity (Cm).

Table 2.7. Parameter estimates of explanatory variables for the best (lowest AIC value) logistic regression model of patch occupancy by *C. vittiger*. Profile likelihood confidence intervals (95%) for estimates are given in parentheses. The landscape variables are neutral-matrix connectivity (Cn) and matrix-matters connectivity (Cm).

Landscape	Life stage	Patch area	Patch quality	Patch shape	Cn	Cm
Low matrix	Nymphs	2.016 (1.642, 2.419)	0.608 (0.292, 0.937)		-0.038 (-0.082, 0.005)	
	Adult	3.625 (3.080, 4.236)	0.907 (0.511, 1.326)			
	Mating adult	1.793 (1.421, 2.191)	0.671 (0.330, 1.027)	-1.100 (-2.217, -0.014)		
High matrix	Nymphs	1.621 (1.162, 2.122)	0.380 (-0.061, 0.835)			-0.285 (-0.462, -0.118)
	Adult	3.960 (3.147, 4.915)	1.170 (0.599, 1.790)			0.217 (-0.002, 0.439)
	Mating adult	1.507 (1.101, 1.958)				

Table 2.8. Parameter estimates of explanatory variables for the best (lowest AIC value) 95th quantile regression model of the abundances of *C. vittiger* among *Opuntia* patches. Confidence intervals (95%) for estimates are given in parentheses. The landscape variables are neutral-matrix connectivity (Cn), matrix-matters connectivity (Cm), and their interaction with patch area (Area*Cn, Area*Cm).

Landscape	Life stage	Patch area	Patch quality	Patch shape	Cn	Area*Cn	Cm	Area*Cm
Low matrix	Nymphs	0.462 (0.410, 0.522)	0.131 (0.067, 0.194)	-0.280 (-0.384, -0.171)	-0.011 (-0.016, -0.006)			
	Adult	0.533 (0.505, 0.601)	0.142 (0.064, 0.184)		-0.018 (-0.033, -0.001)	0.005 (-0.022, 0.012)		
	Mating adult	0.254 (0.164, 0.465)	0.124 (0.001, 0.192)	-0.164 (-0.615, 0.135)	-0.019 (-0.058, 0.055)	0.009 (-0.024, 0.021)		
High matrix	Nymphs	0.403 (0.301, 0.475)	0.044 (-0.064, 0.146)				-0.010 (-0.077, 0.210)	-0.018 (-0.075, 0.021)
	Adult	0.552 (0.523, 0.590)	0.108 (0.027, 0.135)	-0.235 (-0.435, -0.050)			0.025 (-0.016, 0.075)	
	Mating adult	0.228 (0.119, 0.300)	0.062 (-0.065, 0.099)	-0.187 (-0.430, 0.176)			-0.089 (-0.110, 0.195)	0.042 (-0.022, 0.048)

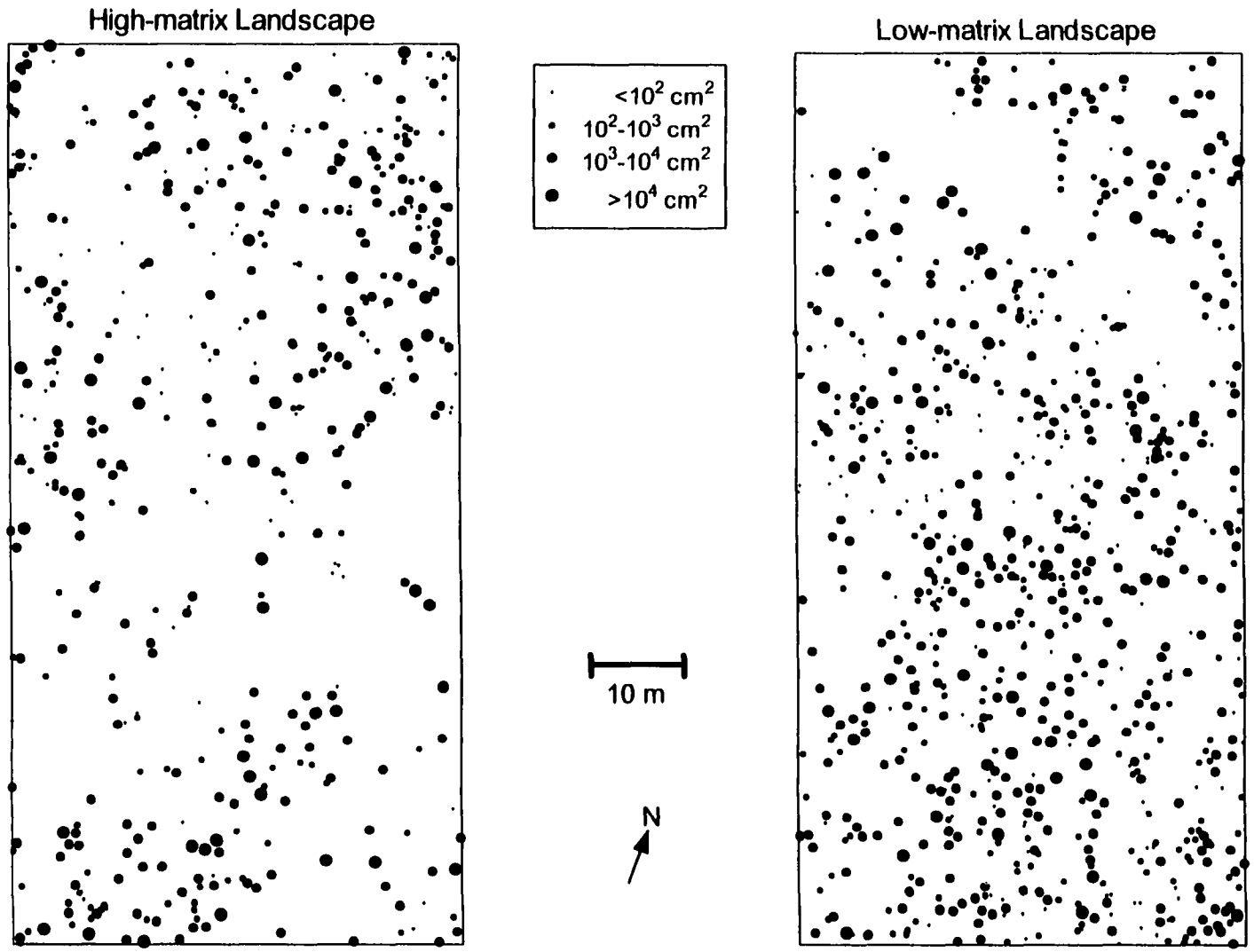


Figure 2.1. Maps of distributions of *Opuntia* patches in two landscapes with differing vegetation structure in the matrix. Symbol sizes indicate the relative areas of the patches. Each plot is 100 x 50 m.

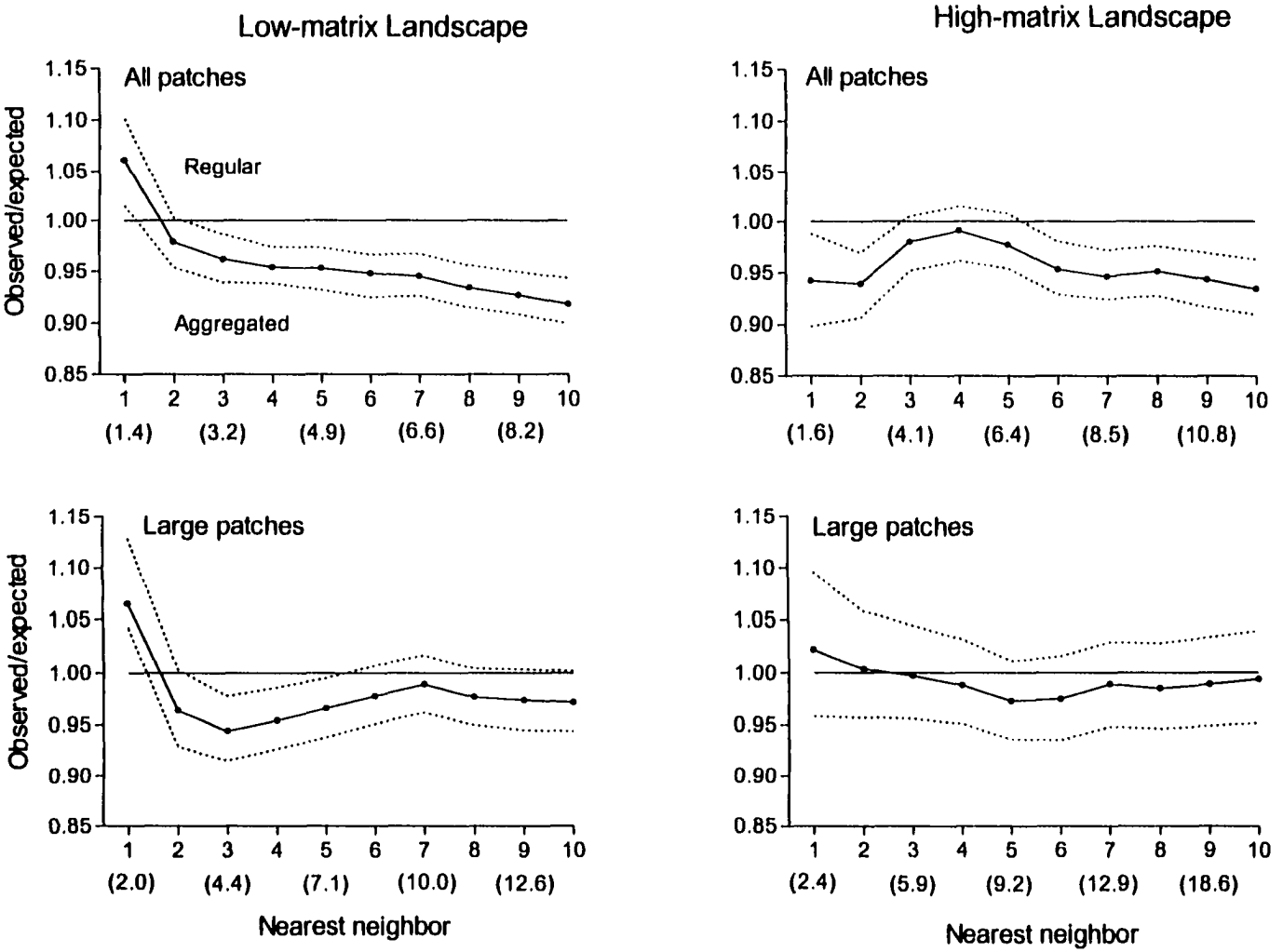


Figure 2.2. The ratio of the observed distance to the expected distance for the 1st through 10th nearest neighbors of *Opuntia* patches. The dotted lines are 95% confidence intervals based on 999 simulations. Confidence intervals >1 indicate a regular dispersion and those <1 indicate an aggregated dispersion. The top panels include all patches, whereas the bottom panels include only those patches with areas $>10^3$ cm^2. The mean distances (m) for selected nearest neighbors are given in parentheses.

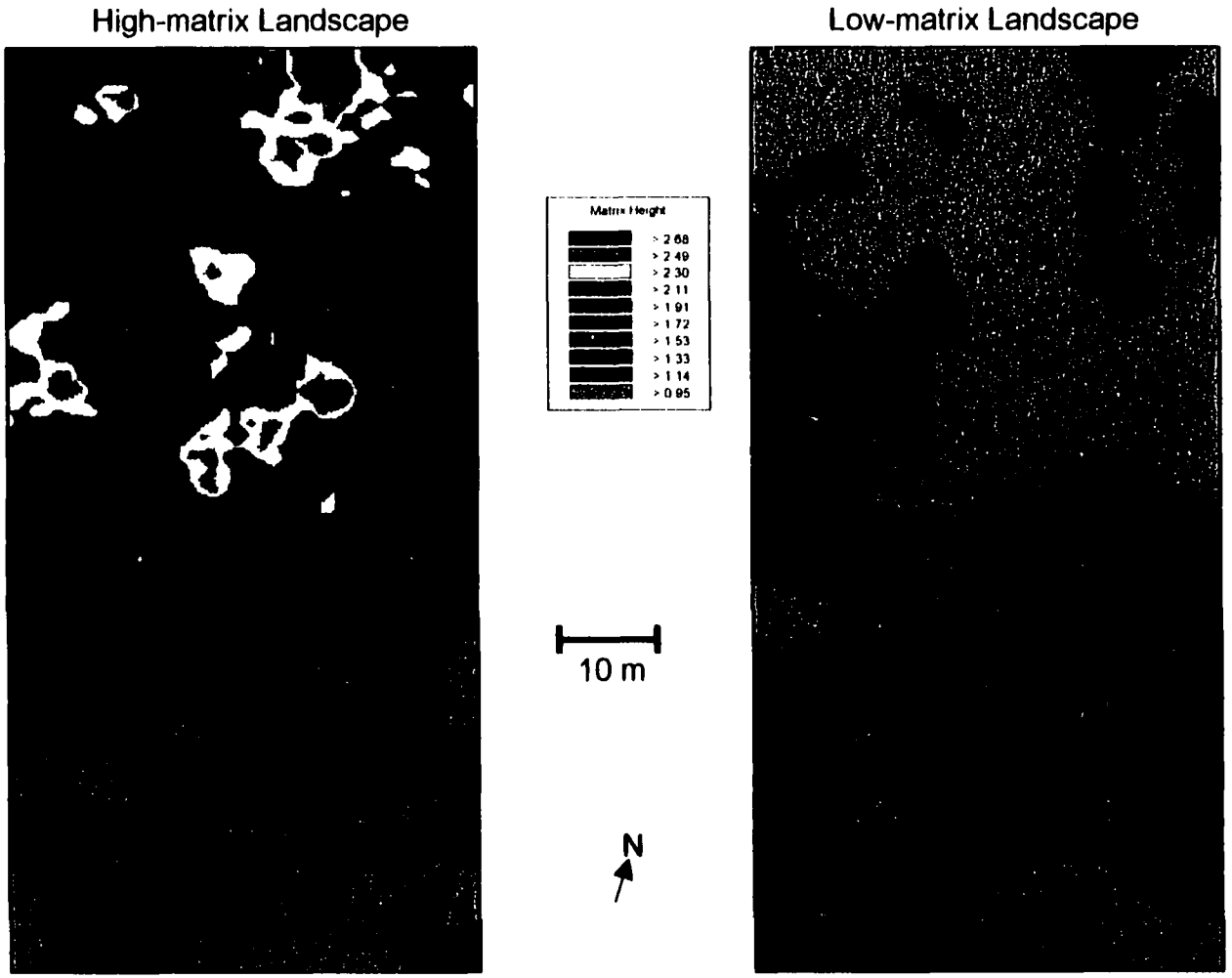


Figure 2.3. Kriged maps of the maximum vegetation height of the matrix on two landscapes. Each plot is 100 x 50 m. The vegetation height was measured in 5-cm intervals so that a value of 1 equals 1-5 cm and a value of 3 equals 11-15 cm.

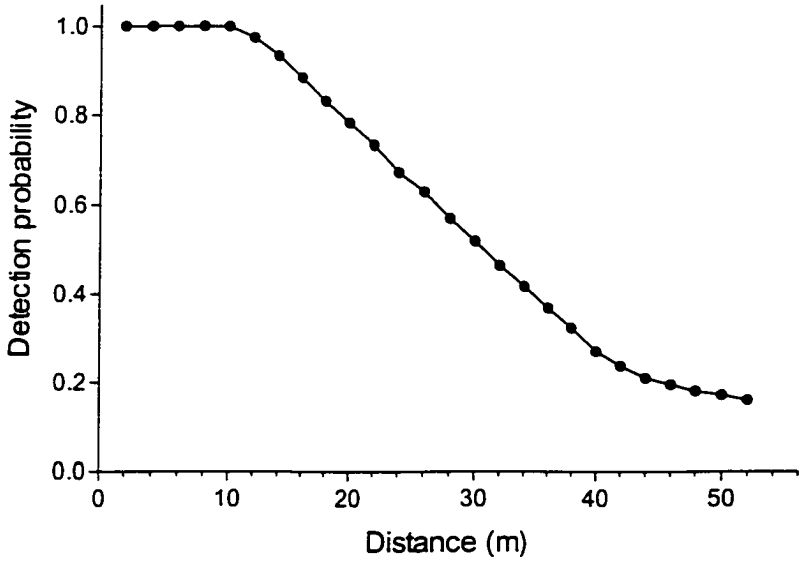


Figure 2.4. The probability of detecting a movement of a given distance based on 10,000 simulated movements for each distance. Movements were detected if they ended within the boundaries of the study plot.

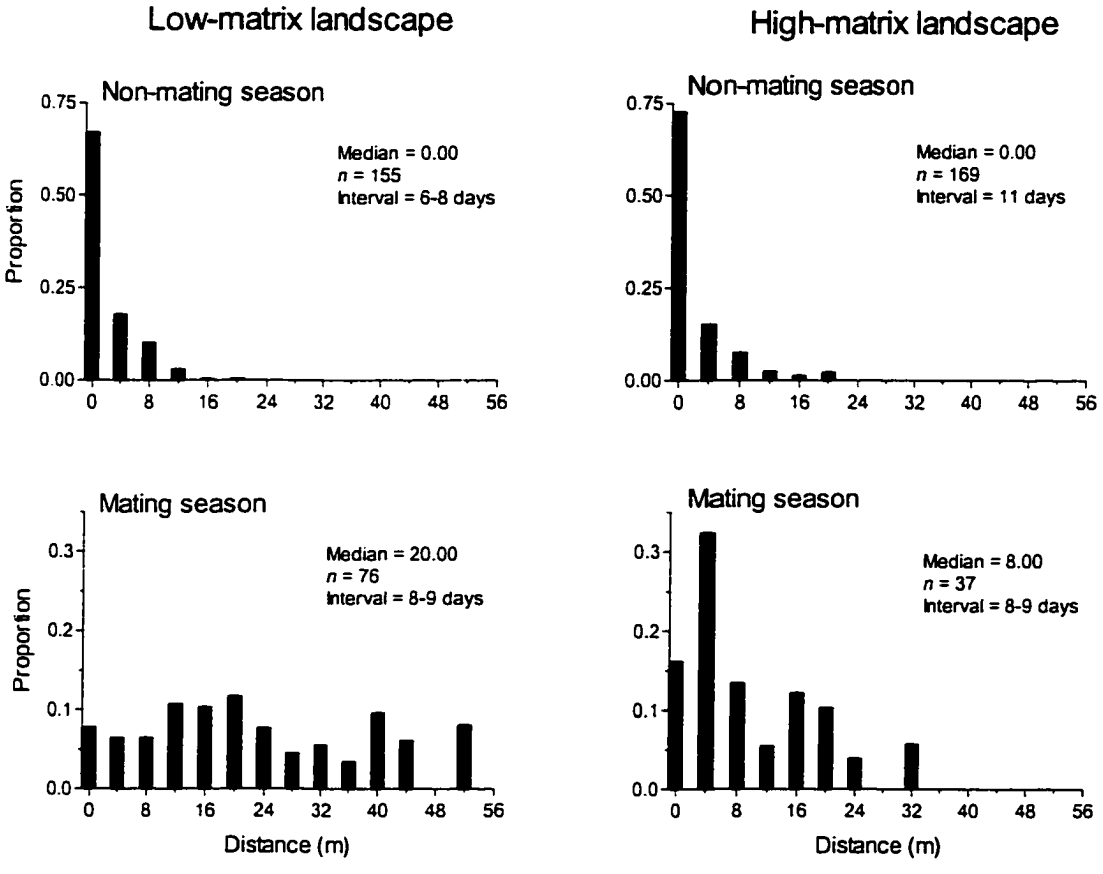


Figure 2.5. Distributions of movement distances of *C. vittiger* during non-mating and mating seasons in two landscapes. The distributions were corrected for distance-dependent detection probabilities (see Figure 2.4). The interval is the number of days between marking and resighting. The sample size (*n*) is the number of individuals.

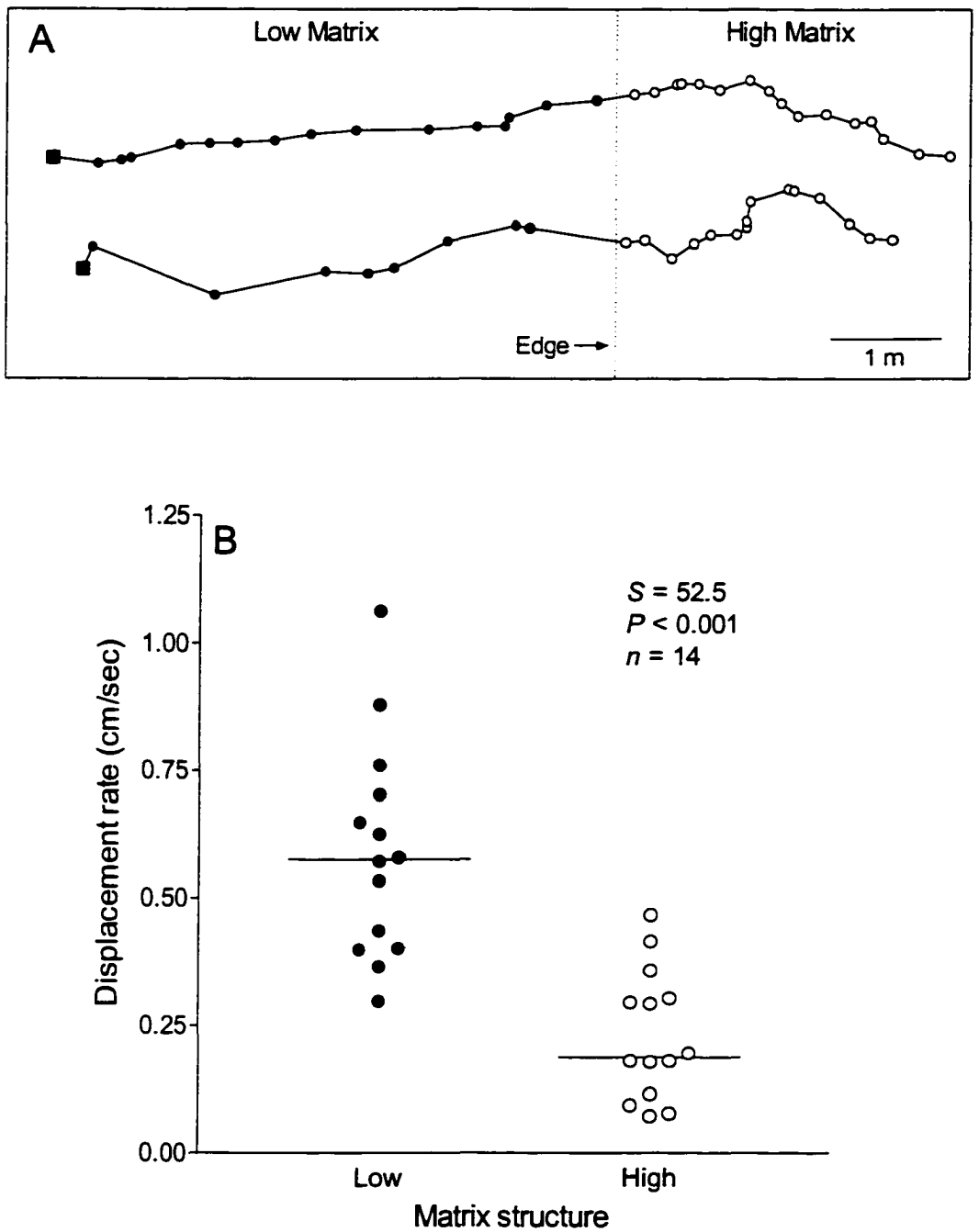


Figure 2.6. Effect of matrix structure and habitat edge on movement behavior of *C. vittiger*. (A) Two representative movement pathways in which the solid squares are release points and the circles are sequential locations at 1-min intervals. (B) Scatterplots of net displacement rates of *C. vittiger* pathways in two matrix elements. The horizontal bars indicate the medians of the distributions. The sample size (*n*) is the number of individuals used in a within-subject design.

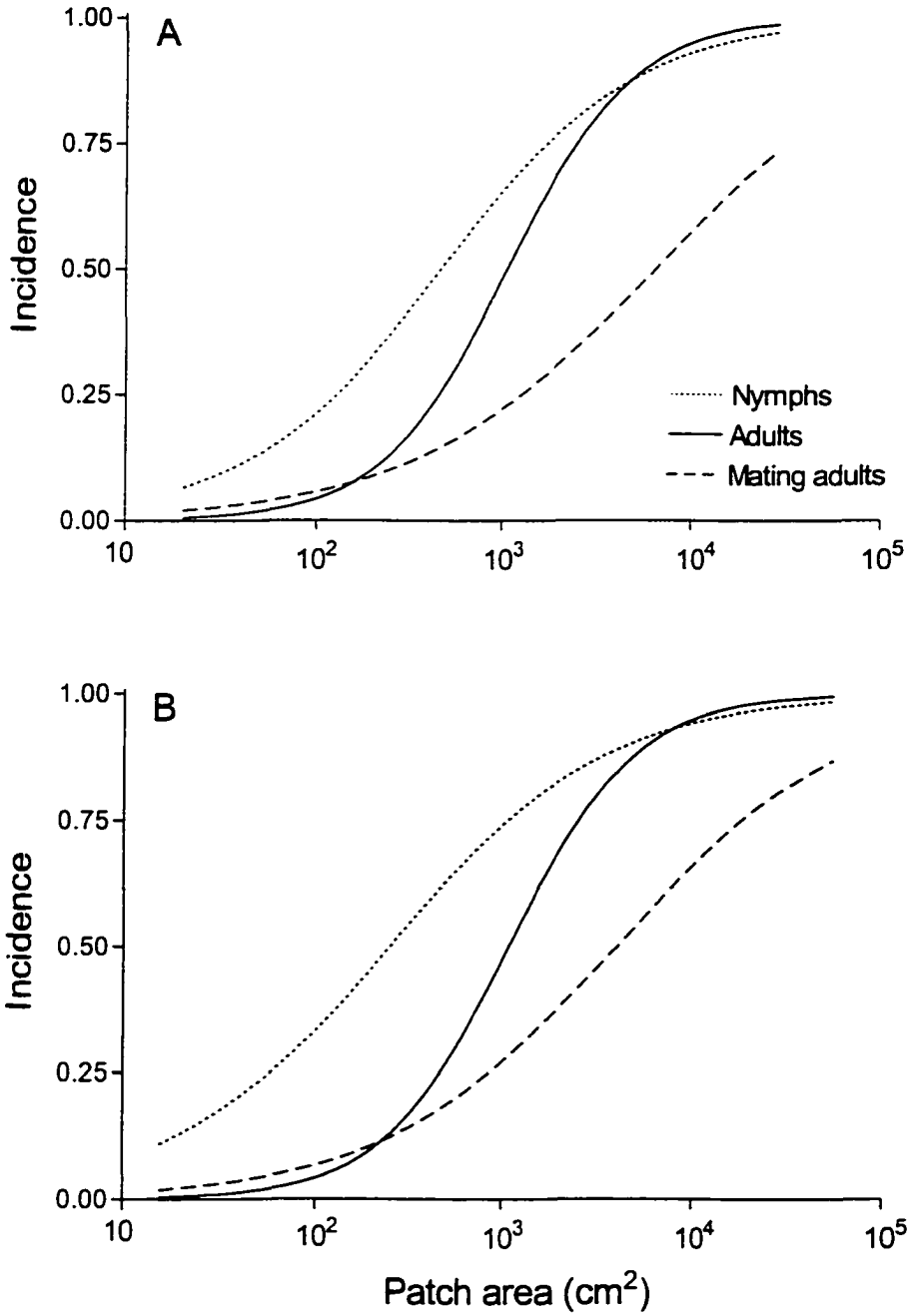


Figure 2.7. Incidence functions for the (A) low-matrix landscape and (B) high-matrix landscape. Each curve represents the predicted probabilities that an *Opuntia* patch is occupied by *C. vittiger* based on logistic regression models. The three life stages represent samples from distinct seasons.

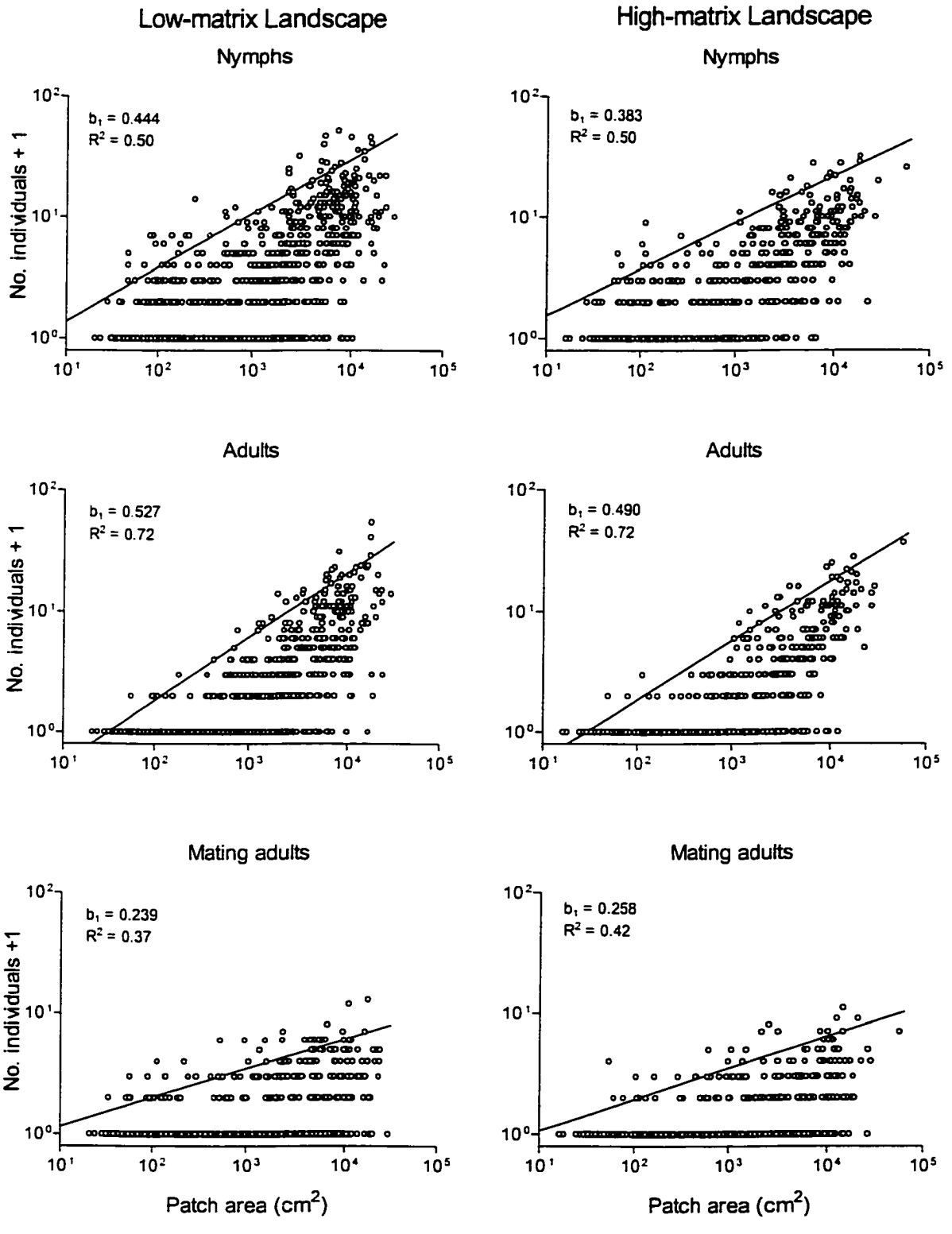


Figure 2.8. Upper-constraint relationships between the abundance of *C. vittiger* and the size of *Opuntia* patches. The fitted lines are 95th regression quantiles. Slopes (b_1) are provided for the regression models. Note that data are plotted on a log-log scale.

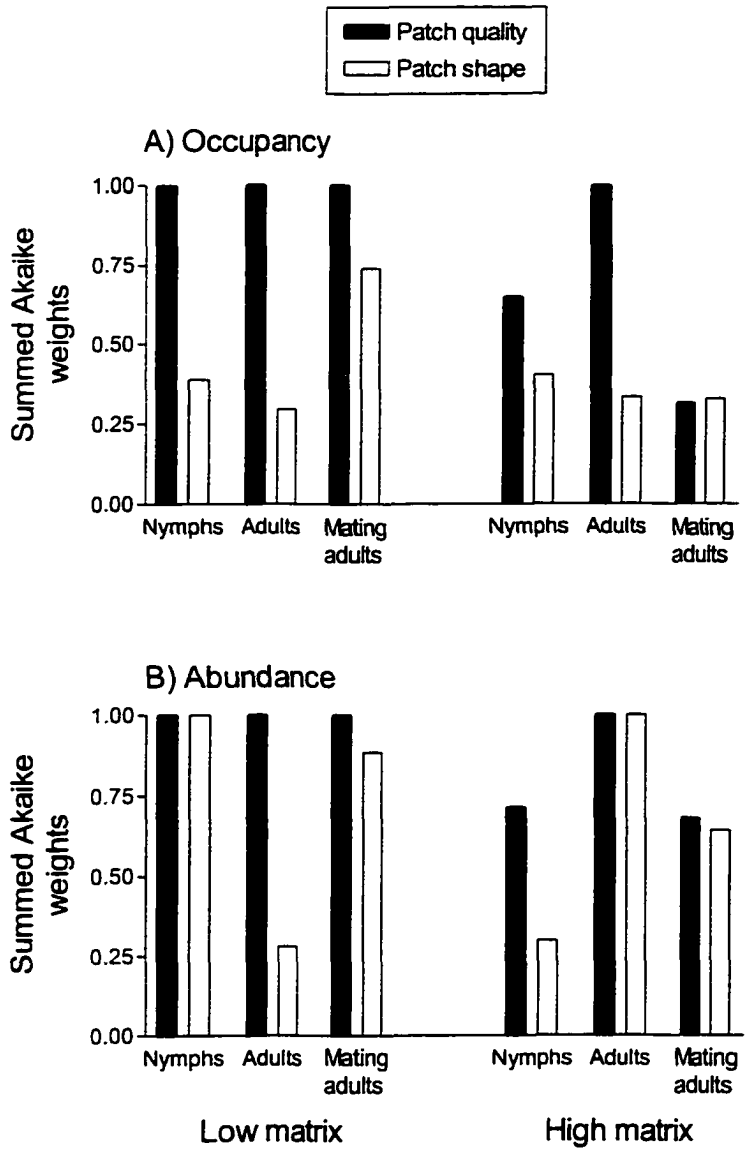


Figure 2.9. Comparison of the relative importance of patch quality and patch shape as explanatory variables based on Akaike weights summed across models. Weights are presented for (A) logisitic regression models of occupancy, and (B) 95th quantile regression models of abundance.

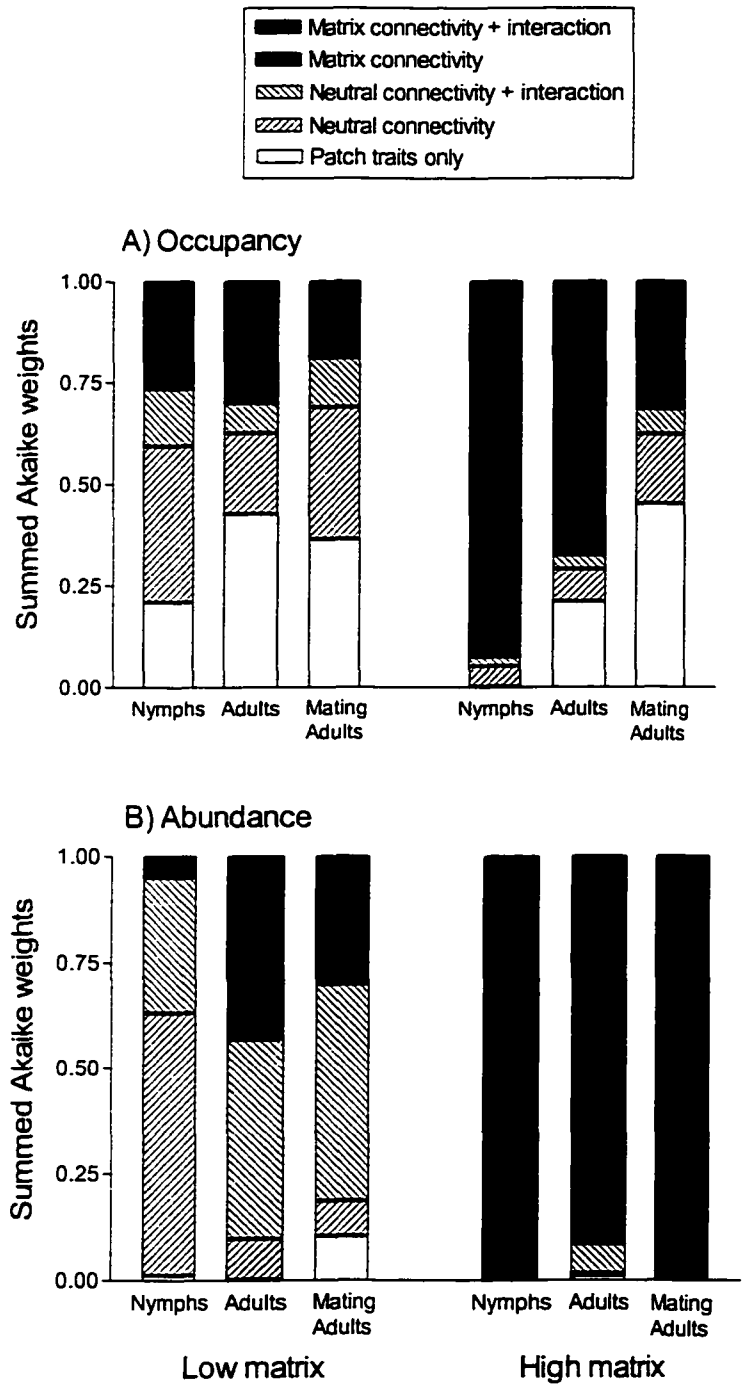


Figure 2.10. Comparison of the relative support for five model categories based on Akaike weights summed across models within each category. The explanatory variables for individual models are preseneted in Table 2.1. Weights are provided for (A) logistic regression models of occupancy, and (B) 95th quantile regression models of abundance.

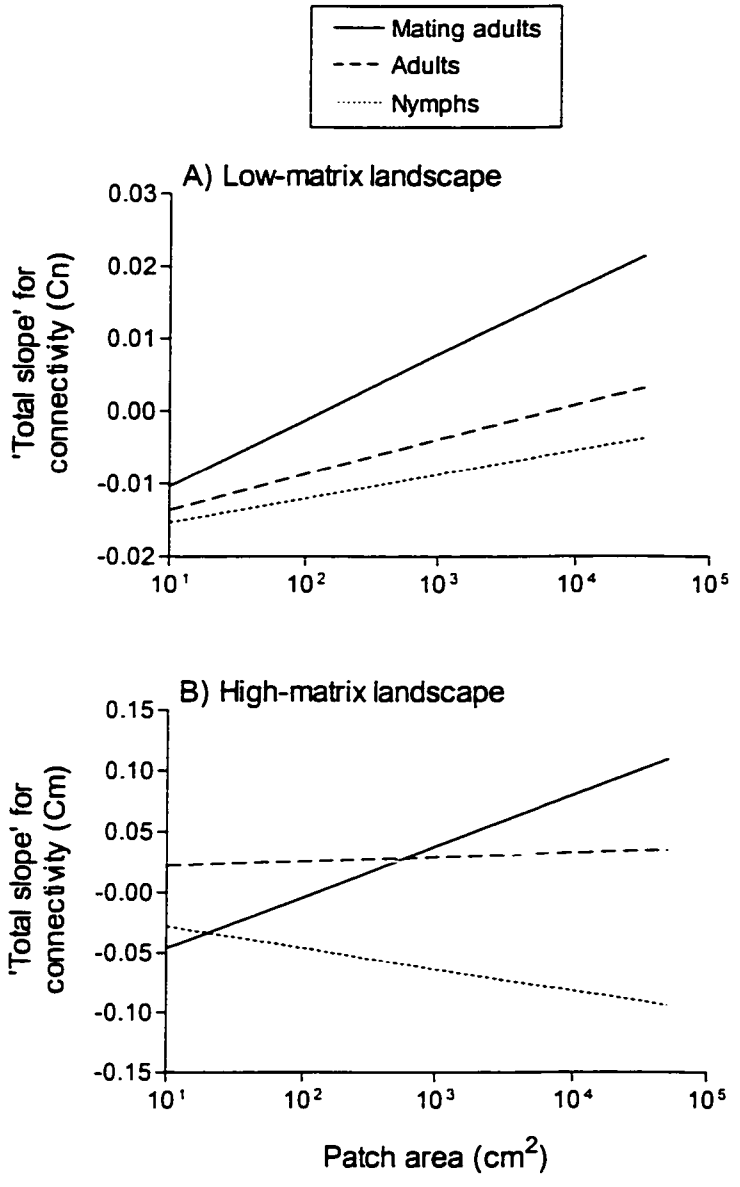


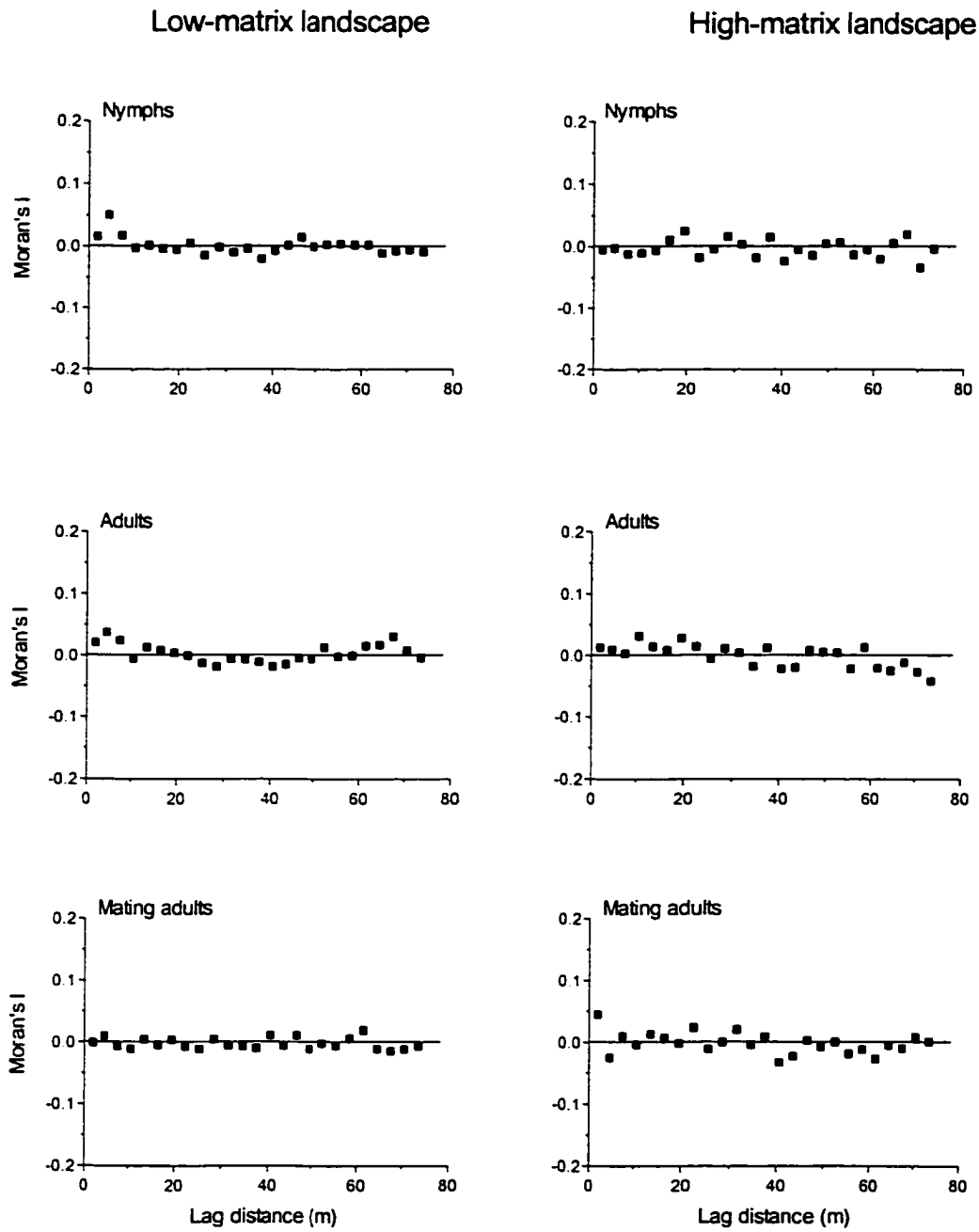
Figure 2.11. Interaction plots of connectivity and patch area based on 95th quantile regression models of *C. vittiger* abundances. The model used for each life stage is the highest ranking model that included the interaction term (either the 1st or 2nd ranked model). The 'total slope' combines the coefficient for connectivity with the coefficient for the interaction (see text).

APPENDIX 2.1

In my field experiment evaluating the effect of matrix structure on the movement behavior of *C. vittiger* (Chapter 2), I always released individuals into a low-matrix plot because I wanted to determine whether the bugs exhibited any deflection behavior after they encountered the edge of the high matrix. If individuals tend to change movement rates over time (i.e., slow down), then any effect that I attributed to matrix structure could have been confounded with time effects. Here, I use data from another movement study of *C. vittiger* (Chapter 3) to demonstrate that my protocol of not alternating releases between the two matrix types was unlikely to have biased my comparisons. Specifically, I asked whether cactus bugs might have lower displacement rates over time even when they are walking in a relatively homogenous matrix.

I used pathways of *C. vittiger* measured in low-matrix habitat and compared net displacement rates for the first segment of pathways (steps 1-10) with those for the next segment (steps 11-26). The number of steps for this comparison roughly equaled those for the low-matrix and high-matrix habitats in the experiment reported in Chapter 1. I compared net displacement rates between the two path segments with a signed ranks test. There was no evidence that net displacement rates of cactus bugs decrease over the examined time scale when individuals are moving through a homogeneous, low-matrix area ($T = 8$, $P = 0.7772$, $n = 20$). Therefore, I conclude that the matrix effects observed in

the movement experiment in Chapter 1 were not confounded by my release protocol that was designed to evaluate simultaneously any potential edge effects.



Appendix 2.2. Correlograms of abundances of *C. vittiger* in *Opuntia* patches. Each panel is for a particular life stage and landscape type. These results indicate that there was no spatial autocorrelation in abundance. Therefore, it was valid to use abundance as a response variable in non-spatial regression models. The correlograms were constructed with GS Plus software (Robertson 2000).

Appendix 2.3. Estimates of the intercepts (b_0) and slopes (b_1) for quantile regression models relating the abundance of *C. vittiger* to patch area ($\log_{10}$-$\log_{10}$ scale). Parameters are reported for the 95th and the 50th regression quantiles. The models are for occupied patches only; patches with zero counts were removed from the data set. The sample size (n) is the number of patches.

Landscape	Life stage	Quantile	n	b_0	b_1
Low matrix	Nymph	95th	442	-0.043	0.376
		50th		-0.787	0.426
	Adult	95th	350	-1.056	0.606
		50th		-1.482	0.575
	Mating adult	95th	191	0.183	0.143
		50th		-0.309	0.180
High matrix	Nymph	95th	306	-0.034	0.340
		50th		-0.650	0.367
	Adult	95th	226	-0.700	0.487
		50th		-1.623	0.618
	Mating adult	95th	149	0.172	0.154
		50th		-0.359	0.177

CHAPTER III

FINDING HABITAT PATCHES AND DIRECTIONAL CONNECTIVITY

You don't need a weather man to know which way the wind blows
–Bob Dylan

Introduction

Many animals are habitat specialists that inhabit landscapes in which suitable habitat is patchily distributed. Individuals must move among suitable patches, across a matrix of unsuitable habitat, to obtain food resources and mating opportunities. For these species, movement behavior (Bell 1991, Wiens et al. 1993*a*, Ims 1995, Turchin 1998) and the distance from which they can detect patches ('perceptual range' *sensu* Lima and Zollner 1996) should be key determinants of individual fitness and of the spatial distribution of individuals within populations and metapopulations. The functional connectivity of patches and landscapes (Taylor et al. 1993, Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001) for a given species is determined primarily by how search behavior and perceptual range of individuals interact with landscape structure.

How should an animal move while searching in the matrix for a patch of suitable habitat? Various theories and models make predictions about what is the most efficient search strategy for individuals attempting to locate resources (e.g., Pyke 1983, Cain 1985, Bell 1991, Bovet and Benhamou 1991, Dusenbery 1989, 1992, Viswanathan et al. 1999).

Here, I focus on the results from a series of simulation models by Zollner and Lima (1999*a*) that examined the relative effectiveness of systematic searches and correlated random walks (with different degrees of correlation) in finding habitat patches in landscapes. Search success was evaluated in relation to patch dispersion, energy reserves, mortality risks, and perceptual ranges. For most situations, the best search strategy was a nearly straight correlated random walk (Zollner and Lima 1999*a*).

Perceptual range is a consequential trait for animals living in fragmented habitats because individuals with a poor ability to detect habitat patches will spend more time searching in the matrix than those with high perceptual range (Lima and Zollner 1996, Zollner and Lima 1997). This extra time could translate into increased mortality risk and reduced mating opportunities. An individual's perceptual range represents its informational window onto its surroundings (Lima and Zollner 1996) and thus it is related to the general issue of how informational constraints affect movements, habitat selection, and the spatial distribution of individuals (e.g., Kennedy and Gray 1993, Ranta et al. 1999). The typical perceptual range of a species may be variable depending on environmental conditions. For instance, the perceptual range of yellow-bellied pond slider turtles (*Trachemys scripta*) depends on the amount of cloud cover (Yeomans 1995), and the perceptual range of nocturnal white-footed mice (*Peromyscus leucopus*) depends on the degree of illumination by the moon (Zollner and Lima 1999*b*). Finally, perceptual abilities may also affect what type of movement behavior produces the most efficient search pattern (Zollner and Lima 1999*a*).

My initial objectives were to examine the movement behavior and perceptual range of cactus bugs (*Chelinidea vittiger* Uhler, Hemiptera: Coreidae), which are habitat

specialists. Specifically, I wanted to determine whether *C. vittiger* had nearly straight pathways while searching in the matrix for suitable habitat, as predicted by Zollner and Lima (1999*a*), and to evaluate their perceptual range under different environmental conditions. My results suggest that olfaction is probably a dominant sense for *C. vittiger* in navigating through landscapes and that current techniques for evaluating perceptual range (Zollner and Lima 1997) may have limitations for olfactory-based species. These concerns are separate from those discussed previously (Goodwin et al. 1999, Zollner and Lima 1999*c*). Moreover, I contend that we need to broaden our conceptual view of landscape connectivity to consider explicitly the natural history of species and the role of abiotic factors such as wind.

Methods

Study area and species

The main study site was at the Central Plains Experimental Range (CPER) in north-central Colorado ($40^0$49'N, $104^0$46'W), 61 km northeast of Fort Collins, at 1650 m elevation. The CPER is located in the short-grass steppe and has vegetation dominated by two bunchgrasses, *Bouteloua gracilis* and *Buchlöe dactyloides* (Lauenroth and Milchunas 1991). Other plant species present included *Aristida longiseta*, *Artemisia frigida*, and *Eriogonum effusum*. Suitable habitat for *C. vittiger* consisted of patches of a single species of low-growing cactus, plains prickly pear (*Opuntia polyacantha*). The climate of the CPER is semiarid, with an average of 321 mm of annual precipitation (Lauenroth and Sala 1992).

The geographic range of *C. vittiger* corresponds to the distribution of flat-jointed *Opuntia* spp. (platyopuntias) in the United States, Canada, and northern Mexico (Mann 1969, Herring 1980). Adult cactus bugs feed on mature pads of *Opuntia*, whereas nymphs are more likely to feed on immature pads and fruits (De Vol and Goeden 1973). Most mating occurs from April to mid June, and females attach eggs to the underneath of cactus spines or to other vegetation nearby the host plant (Mann 1969). *C. vittiger* develops through five nymphal stages. New adults are active for several months during autumn, but they do not mate then. Cactus bugs overwinter in the adult stage (Mann 1969, De Vol and Goeden 1973).

Although adult *C. vittiger* are capable of flight, they are not frequent flyers (Hamlin 1924, Dodd 1940, Mann 1969, De Vol and Goeden 1973). During three years, I witnessed only one flight (a female flew ca. 4 m). Likewise, De Vol and Goeden (1973) observed no flight behavior during two years of field observations. Instead, cactus bugs normally walk between host-plant patches through a matrix of unsuitable habitat. Most inter-patch transfers occur during the mating season, but some individuals switch patches in autumn (Chapter 2). Even during the mating season, the median displacement rates are only 1-2.5 m/day in fragmented landscapes (Chapter 2). This restricted movement probably limited the effectiveness of *C. vittiger* as a control agent against *Opuntia* in Australia during the 1920s (De Vol and Goeden 1973).

Movement behavior in the matrix

The main arena was a 0.8-ha, oval-shaped area with uniformly low vegetation height (median < 5 cm) composed mainly of grasses. It contained no *Opuntia* but was

surrounded all around by *Opuntia* patches. The distance from a release point to the nearest *Opuntia* ranged from 30 to 70 m in different directions. I assumed that these release distances were beyond the perceptual range of *C. vittiger* and that the measured movements represented searching behavior. I will reevaluate this assumption later in the discussion.

I conducted trials from 28 August to 13 September 1999. Individuals (n = 20) were collected from cactus patches in the general area (<200 m from arena), marked with model paint on their pronotum, and released near the center of the arena within 30 min of capture. Each individual was used for only one path. I randomly assigned an individual to one of six release points that were separated by ≥1.5 m with the constraint that no release point was used more than once per day. Trials were conducted between 0945 and 1551 when soil temperatures ranged from 24.8-42.6 °C and windspeeds at 5 cm above ground level ranged from 0.5 to 7.75 km/h.

Using standard procedures for measuring insect movements (Wiens et al. 1993b, 1997, Turchin 1998, Schooley and Bestelmeyer 2000), I recorded the paths by placing sequentially numbered flags at the bug's location at 1-min time steps for 50 min. To avoid disturbing the bugs, I waited ≥1 time step before placing the flag. I mapped the flag locations for each pathway by triangulation with a measuring tape (Turchin 1998).

To measure path directionality, I used mean vector length (MVL), which is a unit vector measure of the dispersion of turning angles (Batschelet 1981, Wiens et al. 1993b). A turning angle is the angle formed by the change in direction between consecutive time steps. MVL varies from 0 (uniform) to 1 (perfectly directional). Zollner and Lima

(1997) concluded that paths with MVL ≥ 0.90 produced the most efficient searches in most situations.

I also examined the directionality (MVL) of pathways of *C. vittiger* in several other matrix situations in which the release points were at greater distances from *Opuntia* relative to those in the main arena. Both sets of trials were conducted in June 2000 using the same general procedures as previously described. First, I evaluated 14 paths from an experiment on the effects of matrix structure on the movements of *C. vittiger* in which no *Opuntia* occurred within 100 m of the release points. The experimental area was located several km from the main arena and included both low and high matrix structure (see Chapter 2 for details). Second, I mapped the paths of five individuals that were released >3000 m away from suitable habitat. These individuals were collected from the CPER, transported to Fort Collins, Colorado, and released within 4 h of capture. They were able to feed on potted *Opuntia* in between their capture and release. The matrix consisted of grass turf (*Poa pratensis*) that had a low structure (median height <5 cm) similar that on the main arena.

Finally, I used the 20 pathways from the main arena to evaluate some assumptions of the correlated random walk model, which may be a useful general model of animal movement under some circumstances (Kareiva and Shigesada 1983, Turchin 1998). The correlated random walk model assumes that there are no serial correlations in step lengths and in turning angles. I tested for serial correlations in step lengths with Pearson's correlation coefficient for time lags 1 and 2, and then treated each path as a replicate and calculated a 95% CI for each lag to determine if it differed from zero (Turchin 1998). For turning angles, I followed Turchin (1998) and categorized consecutive turns as either

in the same direction (S) or in the opposite direction (O) and calculated a measure of autocorrelation as (S-O)/(S+O). This measure ranges from −1 (all turns in the opposite direction) to 1 (all turns in the same direction). Again, I constructed a 95% CI for the autocorrelation measure of turning angles.

Habitat detection: natural patch network

I followed the general approach for evaluating perceptual range advocated by Zollner and Lima (1997) and used in other studies (Harrison 1989, Yeomans 1995, Gillis and Nams 1998, Zollner and Lima 1999*b*, Zollner 2000). Individuals are released into the matrix at specific distances from suitable habitat, and then one measures whether they orient toward the suitable habitat. The key assumption of this assay is that individuals will move toward the closest patch of suitable habitat if they can detect it. That is, the behavioral orientation of an individual is a useful measure of its perceptual range (Zollner and Lima 1997). This assumption seems reasonable for a habitat specialist such as *C. vittiger* because the matrix offers no food resources, little or no opportunity for mating (all observed copulations occurred within patches), and possible thermal stress and increased predation risk. Matrix habitat is unsuitable and has no benefits to balance these potential costs, but it must be crossed during inter-patch movements.

I conducted the releases within two landscapes (0.5 ha each) that were naturally fragmented from the perspective of *C. vittiger*. A complete description of these areas is provided in Chapter 2. *Opuntia* occurred in discrete patches that covered <5% of the landscapes. The median patch size was ca. 1000 cm^2 but varied over several orders of magnitude. The patch distribution was either aggregated or random at all but the finest

spatial scales (<2 m). One of the landscapes had a matrix that was fairly homogenous with low vegetation structure, whereas the other landscape had a matrix with heterogeneous structure.

I released a total of 93 adults either during the mating season (June 1999, $n = 75$) or the non-mating season (August 1999, $n = 18$). Each individual was used for only one trial. I released bugs at either 50 cm or 100 cm from the closest patch of *Opuntia*. Other patches were >2.5 m away. The target patch was either upwind, crosswind, or downwind from the release point. The same release point was not used twice within the same day. In addition to these two main factors (distance, direction) that were controlled by design, I measured several other variables as covariates. Patch area was calculated as an ellipse using the length of the (major) long axis of the patch and that of the (minor) axis perpendicular to the long one. Matrix structure was measured as the maximum vegetation height (in 5 cm increments) every 10 cm between the release point and the target patch. Windspeed was measured before each release at 5 cm above ground level in an interpatch area. Finally, because patch detection might be influenced by conspecifics on the target patch, perhaps due to pheromones cues, I counted the number of adult *C. vittiger* in each target patch at the time of release.

Individuals were captured, transported off site, marked with model paint, and released within 30 min of capture. For most individuals (77%), the target patch was the same patch where they were captured, but during the mating season some individuals (28% of 75) were released at different patches because of logistical constraints. These capture patches are probably not natal patches because *C. vittiger* moves between patches often enough during the mating season that they exhibit a patchy population structure (Chapter

2). Therefore, my assay of patch detection was not confounded with any potential homing behavior during the mating season. Nevertheless, cactus bugs might be more familiar with the matrix surrounding a patch that they had already visited, and this experience could affect their orientation behavior. However, there is no evidence that orientation behavior is influenced by whether individuals are released at their patch of capture or not (Appendix 3.1). Hence, I pooled all data within the mating season but retained 'season' as an explanatory variable.

One should use initial orientations rather than final orientations when evaluating patch detection abilities because even random walkers with no perceptual range are more likely to contact target patches the closer they are released to them (Goodwin et al. 1999, Zollner and Lima 1999*c*). I allowed individuals to move for 2 min after release and then marked their locations. The locations of some individuals (17%) that did not move a substantial distance (10 cm) after 2 min were marked after 5 min to ensure that they had adequate time to exhibit a choice of direction. None of the individuals had reached the target patch after the 2- or 5-min period. I measured the angle from the release point to the initial location of the bug ($\varnothing_1$) and the angle from the release point to the closest cactus pad within the target patch ($\varnothing_2$). For a response variable, I used the absolute value of ($\varnothing_1 - \varnothing_2$). This measure of orientation is termed the angular distance (Batschelet 1981) and it ignores whether the deviation is clockwise or counterclockwise.

The angular distance is a linear variable, not a circular one (Batschelet 1981), which allowed me to evaluate multiple effects on orientation behavior within the framework of generalized linear models. I constructed linear models (Proc GENMOD, SAS Institute 1996) using normal probability distributions and identity link functions. I fit a total of 24

models including the global model that included all seven main effects: distance (50 or 100 cm), direction (upwind, crosswind, downwind), season, patch area, matrix structure, windspeed, and number of conspecifics. I fit seven models that each had six explanatory variables (the global model minus one main effect). I then fit another 14 models with 2-5 explanatory variables that seemed biologically relevant. These models emphasized habitat variables (distance, patch area, matrix), wind (direction, speed), and their combinations with the other covariates. Finally, I fit two single-variable models that included either distance or direction.

I next employed an approach to model selection based on information theory (Burnham and Anderson 1998) that uses Akaike Information Criterion (AIC) to select the best model from the set of candidate models and to rank the remaining models. The AIC approach to model selection balances model fit with the number of model parameters (Burnham and Anderson 1998). I used the second-order criterion, AIC_c, which has an additional bias correction term that is recommended when the ratio of sample size to the number of estimable parameters is <40 (Burnham and Anderson 1998). The model with the lowest AIC_c value is deemed the best model. Because AIC_c is on a relative scale, it is helpful to convey results as AIC_c differences, defined as

$$\Delta_i = AIC_{ci} - \text{minimum } AIC_c$$

across all models (Burnham and Anderson 1998). The best model has $\Delta_i = 0$, and models for which $\Delta_i \leq 2$ have reasonable support and should receive consideration when making inferences (Burnham and Anderson 1998). Moreover, it is useful to calculate a set of 'Akaike weights', w_i, defined as

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_r)}.$$

Each w_i provides the weight of evidence that model i is the best model. Akaike weights are normalized relative likelihoods that sum to 1 (Burnham and Anderson 1998). Thus, I defined a 90% confidence set for the best model by summing the Akaike weights (largest to smallest) until the total was ≥0.90, and I present results only for those models within the confidence set.

I also tested whether the orientation angles ($ø_1$) were nonrandom and clustered around the direction of the closest patch ($ø_2$) using *V*-tests (Batschelet 1981, Zollner and Lima 1997). Based on the AIC model selection results, these tests were conducted separately for the three release directions.

Habitat detection: 'artificial' patch experiment

During October 1999, I evaluated the effect of wind direction on orientation behavior of *C. vittiger* in a more controlled experiment using 'artificial' patches of *Opuntia*. The patches consisted of *Opuntia* potted in shallow circular trays (1300 cm^2). A preliminary study indicated that cactus bugs readily colonized such patches and exhibited normal feeding and mating behavior in them. I conducted the experiment in the center of the main arena for the movement pathways where other *Opuntia* was 30-70 m away. I used four release points within the arena separated by 5 m, and any given point was not used >1 time per day. Individuals were collected, marked with model paint, and released within 30 min of capture. I conducted trials between 1100 and 1665 when soil

temperatures ranged from 26.7 – 36.6 °C and windspeeds at 5 cm above ground level ranged from 1 to 11 km/h.

I released individuals (n = 16) in the center of an array of four patches. Each patch was 100 cm away and either upwind, crosswind (2 patches), or downwind from the release point. To even out any differences among the patches, I randomly assigned each patch to one of the four directions on each trial. There were no adult conspecifics on the patches during the trials, but bugs might have been on the cactus pads before they were transplanted to the trays. The matrix structure was uniformly low between the release point and the patches. I marked the location of individuals after they had moved ca. 50 cm (43-52 cm). Based on results from the natural patch network, I tested for orientation toward the upwind patch using a V-test.

Results

Movement behavior in the matrix

For the 20 movement pathways in the main arena, the mean step length averaged 14.6 cm (range 9.3 – 22.2), the total length of the path averaged 727.9 cm (389.4 – 1108.2), and the net displacement (straight-line distance between the initial and final location) averaged 598.5 cm (363.5 – 1040.2).

Pathways of *C. vittiger* in the matrix were highly directional (Fig. 3.1). The 95% CI for MVL included 0.90 regardless of how far individuals were released from suitable habitat (Table 3.1).

There was positive serial correlation in mean step length at lag 1 ($\bar{r}$ = 0.24, 95% CI = 0.15, 0.32) but none by lag 2 ($\bar{r}$ = 0.08, 95% CI = -0.03, 0.18). Negative autocorrelation in turning angles occurred at lag 1 ($\bar{r}$ = -0.20, 95% CI = -0.29, -0.11). Thus, cactus bugs used counterturning as one mechanism to maintain a high degree of directionality. These paths of *C. vittiger* could not be modeled as simple correlated random walks because key assumptions regarding serial correlation of step lengths and turning angles are violated.

Habitat detection: natural patch network

The best model for explaining the degree of orientation of *C. vittiger* toward *Opuntia* patches was the one that included the release direction relative to prevailing winds, matrix structure, and patch area (Table 3.2). Release direction and matrix structure were in the top four models that received substantial support ($\Delta_i \leq 2.13$), and patch area was included in three of those. An evaluation of the entire set of models indicated that windspeed and release distance were not important variables and that their inclusion in two of the top models (Table 3.2) was simply due to their linkage with the best model. Least squares means for the three wind directions from the best model (Fig. 3.2) indicated that angular distances were smallest when patches were upwind, intermediate when crosswind, and largest when downwind. Based on parameter estimates from the best model, angular distance was positively related to matrix structure (coefficient = 37.5, SE = 14.7) and negatively related to patch area (coefficient = -0.0014; SE = 0.0007). Overall, *C. vittiger* had the strongest orientation toward patches of suitable habitat when large patches were upwind from them and the matrix in between was relatively short.

Given that release distance was an unimportant explanatory variable, I combined data for the 50 and 100 cm releases and conducted *V*-tests for the three release directions. Matrix structure and patch area had similar distributions among the three directions. Only individuals released with the closest patches upwind from them oriented toward those patches (Fig. 3.3; $u = 3.96$, $P < 0.0001$). Those released with patches crosswind ($u = 0.606$, $P > 0.10$) and downwind ($u = -2.00$, $P > 0.10$) did not orient toward the closest patch. In fact, the cactus bugs with downwind releases tended to walk upwind away from the closest suitable habitat (Fig. 3.3).

Habitat detection: 'artificial' patch experiment

Cactus bugs exhibited a strong orientation toward the upwind patch in the experiment using potted *Opuntia* (Fig. 3.4). Their movements were non-random and clustered in the direction of the prevailing winds ($u = 3.20$, $P < 0.001$).

Paths revisited

Given the results from the habitat detection studies, I examined the 20 pathways of *C. vittiger* from the main arena, where they were released 30-70 m from *Opuntia*, and asked whether their movements in the matrix were also directed upwind. I compared the overall angle of each path (angle between first and last location) with the angle of the prevailing wind with a *V*-test. The paths were non-random ($u = 4.76$, $P < 0.0001$) and clustered around the upwind direction (Fig. 3.5). In contrast, the paths were not oriented

toward the patch where individuals had been collected ($u = 0.26$, $P > 0.10$). Finally, the angular distance for the pathways (deviation from upwind) was negatively correlated with windspeed ($r = -0.45$, $P = 0.046$).

Discussion

My original questions regarding search behavior and perceptual range of *C. vittiger* were not answered unambiguously because of the tendency for individuals to walk upwind both within and outside of patch networks of *Opuntia*. However, these results have raised broader questions regarding animal movement, perceptual range, and connectivity.

Movement behavior in the matrix

Initially, the highly directional pathways of adult *C. vittiger* seemed to support the predictions from Zollner and Lima's (1999*a*) simulation models. I had assumed that individuals released 30-70 m from *Opuntia* were not within perceptual range of suitable habitat, so that their movements represented searching behavior. Their pathways were oriented upwind, however, which suggests that they might have been using olfactory cues from host plants within their perceptual range. If so, their movements represented odor-plume tracking (Bell 1984, Murlis et al. 1992) and not search behavior. Still, *C. vittiger* had nearly straight pathways when released >100 m and >3000 m from *Opuntia*. It seems unlikely that a species that has a median net displacement rate of 1-2.5 m/day (Chapter 2) would evolve the ability to detect habitat from such long distances. Unfortunately, I cannot assess whether individuals walked upwind in these other

situations because of possible confounding variables (releases >100 m) and lack of a clear prevailing wind direction (releases >3000 m).

Is there any reason that cactus bugs might walk upwind even when suitable habitat is not within their perceptual range? One might expect that walking crosswind would be the most efficient strategy when olfaction is important because a chemical plume has a larger cross section parallel to the wind flow than across it (Dusenbery 1992). However, Sabelis and Schippers (1984) demonstrated that if the mean wind direction is constant but the instantaneous wind direction fluctuates rapidly within a range larger than $\pm 30^{\circ}$ of the mean direction, then either upwind or downwind movement is the best strategy for searching for an odor plume because the realized cross section of the plume will be larger across the wind than parallel to it. Dusenbery (1990) extended the model of Sabelis and Schippers (1984) and demonstrated that upwind search is more efficient than downwind search because it avoids backtracking to the odor source after the plume is encountered. The model is more applicable to walking insects than to flying insects, and it assumes that wind fluctuations are rapid compared to the movement speed of the animal, that the searcher can determine the mean wind direction, and that it can move efficiently to the source after it enters the plume (Dusenbery 1990, 1992). Although I have not evaluated all of the conditions and assumptions of this model of anemotactic search for the *C. vittiger* system, the instantaneous wind direction at the CPER fluctuated rapidly during the movement trials relative to the speed of walking cactus bugs (pers. obs.). The main point is that there are conditions that are not too restrictive in which upwind searching for an odor plume is best (Dusenbery 1990).

Another possibility is that individuals were using the wind direction to maintain a relatively straight course because such directional movement is the best way to find a patch (Zollner and Lima 1999*a*) or a plume. That is, wind may serve as a collimating stimulus (Dusenbery 1992) that simply serves to maintain a straight course. Without external stimuli, it is difficult for animals to maintain straight routes for very long (Bell 1991, Dusenbery 1989, 1992). Of course, cactus bugs potentially could use wind to maintain a straight path in directions other than upwind, but walking insects probably determine wind direction with their antennae (Bell 1984), so it seems logical that they might lead with these sensory organs and move upwind.

The high directionality of *C. vittiger* pathways in the main arena was partly maintained by counterturning. Alternating turn directions is a behavior exhibited by insects in contact with chemical cues (Bell 1984), but it can also serve to produce a straight path when orientation to external cues is not involved (Kennedy 1986). The *C. vittiger* released >3000 m from *Opuntia* also used counterturning as there was a negative autocorrelation in their turning angles at lag 1 ($\bar{r}$ = -0.29, 95% CI = -0.54, -0.04, n = 5). Counterturning produces more linear paths than would result from simple correlated random walks. Hence, the directionality of my pathways with a MVL of 0.89 (Fig. 3.1) closely resemble those of Zollner and Lima (1999*a*) that had a MVL of 0.99 but no serial correlation in turning angles. Although not a goal of this study, a realistic model of movements by *C. vittiger* would likely involve a biased correlated random walk (Turchin 1998, Schultz and Crone 2001) that allows for movement direction to be influenced both by the absolute direction (bias) and the previous direction (correlation) and that also included the autocorrelation structure observed for step lengths and turning angles.

Perceptual range

The habitat detection trials within a natural patch network demonstrated that the orientation of *C. vittiger* toward *Opuntia* patches depended on environmental conditions. Individuals were most likely to move toward large patches and toward those patches surrounded by a matrix with short vegetation structure. At the release distances of the trials (≤100 cm), these effects of patch size and matrix likely reflected mechanisms related to odor cues. Big patches provide a relatively large source of host-plant chemicals, and odor plumes carry farthest in relatively open environments (Murlis et al. 1992). The effect of the matrix on patch discovery may partly explain the experimental results that *C. vittiger* occurs most often on those pads of *Opuntia fragilis* in mixed grass prairie where the nearby vegetation has been reduced or removed (Burger and Louda 1994, 1995). The matrix also affects perceptual range of white-footed mice, which probably use vision to find habitat patches (Zollner and Lima 1997, 1999*b*). Mice perceive forested habitat from ca. 20 m when in a matrix of bare ground, but they cannot perceive it from just 10 m when in a matrix of crop fields (Zollner and Lima 1997, 1999*c*). The influence of the matrix on animals in subdivided habitats is often considered in terms of its effects on movement rates and behavior (Chapter 2, Hokit et al. 1999, Roland et al. 2000, Jonsen et al. 2001, Ricketts 2001, Wiens 2001). More emphasis should be given to matrix effects on perceptual range of individuals.

Habitat detection by *C. vittiger* could be influenced not only by odor cues from *Opuntia* but also from sex pheromones released by conspecifics within patches. However, the number of conspecifics on target patches was not an important covariate in

the trials. This outcome held when I collapsed the 'conspecifics' variable into a binary one (presence and absence). Furthermore, upwind orientation was as likely during the non-mating season as during the mating season. Additional experiments are necessary to establish whether pheromones and conspecific attraction contribute to patch detection and selection by *C. vittiger*.

What is the perceptual range of cactus bugs? Clearly, the answer depends not only on patch size and matrix structure, but also on where an individual is positioned in relation to the prevailing wind direction. When a patch of suitable habitat is downwind from an individual, its perceptual range must be <50 cm. When a patch is upwind, then its perceptual range would seem to be >100 cm and possibly 30-70 m or more. Again, it is difficult to resolve whether the upwind walking by individuals released in the main arena represented a reaction to *Opuntia* within their perceptual range, upwind search for a chemical plume, or use of wind to maintain a straight course. The key assumption of the technique that I employed to assess perceptual range (Zollner and Lima 1997) was probably met in that cactus bugs likely move toward *Opuntia* if they can detect it. However, they might also move upwind toward *Opuntia* even when they cannot detect it. Hence, this behavioral assay of perceptual range might include 'false positives' for olfactory-based species. Zollner and Lima (1997) did not claim that their technique for assessing habitat detection distances was universally applicable, and it seems to be a practical and informative approach for species in which vision is the dominant sense used in landscape navigation. Nevertheless, it is necessary to caution that the procedure may have serious limitations for olfactory-based species.

Goodwin et al. (1999) suggested that a more insightful approach for testing perceptual range might be to examine movement behavior of individuals at different distances from preferred habitat patches. Perceptual range might be revealed by an increasing tendency for forward movement toward patches, versus more random movement, at a particular distance. However, if highly directional movement is the most efficient search strategy for an animal when suitable habitat is beyond its perceptual range (Lima and Zollner 1999*a*), then it is unclear if any change in movement behavior would be noticeable after the animal perceived the suitable habitat. If a cactus bug were searching upwind (Dusenbery 1990) in a nearly straight path (MVL = 0.90), what sort of detectable change in movement would one expect once *Opuntia* was within its perceptual range?

Despite these potential limitations on measuring habitat detection abilities, it is clear that perceptual range often will be anisotropic for animals that use odor cues to navigate and locate habitat patches. Hence, viewing perceptual range as a 'detection circle' will be inadequate sometimes. Simulation models of movement behavior that have included a parameter similar to perceptual range have typically treated it as an isotropic trait (Cain 1985, Doak et al. 1992, Pulliam et al. 1992, Turner et al. 1994, Gustafson and Gardner 1996, Lima and Zollner 1999*a*, Wiegand 1999). Such models make an assumption, generally unstated, about the primary sensory modality that individuals use to find habitat.

Directional connectivity

Connectivity has been described as the degree that the landscape facilitates or impedes the movement of organisms among patches (Taylor et al. 1993, Tischendorf and Fahrig 2000). Connectivity can be measured either at the patch scale (Moilanen and Hanski 2001) or at the landscape scale (Tischendorf and Fahrig 2001). Measures of connectivity can focus solely on the spatial distribution of suitable habitat (Hanski 1994), or they also can consider how matrix composition affects movements and inter-patch transfers (Chapter 2, Wiens 2001). In all of these approaches, structural connectivity is based on vegetation types and other mappable landscape features. We need to expand our view of connectivity so that it explicitly recognizes the dominant senses that a particular species uses to find habitat patches in fragmented landscapes. For olfactory-based species, the wind direction may contribute substantially to movement behavior, perceptual range, and functional connectivity. These ideas apply to many species beyond just *C. vittiger* because wind-biased movement is not uncommon in other walking and flying insects (e.g., Kalmus 1942, Hawkes 1974, Spencer Johnston 1982, Bell 1984, Nottingham 1988, Visser 1988, Morrow et al. 1989, Wolf and Wehner 2000).

Connectivity between two patches may be asymmetrical if one is upwind of the other. Therefore, the flux of individuals between two patches will not necessarily be balanced. Asymmetrical connectivity between patches has been suggested previously (Gustafson and Gardner 1996, Urban and Keitt 2001), but the envisioned asymmetry was related to landscape features such as patch sizes and matrix structure. I am suggesting that there could be a directional flow of dispersers between two patches with similar areas, habitat

qualities, and surrounding matrices. Such directional connectivity may be more appreciated for aquatic systems in which animal movement can be biased either downstream or upstream (Allan 1995, Wiens 2002), but it may also be common in terrestrial systems where wind replaces water as the directing force. Of course, directional connectivity is also relevant to plants and animals with passive dispersal that is controlled by wind (Bullock and Clarke 2000, Nathan et al. 2001, Cáceres and Soluk 2002).

Patch connectivity has generally been viewed as static across time scales in which vegetation structure does not substantially change. Connectivity may be dynamic on fairly short time scales, however, if prevailing winds shift direction in systems with wind-biased dispersal. The asymmetrical flux of organisms between two patches could even reverse direction over time.

If the direction of prevailing winds shifts often and to all directions, then the effects of wind on movements should even out and traditional measures of connectivity should suffice. I suspect that often there will be a restricted range of prevailing wind directions during the dispersal period for a particular species, and thus directional connectivity measures might be useful. Existing approaches for quantifying patch connectivity could be modified to include wind direction. For instance, in some connectivity metrics the Euclidian distance between two patches is replaced by an effective distance, which is a distance weighted by the structure of the matrix (Chapter 2, Moilanen and Hanski 1998, Petit and Burel 1998, Hokit et al. 1999). Hence, the effective distance accounts for the relative movement resistances of different matrix elements. A similar weighting could be added for directionality. For *C. vittiger*, the 'resistance' from a focal patch to an upwind

patch would be low relative to a downwind patch. A comparable weighting scheme could be applied to a graph-theoretic measure of connectivity (Urban and Keitt 2001).

Conclusions

Humans are a visually oriented species and this tends to bias how we regard other animals. We need to recognize the dominant senses of other species if we are to approach spatial ecology from an organism-based perspective. If a measure of connectivity does not perform well, then constructing a better vegetation map might not be the next best step. Instead, one might need to consider the natural history of the study species, especially how it navigates around its patchy environment. This advice applies to my own work (Chapter 2) as well as to that of others. Broadening our view of perceptual range and connectivity points to the need for more collaboration between spatial ecologists and sensory ecologists. These groups tend to work on different questions and at dissimilar spatial scales, but a shared interest in the mechanisms of animal movement should provide some firm, common ground.

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Table 3.1. Directionality of pathways of *C. vittiger* at different distances from patches of suitable habitat (*Opuntia*). The mean vector length varies from 0 to 1 (perfectly directional). Sample sizes (*n*) are for numbers of individuals.

				Mean vector length	
Distance from suitable habitat (m)	Matrix height	*n*	No. steps	$\bar{x}$	95% CI
30-70	Low	20	50	0.88	0.86-0.90
>100	Low	14	5-14	0.93	0.90-0.96
>100	High	14	6-38	0.85	0.80-0.91
>3000	Low	5	11-16	0.92	0.83-1.00

Table 3.2. Summary of AIC_c selection of general linear models for the orientation of *C. vittiger* toward the closest *Opuntia* patch. The response variable was angular distance. The listed models are a 90% confidence set on the best model. Each model summary includes the number of estimable parameters (K), the log-likelihood, $\Delta_i = AIC_{ci} - \text{minimum } AIC_c$, and Akaike weights ($w_i$).

			AIC_c	
Model[a]	K	Log-likelihood	Δ_i	w_i
Direction, Matrix, Area	5	-488.96	0.00	0.358
Direction, Matrix	4	-490.97	1.77	0.148
Direction, Matrix, Area, Speed	6	-488.77	1.90	0.138
Direction, Matrix, Area, Distance	6	-488.89	2.13	0.123
Direction, Area	4	-492.11	4.06	0.047
Direction, Matrix, Area, Speed, Distance	7	-488.73	4.17	0.044
Direction	3	-493.33	4.31	0.041

[a]The explanatory variables are the release direction relative to prevailing winds (Direction), vegetation height of the matrix (Matrix), patch area (Area), windspeed (Speed), and distance of the target patch from the release (Distance).

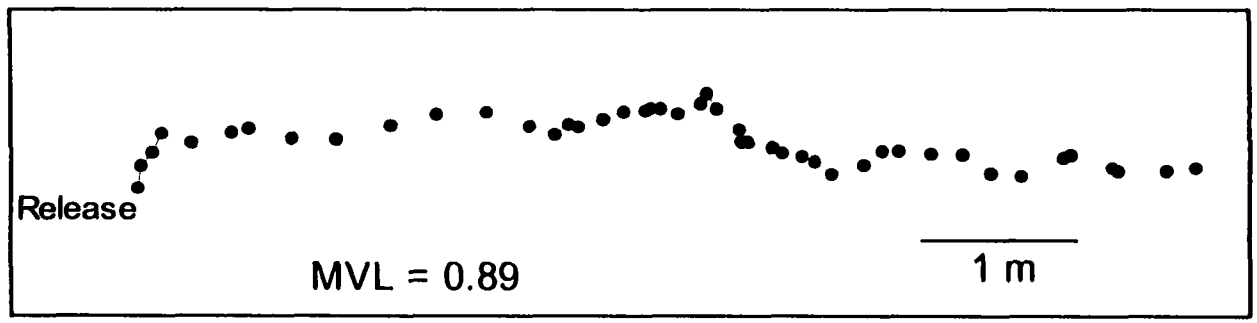

Figure 3.1. Typical pathway of a cactus bug moving though matrix habitat. Each closed circle represents the individual's location at 1-min time steps. The total duration of the path was 50 min.

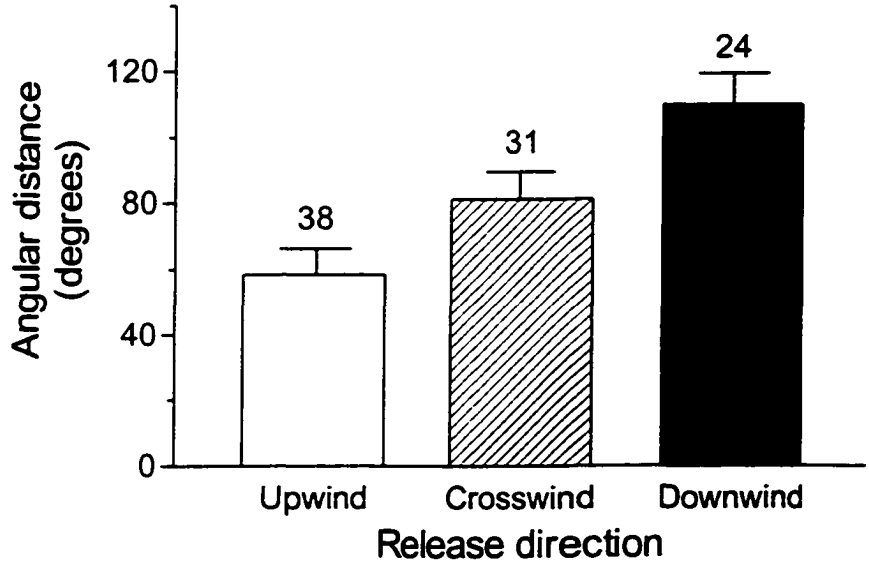

Figure 3.2 Effect of release direction on the ability of individuals to orientate toward the closest patch of suitable habitat. Bars are least squares means (+ 1 SE). Sample sizes are given above the bars.

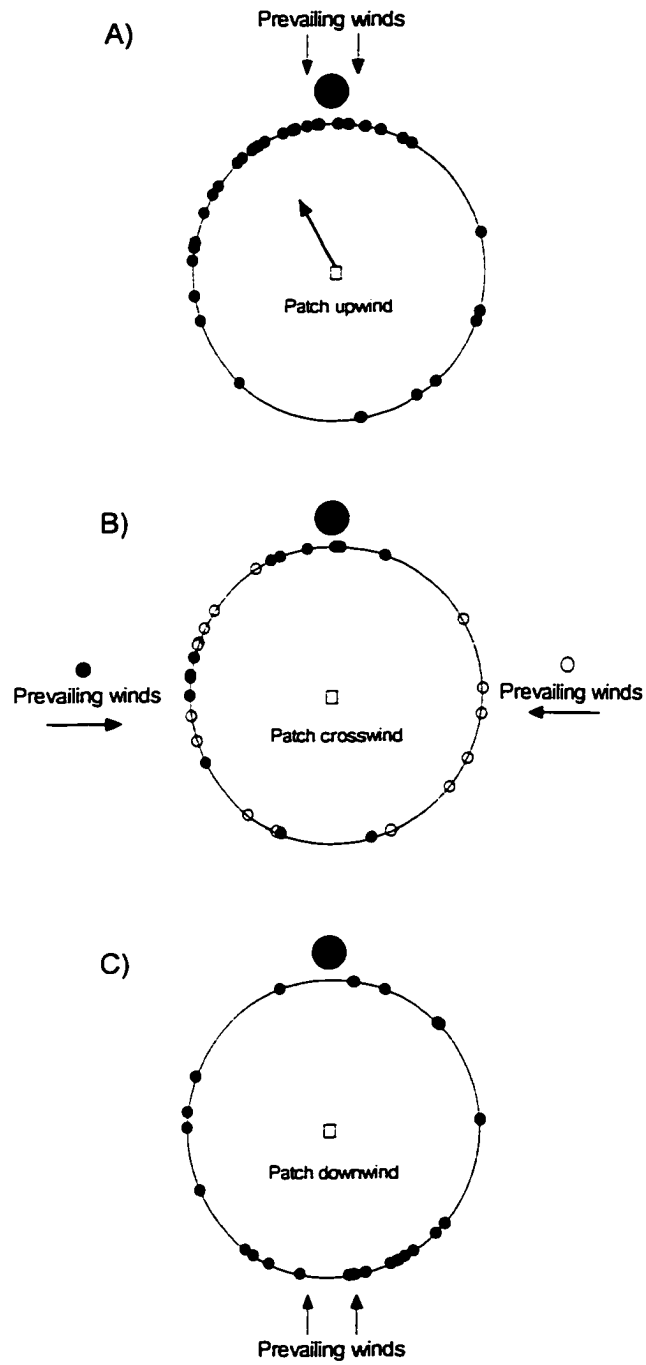

Figure 3.3. Scatter diagrams of initial orientations of *C. vittiger* released either 50 or 100 cm from a patch of *Opuntia*. The closest patch (●) was either upwind (A), crosswind (B), or downwind (C) from the release point (□). Each small circle indicates the angle for a single individual. For the crosswind releases, the wind was either from the left (●) or the right (○) of the release direction. The arrow in (A) points toward the mean angle, and its length indicates the mean vector length.

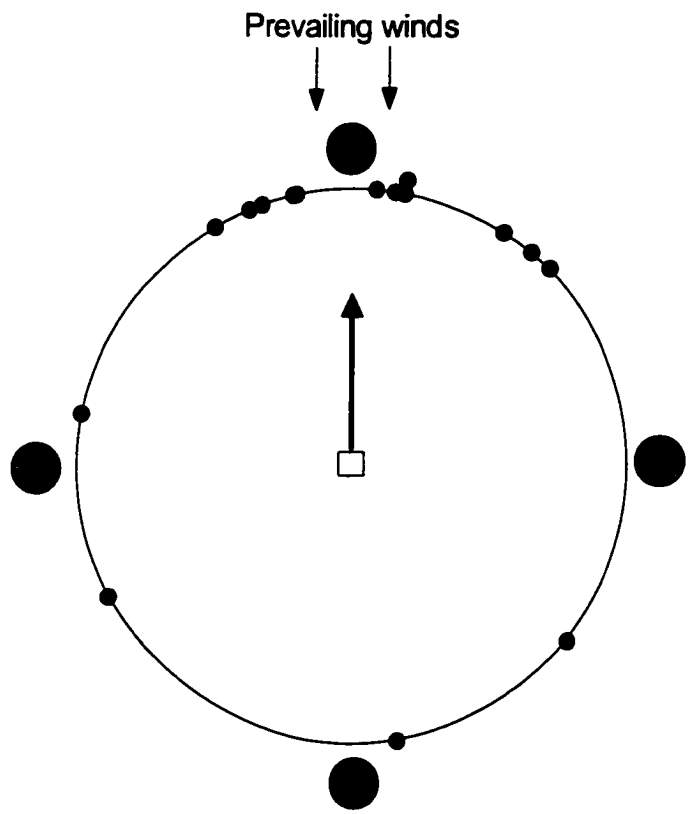

Figure 3.4. Scatter diagram of movement directions of *C. vittiger* during the 'aritificial' patch experiment. The release point (□) was 1 m away from four *Opuntia* patches (●). The small black circles are the angles of movement after 50 cm. The arrow points toward the mean angle, and its length indicates the mean vector length.

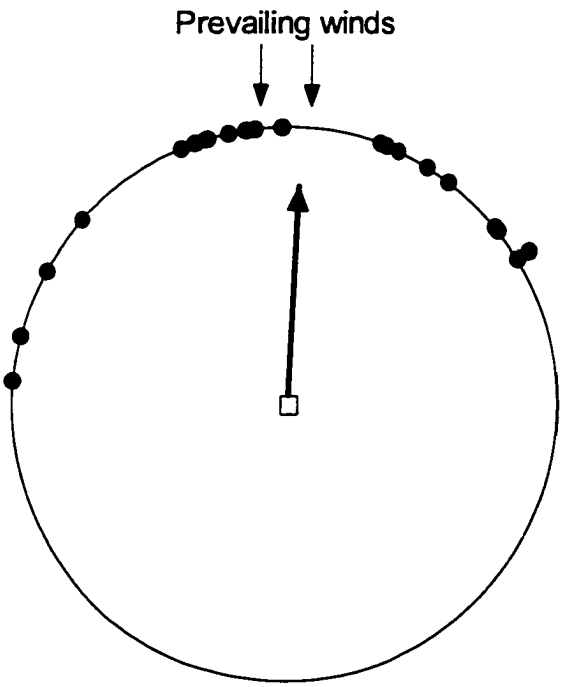

Figure 3.5. Scatter diagram of the overall direction of movement pathways of *C. vittiger* released outside of a patch network. Each black circle indicates the angle of a path relative to the wind direction. The arrow points toward the mean angle, and its length indicates the mean vector length.

Appendix 3.1

In the habitat detection study within a natural patch network (Chapter 3), I released individual *C. vittiger* into the matrix and evaluated whether they oriented toward the closest *Opuntia* patch in different situations. During the mating season, the target patches were either the patches where individuals had been captured or different ones. Here, I evaluate whether the type of target patch (capture, non-capture) influences the orientation behavior of *C. vittiger*. With the data from the mating season (n = 75), I compared the performance of the best model as previously identified by AIC selection (Direction, Matrix, Patch Area) with a model that included these three explanatory variables plus Patch Type. As before, the response variable was the angular distance and the linear models (Proc GENMOD, SAS Institute 1996) were constructed with normal probability distributions and identity link functions.

There was no support for including Patch Type. The best model and the best model plus Patch Type had identical log likelihoods (-391.55) and both explained the same amount of variance (R^2 = 27.6%). The Δ_i based on AIC_c was 0 for the best model and 2.35 for the best model plus Patch Type. Moreover, the least squares means from the model with Patch Type were no different for capture patches (84.54, SE = 6.19) and non-capture patches (83.16, SE = 9.97). Therefore, I conclude that any familiarity of surroundings that *C. vittiger* might have gained prior to capture did not affect subsequent orientation behavior under the conditions of my trials.

CHAPTER IV

GRAIN SIZE, SPATIAL AUTOCORRELATION, AND ANIMAL-HABITAT RELATIONSHIPS

Introduction

Our perception of how organisms interact with their habitat and with other organisms depends on spatial scale (Addicott et al. 1987, Wiens et al. 1987, Wiens 1989, Levin 1992, Caselle et al. 1996, Dale 1999, Fauchald et al. 2000). Spatial scale can be viewed in terms of extent and grain (Wiens 1989). Extent is the overall area covered by a study and it sets the upper bound to generalizations. Grain is the size of the sampling units and it sets the lower limit on the scale of detectable patterns. The variability that we view in spatial data results from how our scale of measurement filters 'reality' (Atkinson and Tate 2000). As grain size increases, more of the variance of a system is averaged within sampling grains, whereas between-grain variance should decrease (Wiens 1989).

One approach for examining the association between organisms and their environment is to conduct a multi-scale correlation analysis in which grain size is progressively changed by aggregating data from the smallest sampling grain to form larger grain sizes. For example, this procedure has been used to investigate the effects of scale on the correlation between the distributions of two tree species (Veblen 1979), vegetation

biomass and topography (Bian and Walsh 1993, Long 1998), beetle species richness and vegetation cover (Hoffman and Wiens *in press*), and bird species richness and a suite of environmental variables (van Rensburg et al. 2002). In these studies, the strength of the correlation often increases with increasing grain size and then sometimes levels off or decreases at the largest grain sizes.

Ecological data often exhibit spatial autocorrelation in which the values of a variable at pairs of locations at some distance apart are either more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for spatially random pairs (Legendre 1993). When ignored, positive spatial autocorrelation poses serious problems for traditional statistical tests such as bivariate correlations and multiple regression analyses (Legendre and Fortin 1989, Legendre 1993, Thomson et al. 1996, Long 1998, Lennon 2000). For bivariate correlations using a Pearson correlation coefficient, when both variables include some positive autocorrelation, then the magnitude of the correlation coefficient is inflated (relative to expectations for zero autocorrelation) with increasing autocorrelation (Lennon 2000). For regression models with some autocorrelation in the response variable, the explanatory variables with positive autocorrelation are most likely to be found significant (Lennon 2000). Moreover, an increase in autocorrelation in the response variable results in an increase in the R^2 value for a model (Lennon 2000). A rise in the R^2 value also can be due to the action of an unmeasured, spatially structured variable that affects the response variable. The inflation of the R^2 value results from an underestimation of the mean square error (Long 1998). In sum, when the key assumption of traditional regression models is violated by having spatially correlated errors, then measures of model fit become suspect.

How does this problem relate to grain size and organism-environment relationships? If the degree of autocorrelation changes with grain size, then making comparisons of measures such as R^2 values becomes difficult. A peak in the R^2 value at a particular grain size might indicate a certain scale at which an organism is responding most strongly to the heterogeneity of its environment, or conversely it might simply represent a grain size where autocorrelation is greatest and inflation of the R^2 value is most severe. In fact, previous research demonstrates that the intensity of spatial autocorrelation for a single variable can change with grain size, although the expected direction of the change remains unclear (Qi and Wu 1996, Fortin 1999).

Here, I examine how the perceived relationship between an insect species and its suitable habitat changes with the spatial grain of measurement. The system includes cactus bugs (*Chelinidea vittiger*), which are habitat specialists, and their host plant, plains prickly pear cactus (*Opuntia polyacantha*). I focus on how the amount of explained variance from regression models *and* the degree of spatial autocorrelation in model errors change with grain size.

Methods

Study site and species

The study was conducted at the Central Plains Experimental Range (CPER) in north-central Colorado ($40^0$49'N, $104^0$46'W), 61 km northeast of Fort Collins, at 1650 m elevation. The climate of the CPER is semiarid, with an average of 321 mm of annual precipitation (Lauenroth and Sala 1992). The CPER is located within the short-grass

steppe and its vegetation is dominated by two bunchgrass species, *Bouteloua gracilis* and *Buchlöe dactyloides* (Lauenroth and Milchunas 1991). Other plant species present included *Aristida longiseta*, *Artemisia frigida*, and *Eriogonum effusum*. Suitable habitat for *C. vittiger* consisted only of *O. polyacantha*, which is a low-growing platyopuntia. Cover of *O. polyacantha* is 1 – 5% on shortgrass steppe (Hart and Ashby 1998) but this succulent may contribute 14 – 56% of the above-ground biomass (Sims et al. 1978).

Adult *C. vittiger* feed on mature pads of *Opuntia*, whereas nymphs are more likely to feed on immature pads and fruits (De Vol and Goeden 1973). During the mating season (mainly April to mid June) ovipositing females attach eggs to the underneath of *Opuntia* spines or to other nearby vegetation (Mann 1969). *C. vittiger* develops through five nymphal stages. New adults are active for several months during the fall but do not mate then. Cactus bugs overwinter in the adult stage (Mann 1969, De Vol and Goeden 1973). Adult *C. vittiger* typically walk between host-plant patches (Hamlin 1924, Dodd 1940, Mann 1969, De Vol and Goeden 1973). Most movement occurs during the mating season when the median displacement rates are only 1-2.5 m/day in naturally fragmented landscapes (Chapter 2).

I focus here on the spatial patterns of abundance of non-mating adults. The distribution of this life stage reflects habitat selection by ovipositing females, survival through the egg and five nymphal stages, and short movements. In a study of the incidence and abundance of *C. vittiger* in patchy landscapes (Chapter 2), non-mating adults had the strongest association with *Opuntia* among the three life stages examined.

Field sampling

I established a 700-m^2 (700 x 1 m) transect across an area in which topography was variable. The transect included uplands, north- and south-facing slopes, a swale, and a yucca (*Yucca glauca*) ridge (Fig. 4.1). The variability in the patchiness of *Opuntia* in the area was highest in the direction of the transect. Given the low movement rates of *C. vittiger*, 700 m represents a fairly large spatial extent for these insects. From 20-26 October 1999, I sampled *Opuntia* and *C. vittiger* with 1,400 contiguous quadrats (Figure 4.1). Each quadrat was 0.5 m^2 (0.5 x 1 m with the wider side positioned perpendicular to the transect). Therefore, 0.5 m^2 represented my smallest grain of observation. Each quadrat was partitioned into eight sub-quadrats (0.25 x 0.25 m each). I measured the frequency of *Opuntia* within each quadrat by recording the number of sub-quadrats that included *Opuntia* (0-8). For all quadrats with some *Opuntia*, I searched the quadrat and counted the number of *C. vittiger*. I did not search for *C. vittiger* in quadrats without *Opuntia* because non-mating adults spend little time in the matrix between cactus patches (Chapter 2). Sampling was conducted between 1125 and 1555 when soil surface temperatures ranged from 26.1 – 33.3 °C.

Statistical Analysis

I summed the data on the frequency of *Opuntia* and the abundance of *C. vittiger* from the 0.5-m^2 quadrats to form data sets for nine larger grain sizes (1, 2, 4, 6, 8, 12, 16, 24, and 32 m^2). I combined quadrats starting from the 0.5-m end of the transect (i.e., moving

left to right on Fig. 4.1). In this approach, any within-grain heterogeneity is ignored and the focus is on a single measure for cactus frequency and bug abundance for any given quadrat. Sampling frames that had no *Opuntia* (after data aggregation) were considered 'structural zeros' and removed prior to analyses so that they would not influence measures of association. For example, the sample size for the 1-m^2 grain size was 377, and not 700, because 46% of the quadrats had no *Opuntia* at that scale of measurement (Table 4.1). Therefore, the analysis was designed to evaluate the association was between *C. vittiger* and *Opuntia* given that there was some suitable habitat present. This approach seemed reasonable for assessing the connection between a habitat specialist and its host plant. For other situations, the retention of quadrats with zero values for the independent and the dependent variable would be valid and sensible.

One general approach for evaluating the relationships among a response variable, environmental variables, and space follows a three-step process (Bailey and Gatrell 1995). First, a non-spatial regression model is fit and then the residuals are examined for spatial dependence. Second, large-scale spatial variations (first-order effects) can be modeled by including terms involving the spatial coordinates of samples into the regression model. For data sampled in two dimensions, often a polynomial function of spatial coordinates is used in this sort of trend surface analysis (Legendre 1993, Bailey and Gatrell 1995, van Rensburg et al. 2002). Third, if the residuals from the regression model still display finer-scale spatial autocorrelation (second-order effects), then a regression model that assumes spatially correlated errors can be developed (Bailey and Gatrell 1995). One approach is to model the spatial dependence of residuals with a

semivariogram and then to incorporate the resultant correlation structure into the regression model (Bailey and Gatrell 1995, Gotway and Stroup 1997).

I developed a non-spatial regression model for the relationship between the abundance of *C. vittiger* and the frequency of *Opuntia* separately for each of the 10 grain sizes. Instead of ordinary least-squares regression, I used quantile regression (Scharf et al. 1998, Cade et al. 1999) to model the association because my previous work strongly supported the notion that *C. vittiger* and *Opuntia* exhibit a limiting-factor relationship (Chapter 2). That is, the amount of *Opuntia* sets an upper constraint on the abundance of *C. vittiger*. A limiting-factor relationship between two variables (Figure 4.2) results in a bivariate scattergram that exhibits a wedge-shaped pattern of variation (Cade et al. 1999, Chapter 2). The variation below the upper constraint is due to the influence of other variables that can pull data points below the upper bound (Thomson et al. 1996). Quantile regression is based on least absolute deviation (LAD) regression, which models the conditional median (50^{th} quantile) so that ca. 50% of the observations are above (and below) the estimated regression line. This approach can be extended to any quantile, and I modeled the upper constraint line as the 95^{th} regression quantile. LAD regression models are fit by minimizing the sum of the absolute values of the residuals and not the sum of the squares of the residuals, which is characteristic of least squares regression (Scharf et al. 1998, Cade et al. 1999). Likewise, quantile regression models minimize the sum of weighted absolute deviations, where the weights equal the quantile (e.g., 0.95) for positive residuals and 1 minus the quantile for zero and negative residuals. Estimates of regression quantiles are insensitive to extreme values of the dependent variable (outliers) because the fit is unaffected by changes in magnitude of the values as long as the values

remain above or below the estimated regression quantile (Cade et al. 1999). Errors are assumed to be independent and identically distributed in quantile regression models (Cade et al. 1999).

For quantile regression models, I followed Koenker and Machado (1999) and calculated a coefficient of determination (R) as 1 – (sum of the weighted absolute deviations of the model of interest / sum of the weighted absolute deviations of the intercept-only model). To convert R to units of measure comparable to R^2 based on squared units of measure, I report R^2 for quantile regressions as $1 - (1 - R)^2$ (McKean and Sievers 1987). All quantile regression analyses were conducted with BLOSSOM Statistical Software (Cade and Richards 1999).

I examined the residuals from the non-spatial regression models for spatial dependency using a correlogram based on Moran's *I* statistic using GS$^+$ software (Robertson 2000). Moran's *I* is a measure of autocorrelation that generally ranges from –1 (negative correlation) to 1 (positive correlation) and is near 0 ($E(I) = -(n-1)^{-1}$) for spatially uncorrelated data (Legendre and Fortin 1989, Rossi 1996, Fortin 1999, Robertson 2000). A correlogram is a graph of the Moran's *I* values against lag distances (i.e., distances among sampling locations).

Next, I constructed a 95th quantile regression model for each grain size that included the frequency of *Opuntia* as an explanatory variable plus the spatial location of the quadrat along the transect. This type of model accounts for any linear trends in *C. vittiger* abundances (first-order effects). After fitting these models, there was still usually spatial dependency in the residuals. I also tried incorporating a more complex trend surface using a cubic polynomial (position + position^2 + position^3 after centering the

position variable by subtracting its mean to reduce collinearity), but this adjustment tended to increase the degree of spatial autocorrelation in the residuals.

The next logical step would have been to construct regression models that explicitly incorporated the spatial dependencies in the residuals (Bailey and Gatrell 1995). Unfortunately, methods for constructing quantile regression models with spatially correlated errors have not been established and evaluated (B. Cade, pers. comm.). Instead, I constructed a third set of models that included *Opuntia* frequency, transect position, and their interaction (*Opuntia**position). This sort of approach has been effective in simulations in which the data were generated to include spatial structuring in an unmeasured process that interacted with the measured habitat variable (B. Cade, pers. comm.). Spatial position serves as a surrogate for some of the information associated with the unmeasured factor. Again, I evaluated the residuals from these fitted models for spatial dependency using correlograms.

Results

A total of 221 individuals of *C. vittiger* was counted on the 700-m^2 transect. These habitat specialist insects do not occur at high crude densities (not constrained to suitable habitat). The density of non-mating adults from this study (0.32 individuals/m^2) is similar to densities on two 0.5-ha plots (0.26-0.38 individuals/m^2) from another study in the same area (Chapter 2). Coefficients of variation for *Opuntia* frequency were small (recall that quadrats with no *Opuntia* were removed from analyses) and insensitive to changes in grain size (Table 4.1). In contrast, coefficients of variation for *C. vittiger* abundance decreased with grain size (Table 4.1).

The amount of variation explained by the 95th quantile regression models depended on the grain size of measurement (Fig. 4.3). The general pattern of R^2 values versus grain size was consistent for the three types of models as it mainly increased from 0.5 m^2 to 12 m^2 and then decreased at 16 m^2 and 32 m^2. The models that included *Opuntia* and transect position had only minor increases in R^2 values relative to the base habitat models that included only *Opuntia* (Fig. 4.3). These results indicate that there was no strong linear trend in the abundances of *C. vittiger* along the transect for any grain size. In contrast, the models that included the interaction term (*Opuntia**position) substantially improved R^2 values, especially for moderate and large grain sizes (Fig. 4.3). A model selection approach based on Akaike Information Criterion (Burnham and Anderson 1998), which considers not only model fit but also the number of model parameters, also identified the interaction model with the habitat*space term as clearly being the best model for all but the 0.5-m^2 grain (Appendix 4.1).

Recall that the main reason for constructing the habitat*space interaction model was to account for some of the spatial correlation of errors so that estimated R^2 values would not be inflated upwards. In general, the interaction model decreased the intensity of spatial correlation in model residuals relative to the base habitat model. For example, for the 24-m^2 grain the Moran's *I* value for the first lag was decreased from 0.63 to 0.37 and the overall correlogram of residuals was flattened (Fig. 4.4). However, there was still significant positive spatial dependence in errors at short lag distances even with the interaction model. As an index to spatial autocorrelation in the errors for different models and grain sizes, I used the Moran's *I* coefficient for the first lag distance (Qi and Wu 1996) because the strongest correlations occurred at this lag (as in Fig. 4.4), and

positive spatial autocorrelation at short lags has the most obvious effect on the inflation of R^2 values. The degree of spatial dependency in the errors changed with grain size (Fig. 4.5). Most importantly, the pattern of correlation intensity across grain sizes (Fig. 4.5) closely mirrored that observed for R^2 values (Fig. 4.3). A naive interpretation of Fig. 4.3 might lead one to conclude that the association between cactus bugs and *Opuntia* increases with grain size until 12-m^2 and then peaks again at 24-m^2. However, this pattern of association and scale almost certainly reflects, in part, the concurrent change in the degree of spatial dependency in errors and its potential to inflate R^2 values. The problem of spatially correlated errors is scale-dependent.

Discussion

The general increase in the amount of explained variance with increasing grain size, at least to a point, for my models of *C. vittiger* abundance is consistent with other 'multi-grain' correlation studies (Veblen 1979, Bian and Walsh 1993, Long 1998, Hoffman and Wiens i*n press*). It is difficult to determine whether my observed pattern represents an ecological response of cactus bugs to the patchiness of their host plant, however, because of the simultaneous change in the pattern of spatial autocorrelation in model errors with changing grain size. At certain scales, I simply may be capturing more of the spatial structure of an unmeasured environmental variable that also influences abundances of *C. vittiger*. For instance, I only measured the frequency of *Opuntia* and various aspects of host-plant quality might vary with soil type and topography in a spatially dependent way. Likewise, any aggregation behavior of *C. vittiger* (perhaps during egg-laying) that was

independent of the mapped *Opuntia* template could create spatially correlated residuals in the habitat models. However, I would expect that such movement behavior would result in unexplained patchiness at finer scales than the observed spatial autocorrelation that occurred over ≥48 m (Fig. 4.4).

I am unaware of other studies that have simultaneously measured changes in correlation coefficients or R^2 values and changes in the intensity of autocorrelation of regression errors across a range of grain sizes. However, Fortin (1999) concluded that correlograms of individual variables (woody plant abundances) based on Moran's *I* statistic had a consistent shape across grain sizes, but that the magnitude of autocorrelation increased with grain size until it reached a plateau. Her results for raw data are fairly consistent with mine for regression model errors. The tendency for Pearson correlation coefficients (Veblen 1979, Bian and Walsh 1993, Long 1998, Hoffman and Wiens *in press*) and Moran's *I* values to increase with grain size (and then perhaps level off) may reflect that these statistics share a common structure (Legendre and Fortin 1989). Both statistics include a covariance term in the numerator and a variance term in the denominator. As Long (1998) suggested for the Pearson correlation coefficient, if the covariance remains relatively stable but the variance term decreases as data are aggregated into larger grain sizes, then the correlation coefficient will increase with grain size. However, Qi and Wu (1996) concluded that the Moran's *I* statistic decreased with increasing grain size for their data sets on topography and biomass. Clearly, continued exploration of the behavior of spatial autocorrelation and grain size is warranted.

The problem of spatial structure and correlation analysis is most obvious for transects or grids in which sampling is conducted within contiguous cells. It can occur in any situation, however, where the sampling locations are within the range of spatial dependency. For example, a common type of landscape ecology study involves using buffers around sampling points or patches to examine how landscape context affects species presence and abundance. A reasonable approach is to try using buffers of different sizes to determine if there is a particular spatial scale where the measured explanatory variables have the strongest relationship with the response variable. With this design, the extent of the study typically remains fixed but the spatial grain size is altered. One needs to be careful in comparing correlations among buffer (grain) sizes to be sure that the selection of the 'best' buffer size is based on the intended criteria and not on the unintended inclusion of excessive spatial autocorrelation.

Thomson et al. (1996) identified two main issues regarding correlational studies. First, many ecological variables exhibit limiting-factor relationships but classical statistical procedures do not adequately deal with such situations. Second, the spatial structure of data is often ignored and this results in spuriously high correlations. Quantile regression has been shown to be a useful approach for estimating upper boundary relationships (Scharf et al. 1998, Cade et al. 1999, Chapter 2), and linear regression models that incorporate spatial correlation (e.g., Hobert et al. 1997, Gotway and Stroup 1997) partially address the second issue. However, there remains a need for approaches explicitly designed for limiting-factor relationships that also involve spatially correlated data. I suspect that this scenario is far from rare in ecological studies.

In sum, attempting to understand how organism-environment relationships change with spatial scale should continue to be a key pursuit in ecology. Interpreting the effects of changing grain size on associations needs to be done carefully. The goal is to identify particular scales where the pattern is the strongest in the hope that this will tell us something about the likely underlying processes. However, the observed results could also reflect the degree of unaccounted for spatial autocorrelation at different scales. When spatial grain filters 'reality' (Atkinson and Tate 2000), it filters both the measured and unmeasured components.

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Table 4.1. Summary statistics for the frequency of *Opuntia* and the abundance of *C. vittiger* measured at different grain sizes along a transect (700 x 1 m). For each grain size, quadrats without any *Opuntia* were removed.

Grain size (m^2)	*n*	Frequency of *Opuntia*			No. of *C. vittiger*		
		Mean	SD	CV(%)	Mean	SD	CV(%)
0.5	614	2.84	1.69	59.5	0.36	1.16	322.2
1	377	4.63	2.89	62.4	0.59	1.57	266.1
2	227	7.70	4.90	63.6	0.97	2.23	229.9
4	131	13.34	8.41	63.2	1.69	2.93	173.4
6	91	19.02	12.38	65.2	2.42	3.75	155.0
8	71	24.38	15.92	65.2	3.10	4.62	149.0
12	48	36.06	22.49	62.3	4.58	6.37	139.1
16	38	45.08	29.79	66.1	5.79	6.23	107.6
24	25	69.24	42.63	61.6	8.80	8.91	101.3
32	19	87.79	57.20	65.2	11.37	10.44	91.8

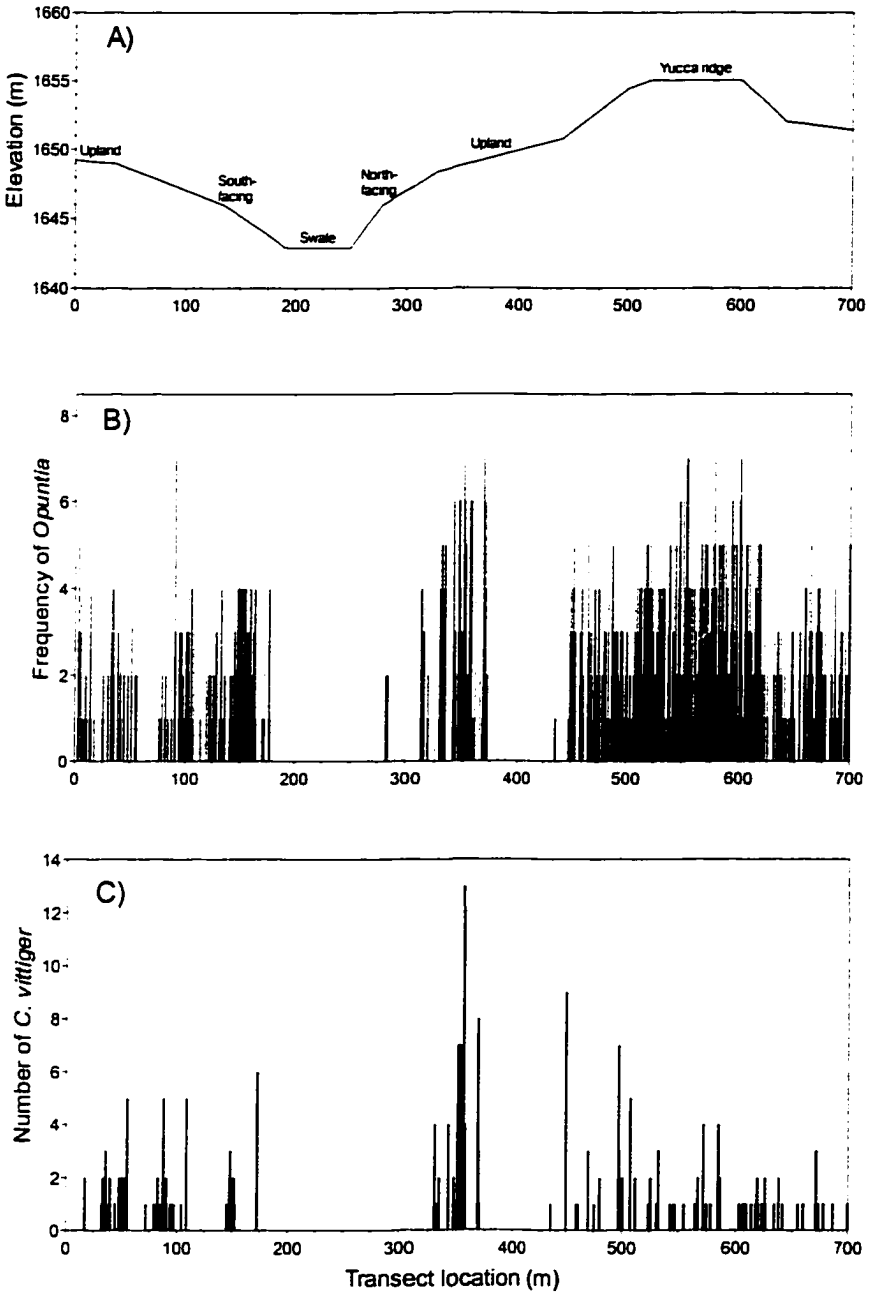

Figure 4.1. (A) Topographic profile of transect. (B) Distribution and frequency of prickly-pear cactus. (C) Distribution and abundance of cactus bugs. The sampling grain for B and C is 0.5 m^2.

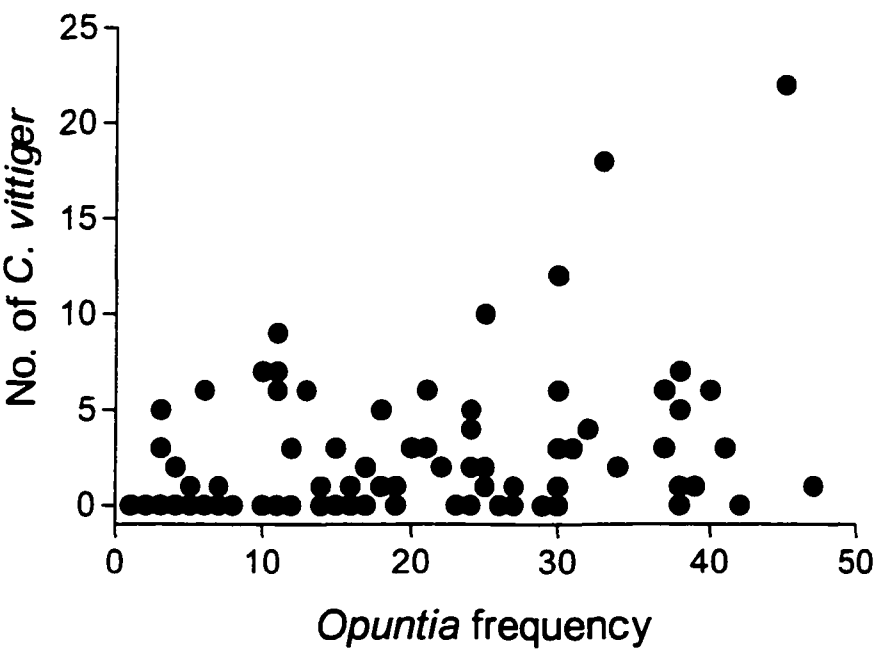

Figure. 4.2. Example of the wedge-shaped pattern of variation between the frequency of prickly-pear cactus and the abundance of cactus bugs. This sort of bivariate scattergram indicates a limiting-factor relationship. These data are from a sampling grain of 6-m^2.

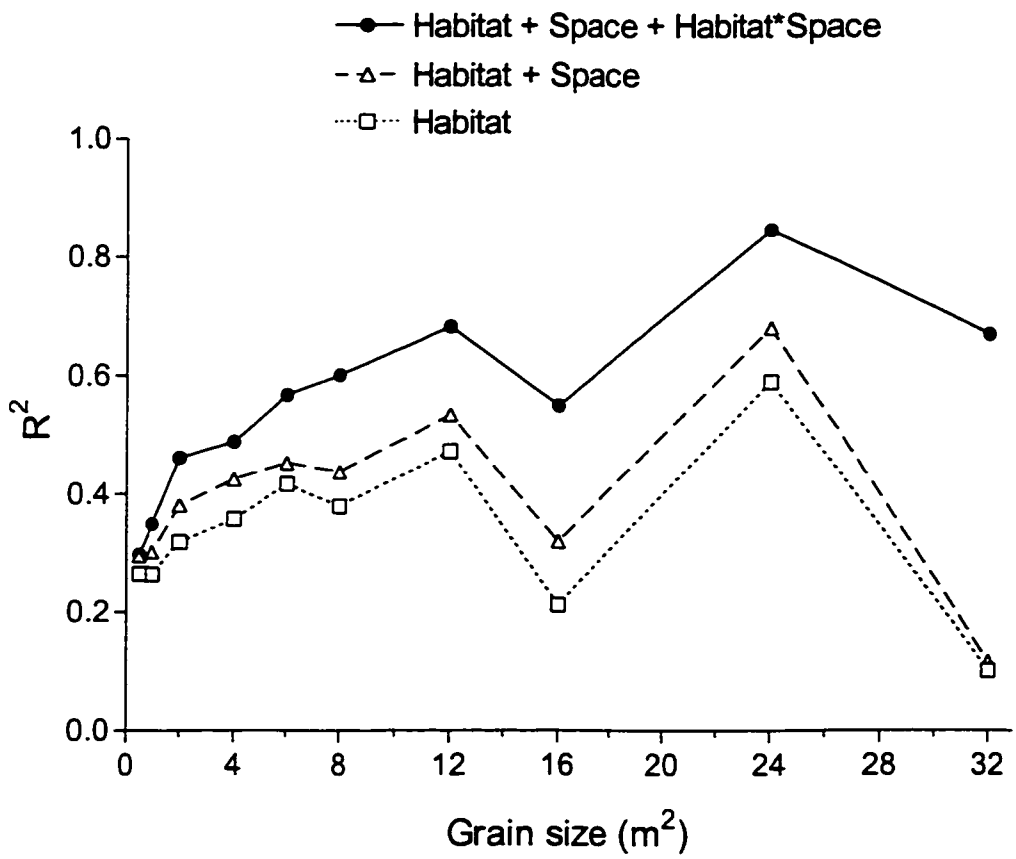

Figure 4.3. Coefficients of determination for three types of 95th quantile regression models of *C. vittiger* abundance. Each model type was evaluated at ten different grain sizes of measurement. 'Habitat' refers to *Opuntia* frequency and 'Space' refers to the spatial location of the sample within the transect.

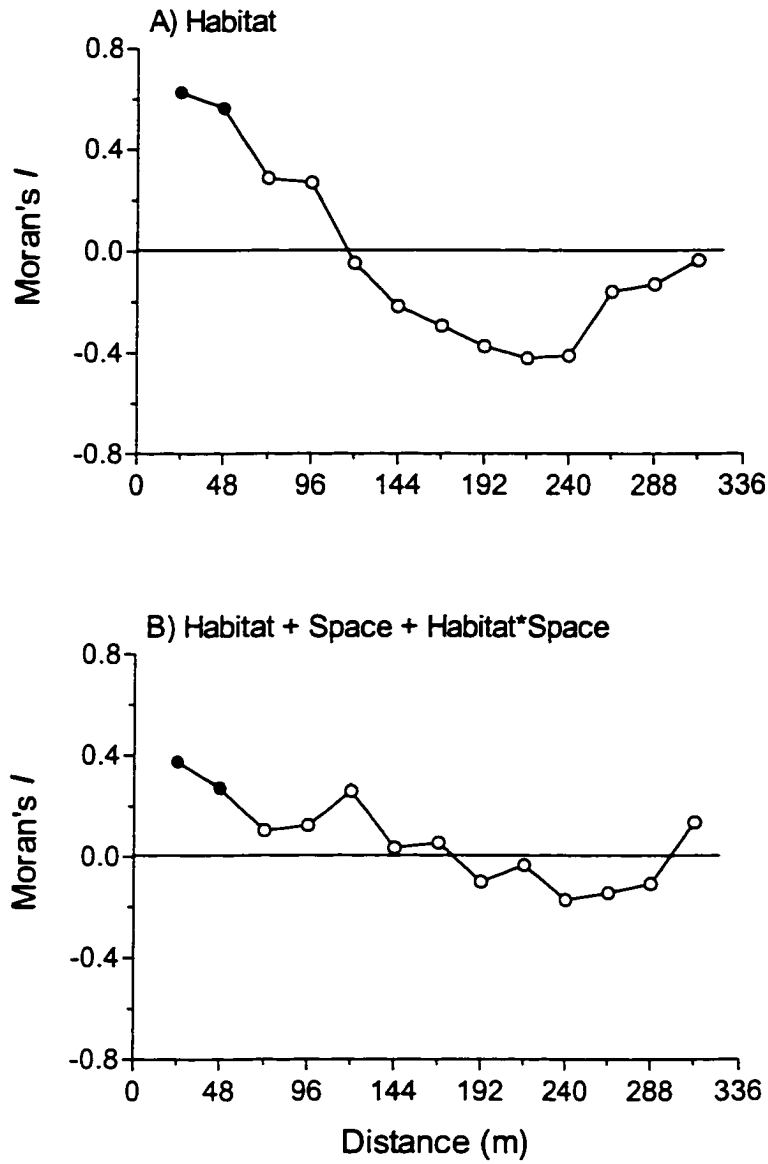

Figure 4.4. Correlograms of the residuals from two 95th quantile regression models of *C. vittiger* abundance. This example is from a grain size of 24 m^2. Filled circles indicate significant values ($P < 0.05$) based on random permutations of the data.

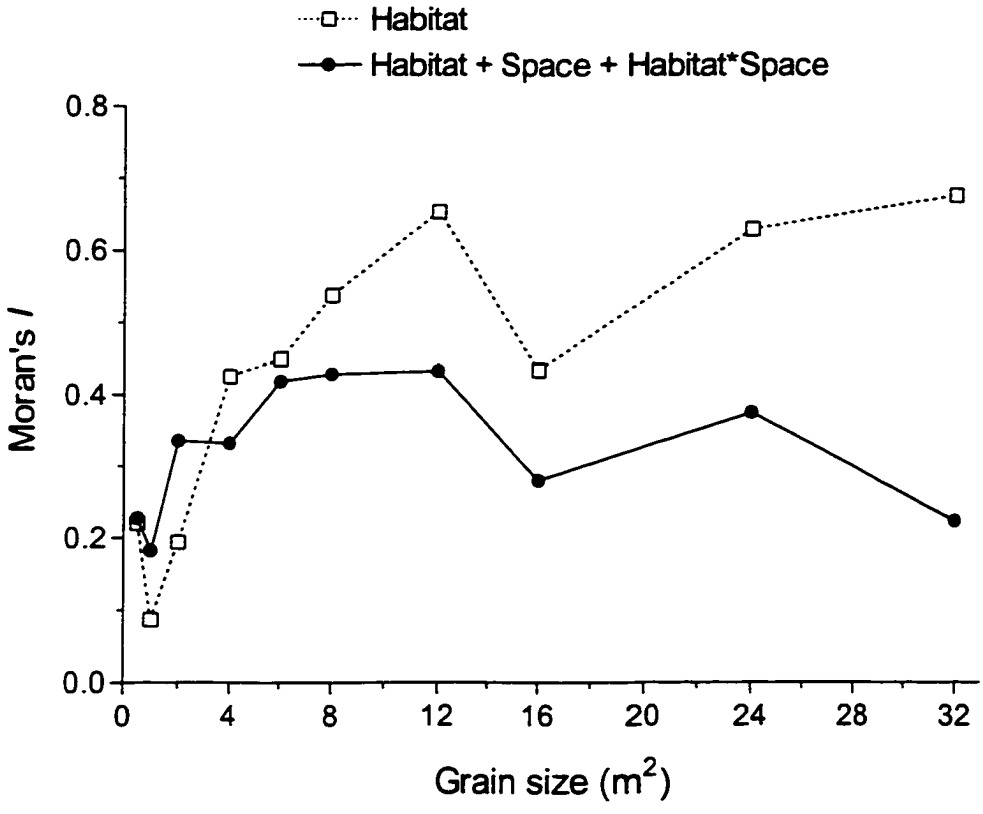

Figure 4.5. Degree of spatial correlation in errors from 95th quantile regression models of *C. vittiger* abundance. Each Moran's *I* value is from the first lag of a correlogram (see Fig. 4.4 for an example).

APPENDIX 4.1

In Chapter 4, I evaluated the relationship between the abundance of *C. vittiger* and the frequency of *Opuntia* along a 700-m^2 transect using ten grain sizes of observation. I compared the amount of variance explained (R^2) by three model types (Habitat, Habitat + Space, Habitat + Space + Habitat*Space) where 'Habitat' was a measure of *Opuntia* frequency and 'Space' was the spatial location along the transect. Here, I also compare these models using an Akaike Information Criterion (AIC) approach, which considers both model fit and the number of model parameters (Burnham and Anderson 1998). I used 95th quantile regression models and calculated an AIC for each model as

$$AIC = n(\log \sigma^2) + 2K$$

where σ is the sum of weighted absolute deviations (Hurvich and Tsai 1990). I then calculated AIC differences and Akaike weights (w_i) for each model (Burnham and Anderson 1998, Chapter 2). Each w_i provides the weight of evidence that model i is the best model. Akaike weights are normalized relative likelihoods that sum to 1 (Burnham and Anderson 1998).

For the 0.5-m grain size, there was similar support for the Habitat + Space model ($w_i = 0.54$) and the Habitat + Space + Habitat*Space model ($w_i = 0.46$) as being the best model. For the other nine larger grain sizes, the best model was clearly the Habitat + Space + Habitat*Space model (all $w_i \geq 0.99$).

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CHAPTER V

FINAL THOUGHTS

I have attempted to include some specific conclusions at the end of each chapter, so I will not reiterate them here. Instead, I will briefly touch on three general viewpoints that I adopted as I conducted my research on *C. vittiger* and its host plant, *Opuntia polyacantha*.

First, in ecology we must continue to struggle with exactly how much complexity must be incorporated into our conceptual view of how organisms interact with landscapes. Historically, we have moved from a simplified view in which space was completely ignored toward a patch-matrix approach in which space is often explicitly considered. This trend toward a spatially explicit ecology has been accompanied by a parallel trend in behavioral minimalism. Too often the behavior of animals is treated in a crude manner, if at all. Such an approach is clearly evident in many simulation models in landscape ecology. For example, dispersal distance is typically considered as a fixed value for a species, individuals are assumed to disperse linearly in random directions, and parameters for perceptual range are isotropic. These sorts of simplifying assumptions certainly make output from models much cleaner, but how often do they generate useful approximations of reality? Likewise, when is a neutral-matrix view of patch connectivity adequate, when is a matrix-matters view required, and when must we consider non-

traditional factors such as wind direction? The key to answering all of these questions is a better understanding of how animals move around landscapes and select habitat patches.

Second, we need to think carefully about when a patch-matrix approach is warranted and when an alternate view of landscapes might be more valuable, such as one that stresses continuous variation and gradients. Clearly, a patch-based approach (Chapter 2, 3) is most justifiable when patches of suitable habitat can be defined fairly easily, such as for habitat specialists like cactus bugs. Even in these situations, the alternative is to not define patches *a priori*, but instead to use sampling and statistical analysis to try to characterize relevant habitat heterogeneity (Chapter 4). My opinion is that the patch-based approach is preferable for habitat specialists *if* patches can be defined from an organism perspective and *if* the landscape texture of the matrix is not ignored (unless it can be demonstrated that a neutral-matrix perspective is defensible). Although one fundamental step in the patch-based approach is to define patches of suitable habitat, we have no 'rules of thumb' in spatial ecology for carrying out this delineation. Too often, patches are defined from remotely sensed data by humans based on our perspective of 'patchiness'.

Third, there has been a recent view in spatial ecology that certain systems may serve as Experimental Model Systems (EMS). Typically, these EMS involve insects and small mammals that operate on small absolute scales compared to larger, less tractable species. I deliberately avoided using the EMS term for my *C. vittiger-Opuntia* system. As for the 'Experimental' part of the term, much of my work was correlative rather than experimental. One key to gaining useful insights is to make sure that the spatial scale of

a study is appropriate for the questions of interest. In my opinion, much of the work with EMS has involved experiments conducted with a spatial extent that was too small for the stated purpose. Few EMS studies have really dealt with systems at a metapopulation scale, for instance, yet inferences regarding metapopulation processes are often stated. Given logistical constraints, I also had to choose between conducting 'landscape experiments' that probably would have been restricted to an extent of ca. 500 m^2, so that there was at least a moderate number of replicates, or conducting correlative studies on two landscapes that each had an extent of 5000 m^2. My point is that systems such as the *C. vittiger-Opuntia* one are perhaps more valuable for conducting correlative studies at appropriate scales than for conducting experiments at inappropriate scales. As for the 'Model' part of EMS, this word suggests too strong of a role for EMS in predicting pattern-processes linkages for other less tractable species. Again, I think that too much behavioral minimalism is needed in this surrogate approach. Nevertheless, systems such as *C. vittiger-Opuntia* are certainly valuable for gaining general insights into how animals respond to landscape structure. These insights should be helpful in our attempts to understand and conserve other species. Hence, I would be more comfortable with applying the phrase 'Correlative Insight System' to cactus bugs, although this clearly does not have the appeal of 'Experimental Model System'.