Social and Vegetative Environments Determine Habitat Use in the Cactus Bug (*Chelinidea vittiger*)

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Habitat selection is fundamental to ecology and evolution because of its broad effects on population dynamics, natural and sexual selection, and rates of speciation. Vegetation structure and ontogeny have been demonstrated as determining factors in the habitat preferences of many populations but have rarely been studied together. Studies of habitat selection are also numerous in avian taxa but rare for other animals such as insects. To address these significant gaps in the literature, we conducted a field study of habitat selection by the Cactus bug *Chelinidea vittiger* aequoris McAtee (Insecta: Hemiptera: Coreidae). We examined the relationship between juvenile and adult distributions (social structure) and the heterogeneity of cactus habitat (vegetation structure). We found evidence of habitat preference in *C. vittiger*, as insects were found more frequently on large patches with tall surrounding vegetation than would be expected by chance. In addition, patch size and the height of surrounding vegetation predicted the social composition of groups present on cactus. These results are important to the study of animal distributions in patchy environments, and more broadly, to the field of habitat selection.

**INTRODUCTION**

A habitat’s *suitability*, or whether an animal can survive and reproduce within it, is often determined by predation pressure and resource availability (Fretwell and Lucas 1969). Populations are typically unevenly distributed, suggesting that not all habitat is equally suitable. One important component of suitability is a habitat’s physical structure, which for many taxa is determined by vegetation (Cody 1981, Spencer et al. 2005, Eifler 2007, Brouwers et al. 2011). Indeed, variation in vegetation structure often explains the patchiness of animal distributions from which we infer habitat use (Wiens 1976). However, individual preference for vegetation structure may vary, generating variation in habitat use.

Social structure may also contribute to variation in habitat use. Life stage is a strong component of social structure, as animals exhibit different resource requirements, behaviors, and morphologies as adults and as juveniles (Werner and Gilliam 1984). With respect to habitat use, distinctions between juveniles and adults have been documented in numerous animal taxa (Eifler 2007, Jeanson and Deneubourg 2007, Roznik et al. 2009). For instance, differences in dispersal ability and predation pressure are strongly associated with distinctions between adult and juvenile distributions in available habitat (Dickman et al. 1991, Brouwers and Newton 2010). Juvenile and adult distributions may determine local densities and patterns of movement across landscapes. Although both vegetation structure and social structure influence habitat use, few studies have investigated how population distributions are affected by both of these factors. Here, we use an insect study system to investigate how habitat use is influenced by both life stage (e.g., social structure) and vegetation (i.e., habitat structure).

**Study Species**

*Chelinidea vittiger* aequoris McAtee (Hemiptera: Coreidae), commonly referred to as the Cactus bug, has a distribution roughly equal to that of *Opuntia* cactus in North America. *Chelinidea vittiger* adults and juveniles feed upon the cladodes of *Opuntia* spp (Mann 1969). Female cactus bugs usually lay their eggs in rows along the undersides of cactus spines. Nymphs are flightless and progress through five instars before reaching adulthood (De Vol and Goeden 1973).

Juvenile and adult *C. vittiger* possess two characteristics that may lead to differences in habitat use. There is no evidence of parental care in cactus bugs, and nymphs and adults differ in their dispersal ability. Adult *C. vittiger* have been used in analyses of movement patterns across patchy landscapes and have been found to travel an average of 7.3 m through cactus habitat when released in an unfamiliar location (Schooley and Wiens 2003). In contrast, juveniles are not expected to travel further than the few patches closest to the location where they hatch (Schooley and Wiens 2004). Cactus grows in discrete patches, which vary in size and density. Patches may be found in open fields or pine forests, with an accompanying range in the height and density of canopy and ground cover. The patchiness of *C. vittiger*’s natural habitat makes this an appropriate system for the study of distributions of individuals across a landscape. The heterogeneity of vegetation structure may cause individuals to be distributed non-randomly. Each patch may also provide a distinct social environment, here
defined as the presence of one or more adults and/or juveniles. The heterogeneity of the cactus landscape, together with differences in mobility between C. vittiger’s discrete life stages suggests that habitat selection may be predicted by juvenile and adult responses to vegetation structure. Due to the limited dispersal ability of nymphs, the author hypothesized that they would be more likely to remain on lower quality food resources than adults. Therefore, we predicted that nymphs would be found on smaller cactus patches than adults. We also hypothesized that nymphs would be more vulnerable to predation than adults, particularly by insect predators, due to their small size, soft exoskeleton, limited mobility, and tendency to remain in large aggregations after eclosion. Thus, we expected to find nymphs in more complex vegetation (with larger grasses surrounding a patch, and a corresponding decrease in canopy cover) than adults, as such vegetation structure could provide more opportunities for escaping and hiding from predators.

METHOD

Transect Point Generation

We conducted field sampling at the Ordway-Swisher Biological Station in Putnam County, Florida from June to August 2011. Before the field season began, we used Geographic Information System (GIS) to generate transect points throughout the biological station. We restricted the transect points to the ruderal habitat areas where prickly pear cactus is found. One hundred points spaced at a minimum of 50m were randomly generated. We deliberately encompassed a large and varied habitat area; as a result, some transects contained no cactus. These points were removed from subsequent sampling.

With another researcher, one of the authors walked two different types of transects with the points we generated: vegetation and insect sampling transects. From vegetation transects, we gathered data on the average abundance of cactus and the nature of surrounding vegetation in ruderal habitat as well as insect presence. From insect sampling transects, we identified features of cactus habitat where we found C. vittiger, as well as number and life stage of all C. vittiger individuals. Vegetation transects were fixed at four points while insect transects were sampled randomly multiple times from the total pool of transect points. Thus, there was little overlap in the two forms of sampling.

Transect Sampling

Transect points were located using a handheld GPS unit, with the GPS coordinates used as the midpoint of transects. Once my research partner and we located a midpoint, one of us flipped a coin twice to designate which of four directions the resulting transect would follow: north-south, northeast-southwest, southwest-northeast, or east-west. We anchored a flag in the ground to secure the two sets of transect tape we used. We then proceeded 25m in two (opposite) directions to walk the 50m distance of the transect. We only checked cactus within 0.5m of the tape as we walked. However, we checked each patch in its entirety, even if it was only partially located within the transect. Any cactus 20cm or further apart was designated as separate patches. We frequently verified our sampling methods with each other to avoid across-observer measurement error.

Insect Sampling Transects

From insect sampling transects, we gathered information on the type of habitat where C. vittiger adults and nymphs occur. We only recorded information on cactus and surrounding vegetation from patches where insects were found along the transect line. To reduce bias in our insect sampling, we selected a different set of transects from the sampling pool each week using a random number function. We placed the transects into eight groups according to areas of ruderal habitat; this allowed us to increase the speed and efficiency of sampling as we completed multiple transects in one area before moving onto the next. Each week, we rotated the first area in which we checked our transects. We checked the remaining areas in ascending order throughout that week. For example, in week one of sampling we checked the areas in the order 1 through 8. The next week, we checked them in the following order: 2, 3, 4, 5, 6, 7, 8, and 1.

If we discovered a C. vittiger nymph or adult on a patch, we recorded several characteristics of that patch. These data included measures of vegetation: the number of reproductive structures (fruit); the height of the tallest vegetation within 50cm of the patch; the presence or absence of canopy cover (cover provided by vegetation exceeding 3m in height); the number of cladodes (cactus pads) in a patch; and a categorical measure (numbered 0–3, according to abundance) of cochineal, a cactus parasite. We recorded insect information such as the instar and number of nymphs and the size, number, and sex of adults.

Vegetation Sampling Transects

From vegetation transects, we collected baseline information on cactus habitat, using the same measures of vegetation as in the insect sampling transects (number of cactus fruit and cladodes, height of surrounding vegetation, amount of cochineal, and presence of canopy cover). We compared this information about general cactus habitat to information on the habitat insects were found in, as provided by the insect sampling transects. From these transects, we also measured change in cactus growth and structure over the field season.

We selected four vegetative transects, one located in each of the four largest areas of ruderal habitat at OSBS. To choose a transect, we used a random number generator to select five points in the area. We explored the potential
transects and chose the first point in each area that had ten or more cactus patches. The majority of cactus habitat at OSBS contains more than ten patches within a 50m transect. We checked vegetation transects every two weeks in rotating order throughout the study period.

Unlike the insect transects, vegetation transects were fixed at the same points and walked in the same cardinal direction throughout the field season. To ensure accuracy, we flagged and numbered each cactus patch within the four transects at the start of the field season. During sampling, we recorded vegetation data for every cactus patch located within a transect, regardless of insect presence.

**Data Analysis**

We explored the relationships between *C. vittiger* adult and nymph presence and vegetation characteristics (i.e., cladode number, vegetation height, and cochineal presence for each patch) using linear regression and generalized linear models (GLMs) with an identity link function and a normal error distribution.

In patches where adult *C. vittiger* were found, we used a linear regression to assess association between cladode number and the number of adult insects in a given patch and between cladode number and the number of nymphs in a given patch. We also used this method to assess association between vegetation height and insect number (both adults and nymphs).

Using a GLM, we tested whether *C. vittiger* social environments are associated with vegetation characteristics. For each type of social environment (i.e., nymphs alone, adults alone, or groups of nymphs and adults), we contrasted each vegetation characteristic (i.e., cladode number, vegetation height, and cochineal presence). All analysis was carried out using SPSS Statistics 19.

**RESULTS**

Insects were distributed at low density in variable habitat. In the four vegetation transects, covering a minimum of 64 cactus patches, we found *C. vittiger* nymphs on cactus patches only 16 times, *C. vittiger* adults on cactus patches 15 times, and *C. vittiger* adult and nymphs together on cactus patches three times during the field season. In total, we found 45 *C. vittiger* nymphs and 24 adults in the vegetation transects. This suggests a less than 5% chance of finding insects in randomly sampled ruderal habitat at OSBS. The four areas where we conducted vegetation transects differed in the composition and abundance of cactus and nearby vegetation (Fig 1–2). Over the season, cochineal scores, cladode numbers, and the height of vegetation surrounding a patch fluctuated. Cactus fruit abundance remained relatively constant over time, but not across space.

![Figure 1](image-url). Total cladode numbers across four areas over time. Numbers of cactus cladodes were summed within each of the four areas where we conducted vegetation transects. We conducted one 50m transect in a permanent location within each area five times during the field season.
Figure 2. Average vegetation height (< 3m) across four areas over time. Vegetation height within 50cm of a patch was averaged for each of the four areas where we conducted vegetation transects. We conducted one 50m transect in a permanent location within each area five times during the field season.

We found a total of 570 *C. vittiger* insects—195 adults and 375 nymphs—in the insect sampling transects. *C. vittiger* nymphs and adults were found together on only 33 patches, whereas nymphs without adults were found on 88 patches and adults without nymphs were recorded on 103 patches. More than half of patches with insects contained just a single adult or nymph (128 of 229 total patches). Most solitary insects were adults (91 adults, 37 nymphs). Nymphs were much more likely to be found in groups than adults, and most nymph groups were larger than adult groups (Table 1).

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<tr>
<th>Table 1. Characteristics of Insect Social Environment in the Field</th>
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<td>Insect Sampling Transects</td>
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Note. Occurrence, size, and life-stage composition of groups in cactus patches (N = 229).

In the insect sampling transects, *C. vittiger* individuals were located in habitat significantly different from that which would be expected from chance, with respect to both patch size (measured by number of cladodes) (Wald $\chi^2 = 11.518$, $p = 0.001$) and height of the surrounding vegetation (Wald $\chi^2 = 52.058$, $p < 0.001$). Also, greater numbers of adult *C. vittiger* were found with increasing number of cladodes in a patch (ANOVA: df = 1, $F_{1,240} = 15.224$, $p < 0.001$). However, nymph numbers did not significantly increase with the number of cladodes in a patch (ANOVA: df = 1, $F_{1,240} = 2.592$, $p = 0.109$). The presence or absence of canopy cover (i.e., vegetation greater than 3m in height) was not significantly related to the presence of *C. vittiger*, although it approached
significance (Wald $\chi^2 = 7.830, p = 0.050$). We found no correlation between the presence of cochineal and the presence of *C. vittiger* (Wald $\chi^2 = 3.153, p = 0.369$).

Insect social environment (i.e., one or both life stages present in a patch) was related to two habitat characteristics: patch size and vegetation height. Patches with insects of both life stages had significantly more cladodes than patches with either groups of nymphs only or with just a single adult or nymph (Wald $\chi^2 = 20.783, p < 0.001$, Tukey’s Post-Hoc) (Figure 4). The height of surrounding vegetation (under 3m tall) was also related to *C. vittiger* social environment (Wald $\chi^2 = 10.726, p = 0.030$). Adult groups and adult-nymph groups occurred in patches with higher surrounding vegetation than did solitary adults, solitary nymphs, or nymph groups. However, these differences were not significant, in part because of a smaller sample size for adult groups ($N = 14$) (Tukey’s Post-Hoc) (Figure 3).

![Figure 3](image1.png)

**Figure 3.** Insect social environment is related to the average height of vegetation around a patch. (Wald $\chi^2 = 10.726, p = 0.030$). Insects were found in taller grasses than expected (Wald $\chi^2 = 52.058, p < 0.001$).

![Figure 4](image2.png)

**Figure 4.** Insect social environment is related to the average number of cladodes within a patch. Groups of both adults and juveniles were found on patches with more cladodes than those of single adults, single nymphs, and adult groups (Wald $\chi^2 = 20.783, p < 0.001$, Tukey’s Post).
DISCUSSION

Cactus bug distributions were influenced by both vegetation and social structure. Insects tended to be on patches with more cladodes and taller surrounding vegetation than are found in average cactus habitat at OSBS. My data also suggest that *Chelinidea vittiger aequoris* McAtee distribution is related to social environment, which varied in the field: an adult or nymph could be solitary on a patch, in a group with individuals of the other life stage, or with individuals of the same life stage. Adults were most often solitary, whereas the opposite was true of nymphs (Table 1). Moreover, nymphal groups tended to be larger than adult groups. Groups containing both life stages (nymphs and adults) occurred relatively infrequently.

The distribution of insects in the field suggests that cactus bugs have a preferred habitat type. Higher numbers of cactus bugs were found in patches with many cladodes and tall surrounding vegetation than in other patch environments. Both descriptive characteristics likely have ecological relevance for the cactus bug: *Chelinidea vittiger* feeds on the surface of cactus cladodes, and thus the abundance of its food resource should be an important factor in habitat use. Taller surrounding vegetation should provide escape and shelter from predators. Cactus bugs frequently hide in the root mass of nearby grasses (KH, pers. obs.). Additionally, surrounding vegetation may produce shade useful for insect thermoregulation.

Although cactus bugs were found more frequently in patches with more cladodes and taller surrounding vegetation, regardless of life stage, we found variation in habitat use across different social environments. Patches with a single nymph, a group of nymphs, or a single adult contained fewer cladodes than patches where adults and nymphs were found together, and the height of surrounding vegetation also differed with *C. vittiger* social environment. Over a reproductive season, larger patches may simply attract more adults, some of which may lay eggs and remain on the cactus patch after the nymphs have hatched. Further research is needed to investigate alternative mechanisms for differential habitat use among life stages, such as oviposition decisions and variable predation pressure; such work would improve our understanding of heterogeneous animal distributions.

My results reflect that various social environments may exist simultaneously within a population, and that population distribution is influenced by life stage and vegetation characteristics. Such patterns of habitat use may underlie observed directions and patterns of animal movement between resources in patchy landscapes (Schooley and Wiens 2004). Also, the covariance between social environment and habitat use could inform investigations of conspecific attraction (Jeanson and Deneubourg 2007). Animals may be attracted to conspecifics for benefits of social interaction (such as group foraging, mating, etc.) or by the conveyance of public information on habitat quality (Stamps 1988). My results suggest that whether juveniles and adults occur separately or together is related to habitat structure (i.e., vegetation). However, it remains unclear why some adults are found in the presence of conspecifics—often in larger patches—and others are found alone. Further work is needed to determine when and why individuals are attracted to conspecifics, and how an animal’s life stage influences the impact of public information about habitat.

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REFERENCES


