

Integrating Environmental Quality and Sexual Selection in the Cactus Bug *Chelinidea vittiger aequoris* McAtee (Hemiptera: Coreidae)

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Knowledge of the effects of variable environments on sexual selection remains incomplete, especially in ecologically relevant settings. This research examines the effects of a spatially and temporally heterogeneous environment on a natural population of the cactus bug *Chelinidea vittiger aequoris* to determine associations between resource quality, male size, and social groupings. Field sampling of *C. vittiger* took place at the Ordway-Swisher Biological Station, located in North-Central Florida, from June 8 to August 12, 2011. Multiple transects were conducted throughout the station, with information recorded on social behavior, adult size, and cactus quality. Males found in close proximity to females showed no significant difference in size, an indicator of male attractiveness in related species, compared to those males found alone, but were located on larger cactus patches. This result suggests that size may not be a reliable indicator of male quality in this population, possibly due to the effects of environmental variation on the processes of sexual selection.

INTRODUCTION

Sexual selection, or the selection of traits driven specifically by competition for mates, has long been a subject of scientific study (Andersson, 1994). Sexual selection is both intersexual and intrasexual. Intrasexual selection involves members of the same sex competing for access to members of the opposite sex, and usually takes the form of male competition for females. Intersexual selection typically takes place when females select males based on male traits that are reliable indicators of male quality. The combined effects of these sexual selection mechanisms help shape the mating system displayed within a population. Sexual selection plays a particularly important role in mating systems where one sex, often males, attempts to control access to the opposite sex. This can occur both directly, by physically defending members of the opposite sex, and indirectly, by monopolizing critical resources (Emlen & Oring, 1977).

Variation in the availability and quality of resources is known to influence the process of sexual selection in many ways (Emlen & Oring, 1977; Ingleby, Hunt, & Hosken, 2010; Mills et al., 2007). Patterns of resource distribution can influence the evolution of mating systems, as more clumped distribution patterns provide greater potential for monopolization of critical resources. Environmental variation can also affect the reliability of sexual signals within a population. Spatial or temporal variation in a critical resource may affect an individual's development of traits involved in sexual selection, possibly resulting in these traits becoming unreliable signals of mate quality. If

such effects persist, this may alter the mechanisms of sexual selection, resulting in a decline in preference for a specific trait.

Although environmental variation may strongly influence sexual selection, the effects of environmental variation on sexual selection and mating systems remain unclear. Purely gene-focused experiments are unable to adequately address these questions, particularly in artificial laboratory settings. Thus, in order to advance sexual selection theory, research needs to integrate development, ecology, and evolution in ecologically relevant environments (Cornwallis & Uller, 2010). To address this gap in knowledge we examine a natural population of cactus bugs, *Chelinidea vittiger aequoris* McAtee (Hemiptera: Coreidae), to determine associations between resource quality, male size, and social groupings.

Study Species

Chelinidea vittiger is found throughout the United States, extending northward to Montana and as far south as Florida and northern Mexico. It feeds on the cladodes (cactus pads) of the prickly pear cactus *Opuntia spp.* Females lay eggs on the underside of cactus spines. Once hatched, juveniles, or nymphs, progress through five instars, often remaining on the same cactus patch due to limited mobility (Hamlin, 1924). Adult *C. vittiger* vary in size, a trait that has been shown to be predictive of male attractiveness as well as mating success in related species, and so male size is used here as a metric of male quality (Gillespie, Tudor, Moore, & Miller, n.d.; Partridge & Farquhar, 1983; Procter, Miller, & Moore, 2009).

In this study we examined a population of *C. vittiger* (subspecies *aequoris*) found at the Ordway-Swisher Biological Station. This insect feeds on *Opuntia humifusa* cactus in North-Central Florida, and cactus patch size is highly variable. Cactus plants produce areas of new growth only once a year in spring, and cladodes gradually mature through summer. Throughout this time cactus undergoes herbivory from animals such as deer and tortoises. Together, seasonal growth and herbivory add spatial and temporal variation to a fundamental resource for *C. vittiger* populations. Such resource variation has been found to be important for sexual selection in laboratory studies of related species, as variable resource quality in developmental environments can affect the expression of traits important to sexual selection processes as adults (Miller & Emlen, 2010; Nageon de Lestang, 2010).

Male proximity to females was used as a proxy for male attractiveness (Shelly & Kennelly, 2007). Those males found paired with females on the same patch were assumed to be more attractive than solitary males. This assumption was based on the relatively low population density of *C. vittiger* within the station as well as observations that uninhabited cactus patches are often located nearby male-female pairings. Low population density reduces the likelihood of close proximity of males to females due to chance encounters, while the presence of uninhabited patches close by suggests attraction to a specific patch. We predicted that 1) larger *C. vittiger* males would be found more frequently on larger cactus patches, 2) males found paired with females would be larger than solitary males, and 3) males found paired with females would be found on larger cactus patches than solitary males.

METHODS

Transect Point Generation

We conducted field sampling at the Ordway-Swisher Biological Station, located in North-Central Florida, from June 8 to August 12, 2011. Prior to the field season, transect points throughout the biological station were generated using GIS. These points were limited to those areas of the station designated as ruderal habitat, as the majority of prickly pear cactus is found in this habitat type within the station. To ensure an adequate range of environments and coverage of habitat area, 100 transect points with a minimum of 50m between points were randomly generated within ruderal habitat for use in field sampling. Because of the large and varied coverage area, some transects were found to contain no cactus and were removed from subsequent sampling.

Transect Types

We conducted two types of transects during the field season, insect sampling transects and vegetation sampling

transects. Insect sampling transects were designed to provide information on the habitat quality and social interactions of *Chelinidea vittiger* adults and nymphs. Vegetation sampling transects were designed to provide data on cactus patches regardless of insect presence, yielding a baseline for vegetation throughout the station.

Insect Sampling Transects

We conducted insect sampling transects each week throughout the course of the field season. To reduce bias in field sampling for insects, a different set of transects was selected from the total pool each week using a random number function. To increase the speed of sampling, transects were placed into eight groups according to area, allowing multiple transects to be completed within the same area before moving onto the next. To reduce any effect time of day had on insect activity, the first area of transects visited was rotated each week. The remaining areas were then visited in ascending numerical order each week. As an example, in week one of sampling we visited areas in the order of 1,2,3,4,5,6,7,8; the following week's order was then 2,3,4,5,6,7,8,1, and so on. We visited transects between the hours of 8:30am and 2:30pm.

Transect points were located using a handheld GPS unit, with the GPS coordinates used as the midpoint of transects. Once a midpoint was located a coin was flipped twice to determine one of four directions the resulting transect would follow, Northeast-Southwest, Southwest-Northeast, North-South, or East-West. A flag was then anchored into the ground to secure the two sets of transect tape used by my field partner and myself. We would then proceed 25m in opposite directions, resulting in a total transect distance of 50m. Transects were 1m in width. When a patch was located, it was checked in its entirety even if only partially located within the transect. A distance of 20cm designated separate patches.

If a nymph or adult *C. vittiger* was found on a patch, data on the patch were recorded. These data included the number of cladodes contained in a patch, the number and instar of nymphs, and the number, sex, and size of adults. Insect size was measured in terms of pronotum width using digital calipers.

Vegetation Sampling Transects

For vegetation sampling, four randomly selected transects were constructed in the same manner as insect sampling transects. Unlike transects used for insect sampling, we collected data on every cactus patch located within vegetation transects despite insect presence or absence. Vegetation transects remained at the same points and in the same direction throughout the course of the field season in order to provide consistent baseline information

on cactus in the biological station. All four vegetation transects were checked once every two weeks in rotating order. To ensure accuracy each cactus patch within the transects was flagged and numbered.

Statistical Analyses

To determine relationships that should be relevant to sexual selection, each cactus patch was assigned a classification based on the number of male and female *C. vittiger* present. The classes are as follows, solitary: one male found with no females, paired: one male found with one or more females, multiple male: more than one male found with no females, mixed: more than one male found with one or more females. To avoid pseudoreplication, male size was taken as the average size of all males measured on a patch. We used generalized liner models to compare solitary and paired males in terms of size as well as number of cladodes per patch. A generalized liner model was also used to analyze changes in male and female size over the course of the field season. An additional linear regression analysis was performed to determine the relationship between number of cladodes present in a patch and male size. SPSS 19 was used for all statistical analyses.

RESULTS

Male Size and Cladode Number

We found 196 adult *Chelinidea vittiger*, 97 of which were male, on cactus patches of varying size. Of the 97 males found, 12 escaped before size was recorded. Cactus patches containing males showed high variation in cladode number, ranging from 2 to 225 cladodes. Male size was found to have no association with the number of cladodes present in a patch ($F_{65}=0.421, p=0.519$).

Social Behavior

C. vittiger males were found on 85 total patches, with nymphs also present in 33% of these patches. Of the patches containing both a male and nymphs, a female was also present 46% of the time. Females were found on 84 total patches, with nymphs also present in 20% of these patches. Of the patches containing both females and nymphs, a male was also present 76% of the time. Males and females were found together on 29 total patches, with nymphs also present in 45% of these patches (Fig. 1). Only four males were found mating.

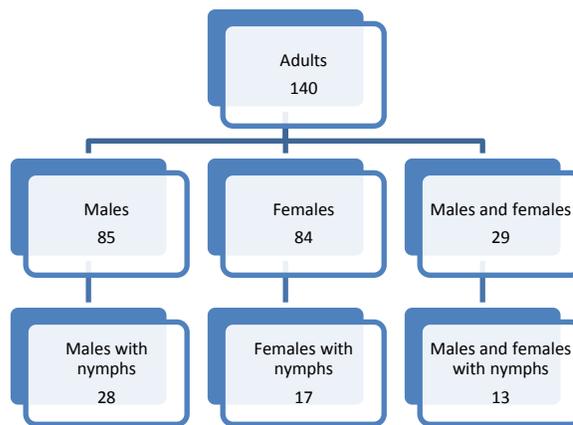


Figure 1. Social Distribution of cactus patches containing *C. vittiger* adults.

Comparison of Solitary and Paired Males

Of the 97 male *C. vittiger* located during field sampling, 53 were solitary. An additional 25 males were paired with one or more females. Nine males were found in a total of four male-only groups, while 10 males were found in four mixed-sex groups (Fig. 2). We did not include these groups in further analyses because of their rarity.

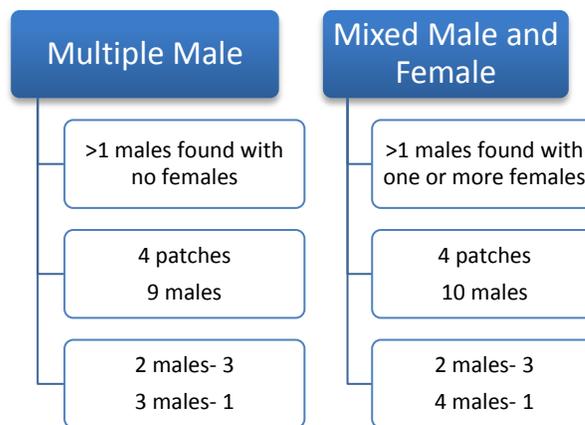


Figure 2. Number of cactus patches and male *C. vittiger* found in multiple male and mixed groups. Of the remaining 78 males in the study, 25 were found paired with females and 53 were solitary.

No significant difference was found in the body sizes of solitary and paired males ($\chi^2=0.073$, $df=1$, $p=0.787$; Fig. 3). The number of cladodes per patch where paired males were located tended to be higher than the number of cladodes where only solitary males were found, approaching significance ($\chi^2=3.609$, $df=1$, $p=0.057$; Fig. 4).



Figure 3. Solitary males and males paired with females did not differ in body size.



Figure 4. Males paired with females were found on larger cactus patches ($p=0.057$) than solitary males.

Changes in Size Over Time

Males were smaller later in the season ($\chi^2=16.240$, $df=6$, $p=0.013$; Fig. 3), but no significant difference was seen in female size over time ($\chi^2=9.486$, $df=6$, $p=0.148$; Fig. 5).

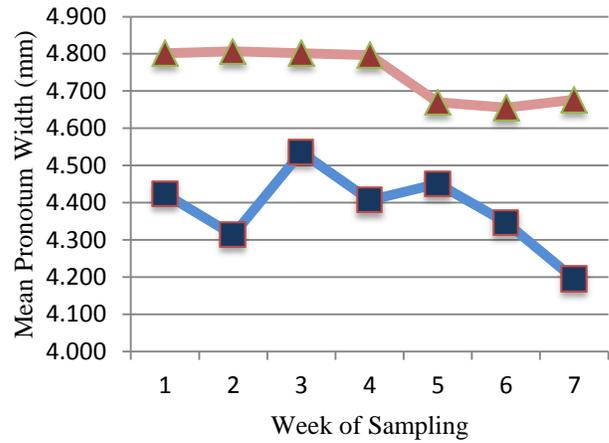


Figure 5. Male (blue) and female (pink) size trends over the sampling period.

DISCUSSION

Male Size Effects

Contrary to our predictions, no significant difference was observed between the body sizes of *Chelinidea vittiger* males found paired with females and those found alone. This is a surprising result, as studies of other species of coreids have shown male size to be an important factor in both male-male competitions (Procter et al., 2009) and female mate choice (Gillespie et al., n.d.). It is possible that proximity to females does not accurately represent mating success for males in this case. However, it is also possible that male size is unreliable as an indicator of male quality, that male size plays only a small role in the mating system of the population, or that females value resource quality over male quality.

Male size may not be reliable as a sexual signal for the population of *C. vittiger* at the Ordway-Swisher Biological Station. For a female mating preference to develop, male sexual traits must be reliable indicators of male quality, allowing females to benefit from potentially costly mate choice (Andersson & Iwasa, 1996). If no such correlation between male traits and quality exists, mate choice may fail to evolve within a population (Kokko, Jennions, & Brooks, 2006). In recent years models have been developed to predict possible environmental effects on sexual signals (Ingleby et al., 2010). One study made four predictions

regarding what conditions may lead to sexual signals becoming unreliable signals of male quality: highly heterogeneous environments, low variation in genetic quality, harsh environments with high levels of juvenile mortality, and strong environmental influence relative to genetic quality influence on sexual trait expression (Higginson & Reader, 2009).

While no measure of genetic quality was recorded for the study population of *C. vittiger*, the presence of a harsh and heterogeneous environment is highly plausible. Cactus within the Ordway-Swisher Biological Station is highly heterogeneous, especially on the habitat scale of *C. vittiger*, as the cactus naturally grows in distinct patches with different areas of the station varying in density and size of patches found (Thickman, unpublished data). Natural predators such as ants or spiders were also frequently found in areas containing cactus, suggesting potential for high predation on nymphs that lack mobility (Thickman, unpublished data). Size in many other insects can be adversely affected by resource quality and predator presence during development (Danner & Joern, 2004; Nageon de Lestang & Miller, 2009).

While no significant relationship was found between patch size and adult male size, it was not possible to distinguish rearing environment from adult location in this study. Adult size is influenced by developmental environment, the cactus patch on which *C. vittiger* progress through 5 instars. Once fully developed, adults may travel between different cactus patches, though their mobility is somewhat limited by short flight distances. Further research on the effects of patch size during nymphal stages is needed to more accurately determine the level of environmental influence on size in *C. vittiger*.

The effects of this harsh, heterogeneous environment may be the cause of the downward trend in male size that was observed over the course of the sampling period. Although we are unable to identify causal environmental factors from these data, herbivory or the maturation of cactus cladodes may play a role. Herbivory by populations of deer or tortoises in the station depletes patches of cladodes, reducing the quantity of resources available. New cactus cladodes are produced only early in the year, and *C. vittiger* are often found feeding on areas of new growth. Prickly pear cladodes in other *Opuntia* species have been shown to vary in chemical composition as they mature, exhibiting a decline in protein content over time (Rodriguez-Felix & Cantwell, 1988). This may affect the quality of food resources available to *C. vittiger* populations. In any case, this observed decline in male size over the course of the mating season could potentially weaken selection for mate choice based on male size within the population as size becomes an unreliable indicator of male quality.

It is also possible that size is not a determinant of male attractiveness within the mating system present in the

population of *C. vittiger* at the Ordway Swisher Biological Station. In either female-defense or resource-defense polygyny larger males may be better suited to defend females or resources critical to females from competitors, resulting in higher levels of mating success (Thornhill & Alcock, 1983). In the absence of aggressive behavior between males (none was witnessed during the field season) scramble-competition polygyny may develop, in which a male's mating success depends on his ability to locate receptive females rather than his ability to aggressively exclude other males (Alcock, 1980; Nishida, 1989). In such a mating system male size could potentially play a much smaller role, as any advantage larger males might hold in direct competition or exclusion would be lost. *Chelinidea vittiger* were found at relatively low density throughout the station (Thickman, unpublished data), suggesting that to spend energy efficiently, adult males should attempt to increase female encounters rather than defend territories. Further knowledge of adult movement patterns and social interaction is required to fully examine the mating system of *C. vittiger* within the station.

Cactus Patch Size Effects

While no significant difference in body size between solitary and paired males was found, analyses showed a potential difference in cactus patch size between the two groups, with paired males being found on larger overall patches. This result suggests that the size of the cactus patch a male is located on may play a role in sexual selection within the population. The distribution of resources within a population can shape the development of mating systems, as more clumped distributions of important resources provide greater potential for individuals to monopolize them (Emlen & Oring, 1977). The uneven distribution pattern of cactus in the station holds potential for the monopolization of large cactus patches by *C. vittiger* males. Patches may also be economically defendable from an energetic standpoint, as no parental care is exhibited (Emlen & Oring, 1977). This potential for monopolization is somewhat supported by the lack of multiple male and mixed male and female groups found during the field season, presumably due to the possible monopolization and defense of cactus patches by individual males.

It is possible that cactus patch size may represent a valuable resource to female reproduction. Cactus cladodes are the primary food resource for *C. vittiger* and nymphs lack mobility. It is highly plausible that nymphs remain on the same patch on which eggs were laid until adulthood; therefore the quality of the rearing environment selected by females could play a role in nymphal development (Miller, 2008). Large patches may also provide greater defense from predators. When discovered in the field, both nymphs

and adults often traveled downward into the cactus patch and leaf litter when disturbed, taking advantage of the natural defenses of the cactus. A larger patch may increase the effectiveness of such behavior, providing a greater area in which nymphs can seek cover.

If certain *C. vittiger* males were able to monopolize larger cactus patches, a potentially valuable resource to females, then female choice should be affected by both male and patch quality (Emlen & Oring, 1977). Because male size may be an unreliable signal of male quality in this *C. vittiger* population, it is possible that females place more emphasis on patch size when selecting a mate. To test this hypothesis, further information is required regarding

the potential mechanisms for male resource monopolization and environmental effects on nymph development.

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