

**The effects of habitat patch and time of day on *Melanoplus sanguinipes*
susceptibility to predation**

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Abstract

Organisms respond to both bottom-up and top-down forces during habitat selection, particularly vegetation structure and predation, respectively. Sex, body size, vegetation cover, and time of day have been shown to significantly affect adult grasshopper susceptibility to predation by vertebrates, predominantly avians and small mammals. This study examined *Melanoplus sanguinipes* vulnerability to such predation. Differences in predation rates were determined for tethered individuals placed overnight in five pairs of distinct patches within Palouse prairie habitat on the National Bison Range, Montana. Predation was negatively related to percent cover and female body mass. As *M. sanguinipes* was more abundant in dense patches of forbs, predation probably acted as a top-down force influencing habitat patch choice. By examining these links between susceptibility to predation and prey habitat selection, understanding of community dynamics can be advanced and applied to management of grasshopper populations.

Introduction

Understanding factors influencing susceptibility to predation may aid in the prediction of prey habitat patch selection, thus providing a better concept of community dynamics (Rosenzweig 1991). Individuals respond to both bottom-up and top-down forces during the habitat selection process (Rosenzweig 1991; Sih et al. 1985). Environmental characteristics including vegetation structure (habitat structural features), soil characteristics, microclimate, and plant species composition can be classified as exerting bottom-up control on an organism's use of various habitat patches. Habitat structural features play a particularly important role in grasshopper habitat patch selection. Vegetation structure is correlated with abiotic factors including soil characteristics and microclimate and thus may be the primary source of cues used by grasshoppers to distinguish suitable habitat patches (Joern 1982).

Factors such as predation also can influence habitat choice. As organisms often select habitats to reduce risk of predation (Sih et al. 1985), predators can exert top-down control with respect to prey patch choice. Habitat characteristics can affect predatory defense mechanisms such as crypsis and motion detection. Specifically, differences in vegetation structure may alter the efficacy of these antipredator strategies (Rosenzweig 1991).

Understanding variation in predatory defense mechanisms has been facilitated by studies on grasshopper susceptibility to predation. Adult grasshopper sex and body mass have been shown to significantly affect vulnerability. Belovsky et al. (1990) found that males are more than twice as likely to be preyed upon than females. While larger species tend to be more readily consumed (Belovsky et al. 1990), individuals of intermediate body size are at the greatest risk to predation (Kaspari and Joern 1993). As females tend to be significantly larger than males, these findings were unexpected. Explanatory hypotheses cite behavioral differences between males and females as the cause of these conflicting results. Males are more active and conspicuous when searching for mates. They frequently hop and fly, resting on bareground or high in the vegetation. Females walk more often and tend to burrow into the vegetation, thus remaining less noticeable to predators (Belovsky et al. 1990).

Additional factors affecting predation on grasshoppers include cover and time of day. Fuller and Joern (1996) found greater predation from vertebrates in habitats with 80-85% vegetation cover than in habitats with 15-20% cover in Sandhills grassland habitat. This difference suggests prey may possess qualities enabling them to lower their predation risk in specific habitat patch types (Fuller and Joern 1996). Also, predation on grasshoppers is greater during the day than at night (Belovsky et al. 1990; Fuller and Joern 1996).

Both of these findings reveal the importance of various predators on grasshopper populations. Invertebrates are the dominant predators on nymphs, while the majority of

predation on adults is due to vertebrates, primarily birds and small mammals (rodents) (Belovsky et al. 1990). Most predation by small mammals occurs at night as rodent predators tend to be nocturnal. Avian predation primarily occurs during the day (Belovsky et al. 1990) in patches of dense vegetation (Fuller and Joern 1996). Greater predation rates in the daytime thus indicate that birds are more important predators on grasshoppers than rodents.

While grasshopper susceptibility to vertebrate predation has been examined with respect to structural features in Sandhills grassland habitat, such a direct study of the effects of vegetation structure on grasshopper predation is lacking for Palouse prairie habitat. This grassland type is comprised predominantly of shortgrass prairie species, making it distinct from Sandhills grassland, which consists of both short- and tallgrass species (Fuller and Joern 1996). Common Palouse grasses include *Pascopyrum smithii* (Rybd.) and *Poa pratensis* (L.), while dominant forbs are identified as *Achillea millefolium* (L.), *Symphyotrichum falcatum* (Lindl.), and *Erigeron* sp. (Belovsky and Slade 1993). Dense and sparse patches of graminoid and forb vegetation create a heterogeneous landscape occasionally including shrubs such as *Symphoricarpos albus* (L.).

One of the most abundant grasshopper species in the Palouse prairie habitat of western Montana is *Melanoplus sanguinipes* (Fabricus) (Belovsky and Slade 1993). *M. sanguinipes* is widespread across North America. It commonly occupies meadows and grasslands (Pfadt 1994), preferring dense forb vegetation (Fuller and Joern 1996). Its most common avian predators in Palouse prairie, as identified by Belovsky and Slade (1993), are the western meadowlark (*Sturnella neglecta*), the grasshopper sparrow (*Ammodrammus savannarum*), and the eastern and western kingbirds (*Tyrannus tyrannus* and *T. verticalis*). The major small mammal predators are *Peromyscus maniculatus* and *Microtus pennsylvanicus* (Belovsky et al. 1990).

This study examined *M. sanguinipes* susceptibility to vertebrate (avian and rodent) predation by determining differences in predation rates for individuals placed in distinct habitat patches of Palouse prairie. Based on the results of previously described research, predation rates were expected to be greater for males than females. There should be a positive relationship between predation rate and body size. More predation should occur during the day than at night, and predation rate should be positively related to percent cover.

Materials and Methods

Experimental Plot Selection

Grasshopper tethering experiments were conducted in patches of two distinct habitat types at an elevation of 830 m within the Palouse prairie in the National Bison Range, Montana (Lake and Sands Counties). The distinct habitat types were 1) dense patches of graminoid and *S. albus* vegetation and 2) sparse patches of graminoid vegetation. Five plots of each habitat type were used as paired replicates during the experimental trials. Differences between habitat types 1 and 2 were verified using comparative measures of vegetation biomass and percent cover. A t-test was used to statistically confirm significant variation in biomass and percent cover between patch types. Plant biomass was measured by clipping all vegetation within three random 0.1 m² areas in each experimental plot. To determine percent cover, 25 point counts were taken in five random sites within each plot to determine the percent of the patch consisting of bareground, litter, or graminoid, forb, and *S. albus* vegetation.

Grasshopper Tethering

Grasshoppers used in the experiment were collected on west-facing hillsides in Moiese Valley, Montana no more than two days before tethering. Methods employed in tethering closely followed those used by Belovsky et al. (1990). Based on additional results of this study indicating that tethering does not significantly alter acridian behavior so as to increase risk of predation, it was assumed that tethering does not modify grasshopper behavior other than by restricting the linear distance capable of being traveled. Individuals were attached to a 60-cm length of 0.152-mm diameter monofilament using a noose. The noose was secured with a square knot after the loop slid under the metazonal disk of the pronotum. Only adult grasshoppers were used to ensure that vertebrates predominantly were responsible for observed predation events. By measuring adults not used in the experiment, a standardized regression was created for each sex to estimate body mass from length. Tethered individuals were housed in cells 121 mL or larger for no longer than nine hours prior to being placed in the field. Once tethered, individuals were anchored by tying the free end of the monofilament to a nail inserted into the ground. Each nail was marked by a 4-cm² piece of orange plastic flagging numbered for grasshopper identification to aid in relocation.

Presentation

On a single day, 25 grasshoppers were placed in each of two plots, one with dense and one with sparse vegetation, between 1730 and 1830. In each plot, individuals were arranged in five rows of five at 1.5-m intervals to form a grid. Plots were oriented so that the patch edges were at least 1 m from grid edges. The presence or absence of each tethered individual was noted 2, 13, and 15 hr after placement. Absent individuals or invalids were replaced and the cause of absence determined when possible. The grasshoppers were removed from the plots 15 hr after placement and stored for reuse the following evening.

The tethering experiment was conducted for five consecutive nights using five pairs of dense and sparse habitat plots. A different pair of plots was used each night, and these plots were reused during a second five-night trial period. Trials were conducted 22-27 July and 29 July – 3 August 2007.

Statistical Analyses

Based on presence and absence data, predation rates were calculated as the number of individuals preyed upon out of the total number presented per hour. Rates were determined for each time period (evening, night, and morning) and for each body mass category and compared between habitat types. Statistical analyses were conducted with arcsine transforms of predation rates using SYSTAT 10.0. An ANOVA was used to investigate differences between predation rate and time of day. Body mass was compared between sexes using a t-test to confirm sexual dimorphism. An ANCOVA was used to examine the effect of body mass on predation rate considering sex. Significant variation in predation rates between habitat patch types was examined using a t-test. The relationship between predation rate and percent cover was determined with a linear regression comparing the 10 experimental plots.

Results

Grasshopper body mass was estimated using a standardized regression calculated for both males (Figure 1) and females (Figure 2). Dense and sparse habitat patch types significantly differed in terms of plant biomass (Figure 3) and percent vegetation cover (Figure 4). Time of day had no significant effect on predation rate ($F = 0.436$, $df = 57$, $p = 0.648$). Females were significantly larger than males (Figure 5). Body mass and sex interacted significantly when considering their effect on predation ($p = 0.034$). A linear regression examined the relationship between predation and body mass for each sex by establishing male and female groups. Predation rate was not significantly related to male

body mass ($R^2 = 0.115$, $n = 10$, $p = 0.338$). For females, predation rate was negatively related to body mass (Figure 6). Predation was significantly higher in sparse habitat patches than in dense patches (Figure 7). A negative relationship was observed between predation rate and percent cover (Figure 8).

Discussion

The lack of effect of time period on predation rate was unexpected based on the literature, which found more predation during the day than at night. This was most likely due to the delayed start of morning observations. Grasshoppers were not checked until after 0700, by which time birds had been foraging for approximately two hours. In order to more closely estimate day- versus nighttime predation, individuals should have been assessed at sunset (around 2130) and sunrise (about 0500) to calculate predation rates more accurately reflecting nighttime predation.

Males and females exhibited different responses to predation with respect to body mass. Size did not affect predation on males probably because their behavior in terms of higher activity levels and conspicuous resting sites increased their risk of predation, negating any effect of size. Smaller females were more likely to be eaten (Figure 6) as they are generally weaker, which may reduce their ability to escape predators.

Predation rate exhibited an unexpected negative relationship with percent vegetation cover. Grasshoppers in the sparse habitat were more likely to experience predation than those in the dense habitat. Should an additional study find that rodents feed more frequently in areas with lower percent cover, these findings support a shift in the dominant predator from birds in the day to small mammals at night.

These results also may explain the tendency for *M. sanguinipes* to inhabit patches of dense forb cover within the Palouse prairie study site (*personal observation*). Fuller and

Joern (1996) also found that *M. sanguinipes* tended to be less vulnerable to predation in habitat types most similar to its preferred patches of dense vegetation. Such findings indicate that *M. sanguinipes* antipredatory mechanisms may be less effective in sparse patches, causing them to select dense habitat patches due to top-down predation pressure.

Understanding this link between predation and habitat selection has various implications on grasshopper management. Altering the area of preferred habitat may control grasshopper abundance, which becomes particularly important should populations reach outbreak densities. These results also contribute to the understanding of mechanisms underlying prey habitat choice. By quantifying the pressures of additional bottom-up and top-down forces on organism habitat selection, community dynamics eventually may be predicted within given parameters.

Acknowledgements

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Figures

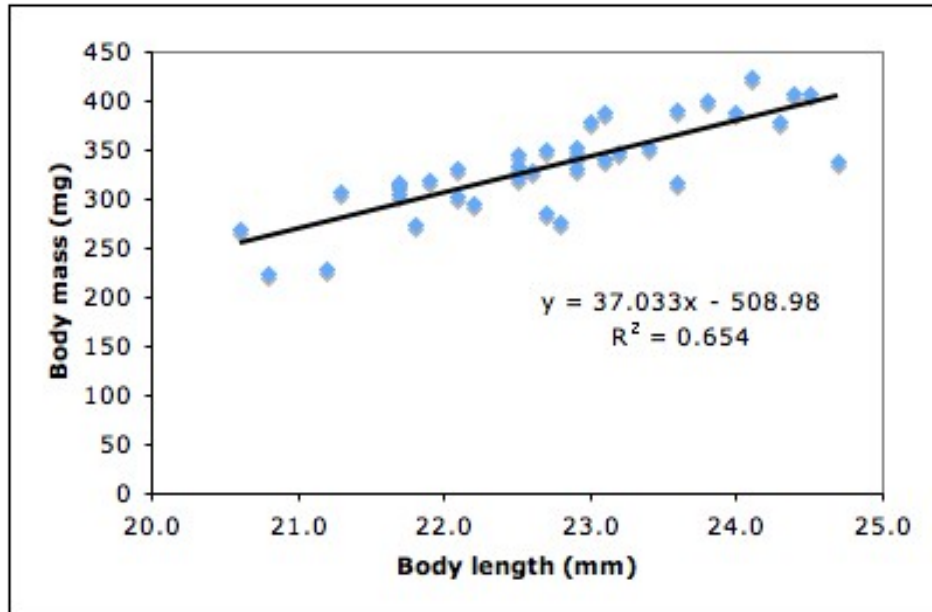


Figure 1 The relationship between body mass and length for male grasshoppers. Body mass was estimated with the equation given above using the measured value for body length.

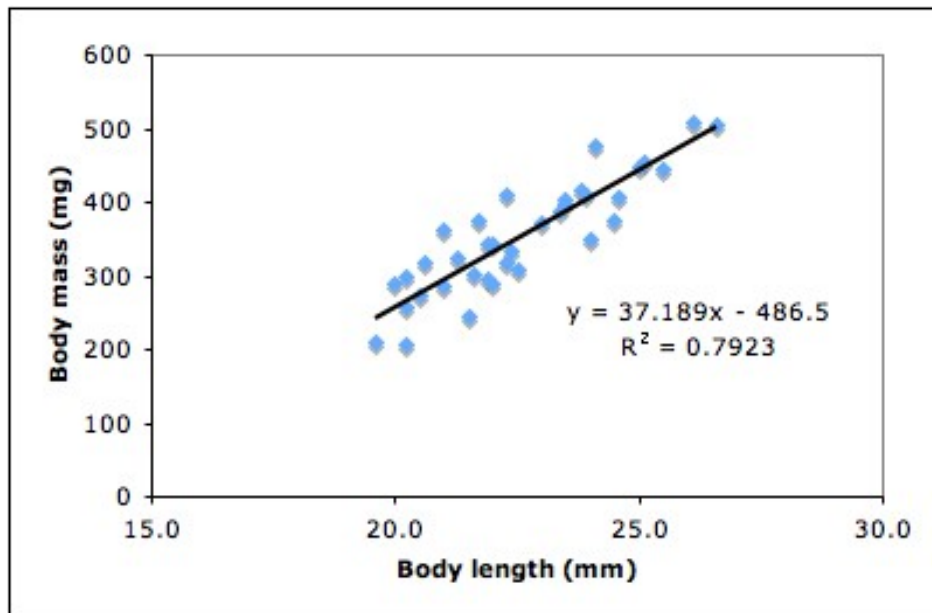


Figure 2 The relationship between body mass and length for female grasshoppers. Body mass for each female was computed with the equation given above using the measured value for body length.

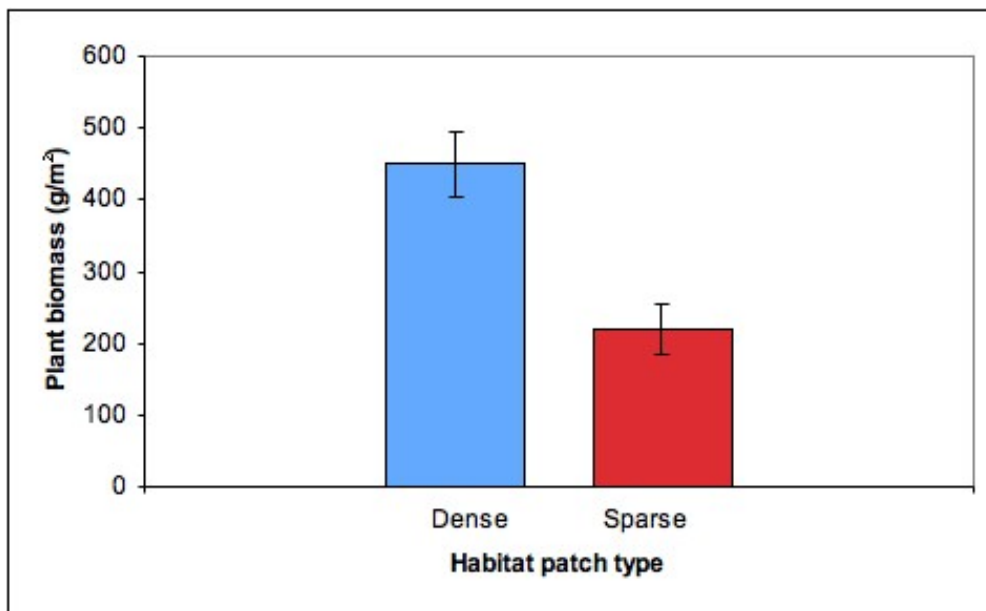


Figure 3 The difference in plant biomass for each habitat patch type. Patches of dense vegetation have significantly higher plant biomass than sparse patches, confirming differences between habitat types ($t = 4.064$, $df = 28$, $p < 0.001$). Variance is shown as standard error.

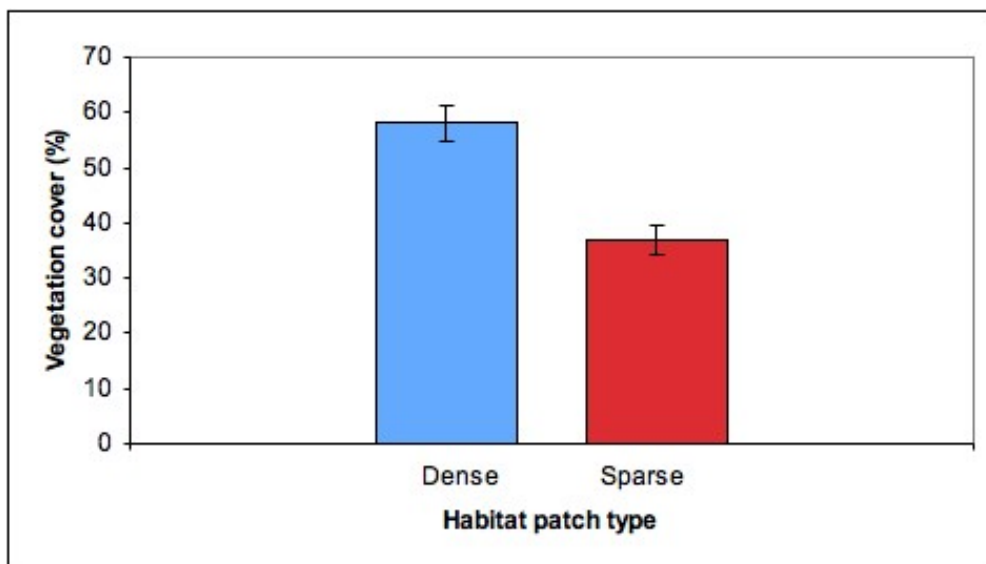


Figure 4 The difference in percent vegetation cover for each habitat type. Dense habitat patches are significantly more covered with vegetation than sparse habitats ($t = 5.031$, $df = 48$, $p < 0.001$). Variance is shown as standard error.

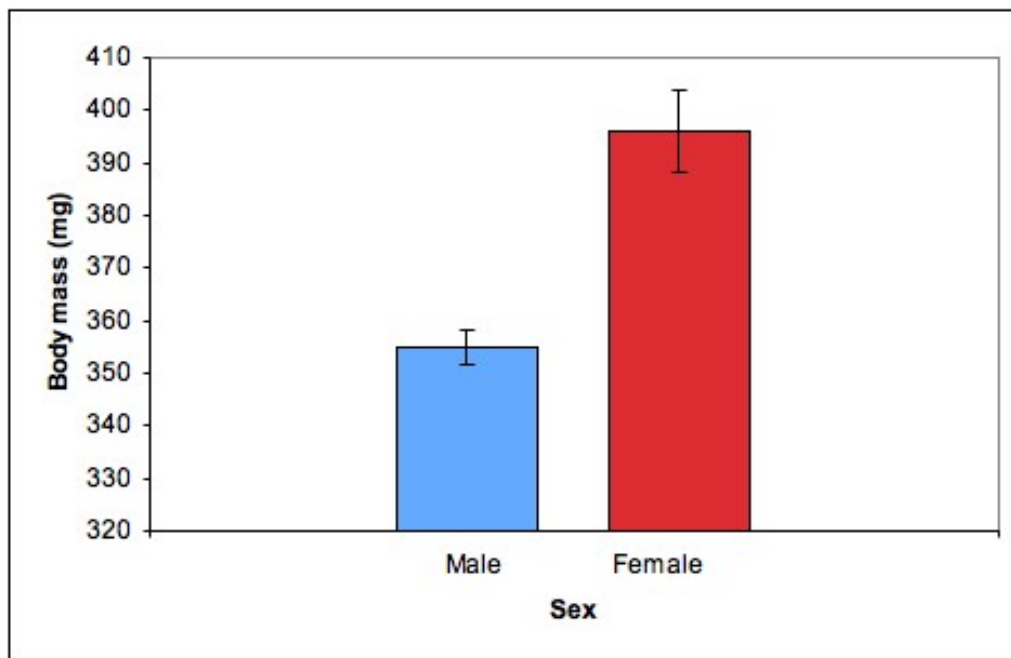


Figure 5 Body mass differences between male and female grasshoppers. Females were significantly larger than males ($t = 5.458$, $df = 351$, $p < 0.001$).

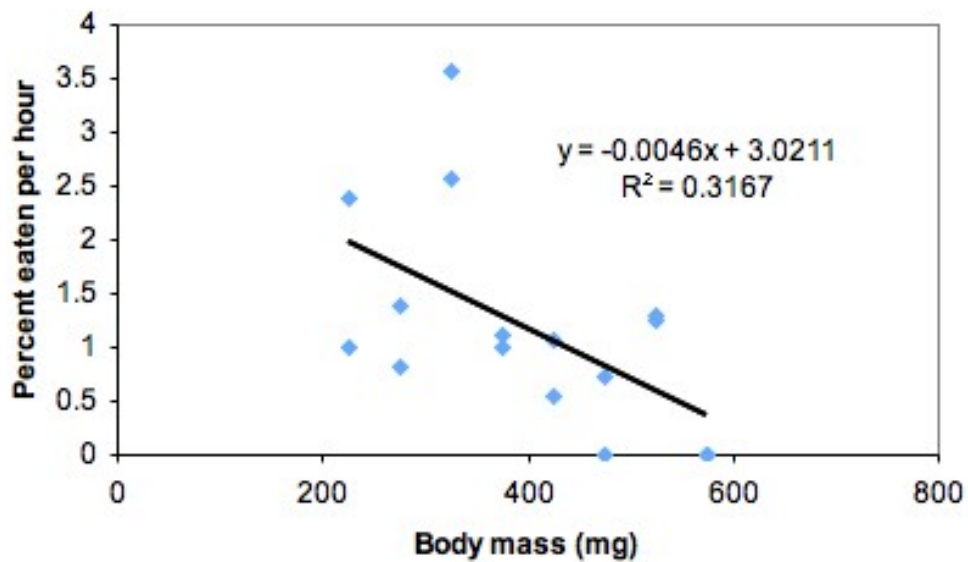


Figure 6 The relationship between predation rate and female body mass. Predation varies significantly with female body mass, decreasing while body mass increases ($R^2 = 0.413$, $n = 16$, $p = 0.007$).

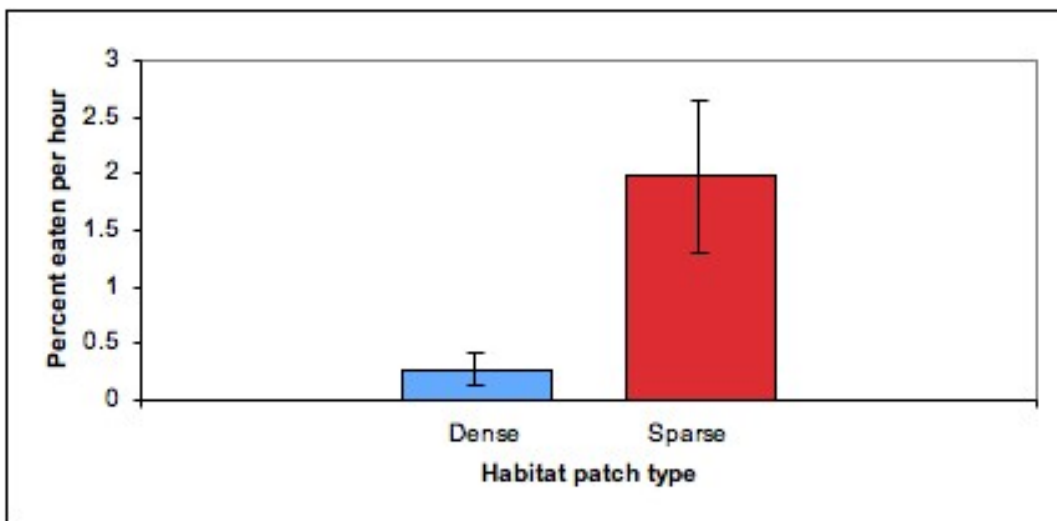


Figure 7 Effect of habitat patch type on predation rate. Significantly more grasshoppers are consumed per hour in the sparse vegetation patches than in the dense patches ($t = -4.011$, $df = 58$, $p < 0.001$). Variation is shown as standard error.

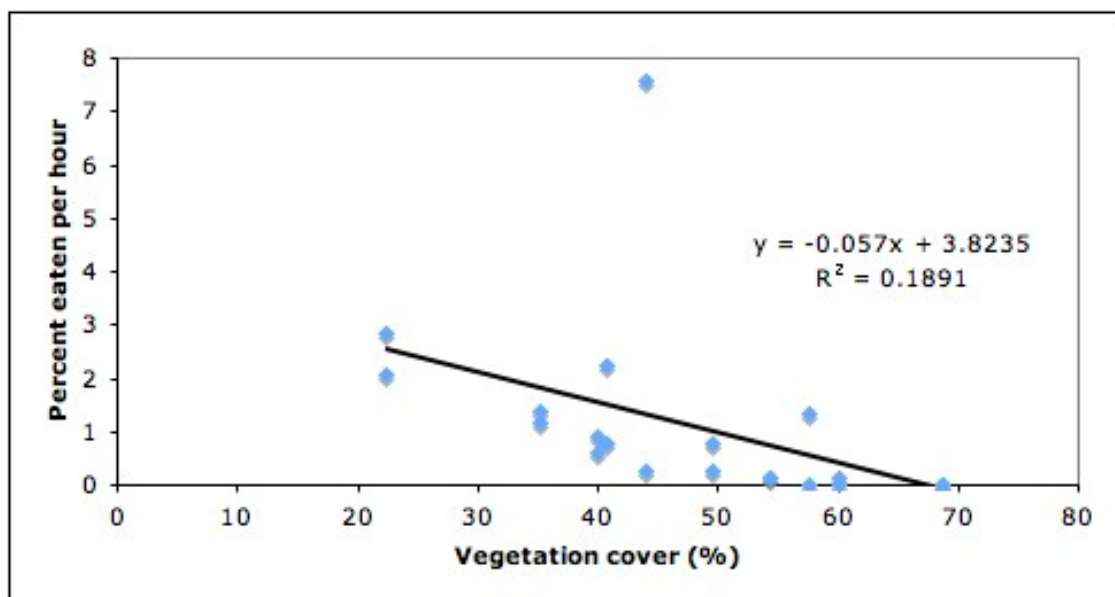


Figure 8 The relationship between rate of predation and vegetation cover. Predation varies significantly with percent cover, decreasing as cover increases ($R^2 = 0.454$, $n = 20$, $p = 0.001$). The equation and R^2 value displayed above give the relationship for the raw data graphically represented.