



Research paper

Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging, and thermoregulation

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Abstract. Predation risk can influence habitat use and activity of potential prey. I explored how the risk of predation by vertebrates influenced the behavior of grasshoppers. I monitored the height in vegetation and the frequency of resting, moving, and feeding behaviors of both tethered and free-ranging grasshoppers under exposure to various predators. Grasshoppers protected from birds remained high in the vegetation, while those protected only from small mammals and lizards remained low in the vegetation. Grasshoppers exposed to all predators occupied an intermediate height. Lower positions in the vegetation were associated with cooler thermal conditions, lower feeding rates, and lower food availability. My results are consistent with the hypothesis that grasshoppers utilize different microhabitats to balance the trade-off between reducing mortality from predators and experiencing greater food availability, and warmer conditions.

Key words: behavior, birds, grasshoppers, habitat selection, lizards, Minnesota, predation risk

Introduction

Predators have well-known effects on prey behavior, including reducing activity (Lawlor, 1989; Schmitz *et al.*, 1997), altering behavior that reduces encounters with predators (Schultz, 1981; Losey and Denno, 1998), modifying habitat selection in time and space (Werner and Hall, 1976; Wootton, 1993; Gotelli, 1996), and increasing vigilance (Caraco, 1979; Bertram, 1980; Rothley *et al.*, 1997). In all these cases, prey must balance the benefits of reducing predation with the costs of reducing foraging gains or other fitness benefits (Lima and Dill, 1990; McNamara and Houston, 1994; Peckarsky and McIntosh, 1998). It is intuitive that resource rich patches should contain high numbers of prey, whereas resource poor patches should contain fewer prey (Fretwell, 1972). However, patches with more abundant prey may attract

greater numbers of predators (Neil, 1990; Huang and Sih, 1991). Consequently, the fitness gain from additional food may be reduced or overcome by the fitness cost of predation risk (Abrahams and Dill, 1989). Thus, patch choice by prey is dependent upon the net fitness of the patch, fitness from energy intake reduced by the fitness lost due to predation risk.

In field environments, prey face the risk of predation from multiple predators (Soluk, 1993; McIntosh and Townsend, 1996). In addition, different aspects of the environment (e.g., food and thermal conditions) may vary with risk and provide for additional considerations when avoiding predators (Belovsky and Jordan, 1978; Belovsky, 1984; Ritchie, 1996). In these environments, prey must balance the risk of predation by different predators with potential benefits from available resources and abiotic conditions (Sih, 1982; Neil, 1990; Rothley *et al.*, 1997). Grasshoppers have many predators, including birds, small mammals, lizards, and spiders (Joern, 1986, 1992; Belovsky *et al.*, 1990; Joern and Gaines, 1990; Bock *et al.*, 1992; Chase, 1996; Schmitz *et al.*, 1997). At different heights in grassland vegetation, grasshoppers may experience different levels of predation risk, abundance and quality of food resources, and microclimates. Grasshoppers may move lower in the vegetation to escape aerial predation or higher to escape ground predators. In addition, the location of grasshoppers may be further influenced by their need to find abundant high-quality food items or preferred thermal environments (Ritchie and Tilman, 1992; Harrison and Fewell, 1995). I explored how risk of predation by birds and ground-dwelling vertebrates, mainly lizards, influenced selection by grasshoppers (Orthoptera: Acrididae) of microhabitats (i.e., height in the vegetation) that differed in food availability and thermal conditions.

The thermal environment is extremely important to grasshoppers, because temperature affects all biological functions and ultimately fitness (Willott and Hassall, 1998). To survive and reproduce, grasshoppers must maintain their body temperatures within a range of temperatures. At cool body temperatures ($< 15^{\circ}\text{C}$) grasshoppers move very slowly and are unable to feed, whereas at high body temperatures ($> 45^{\circ}\text{C}$) enzymes denature and death occurs (Chappell and Whitman, 1990). Nonetheless, the range of body temperatures for optimal growth and survival is much narrower as most species prefer body temperatures between $35\text{--}42^{\circ}\text{C}$ (Chappell and Whitman, 1990), although most species are likely biochemically adapted to function at temperatures they are subjected to their natural habitats (Heinrich, 1977). Grasshoppers living in ambient temperatures outside of their preferred body temperature range behaviorally thermoregulate to achieve more preferred body temperatures. In most environments, grasshopper gain heat from solar radiation and lose heat by means of convective exchange (Chappell and Whitman, 1990). Thus, grasshoppers may change their posture (e.g., crouching close to the ground),

orientation to the wind or sun, or microhabitat (e.g., shade or sun) to gain or lose heat (Chappell and Whitman, 1990). In warm ambient temperatures, grasshoppers may move lower in the vegetation to be shaded by plants, whereas in cooler environments grasshoppers may move up in the vegetation to gain heat (Harrison and Fewell, 1995).

Grasshopper food resources vary with the quality and abundance of plant tissue. Plant tissue quality is dependent on chemical constituents (i.e., chemicals of nutritional quality and secondary compounds which may reduce quality), water content in relation to the state of hydration of the individual, and physical qualities of the tissue (e.g., hairs, hardness, and leaf thickness) (Chapman, 1990; Bernays and Bright, 1993). Plant leaves are of higher quality than stems and young tissue is of higher quality than older tissue. Stems and older tissue have lower protein levels and more indigestible tissue (Field, 1983; Anten *et al.*, 1998). In addition, higher quality tissue (e.g., more nitrogen) is found higher in the canopy (Hirose *et al.*, 1989; Werger and Hirose, 1991). Abundance of plant tissue may vary depending on the growth form of the plant (Strong *et al.*, 1984). For most canopy forming plants, more leaves and younger tissue will occur higher in the canopy than closer to the ground (Rauner, 1977; Hirose *et al.*, 1989).

Potential predators of grasshoppers include birds, mammals, reptiles, and spiders, as well as other arthropods (Churchfield *et al.*, 1991; Bock *et al.*, 1992; Belovsky and Slade, 1993). Most small mammals and reptiles in grasslands forage near the ground and grasshoppers may avoid detection by remaining higher in the vegetation. However, birds fly to forage or locate potential prey and grasshoppers may be able to avoid detection by remaining lower in the vegetation. Arthropods forage throughout the vegetation and grasshoppers are unlikely to find locations that do not contain these predators. The optimal location to reduce predation may depend on the relative abundance of birds vs. reptiles and small mammals.

To assess such potential grasshopper responses to predators, I monitored the behavior of grasshoppers exposed to different types of predators in successional grasslands in Minnesota. Birds are major grasshopper predators in many North American grasslands (Fowler *et al.*, 1991; Bock *et al.*, 1992; Joern, 1992; Belovsky and Slade, 1995), so grasshoppers may exhibit behavioral responses to the risk of bird predation (Schultz, 1981). In addition, insectivorous small mammals and lizards may have a major effect on invertebrates in grasslands (Churchfield *et al.*, 1991; Bock *et al.*, 1992). I included lizards to evaluate whether various kinds of predators have different effects on behavior. I recorded detailed time budgets of tethered grasshoppers in areas with and without birds and measured the height in vegetation of both tethered and free-ranging grasshoppers inside areas exposed to different combinations of vertebrate predators. To test for potential trade-off with predation risk, I measured

the food available, feeding rate, and thermal environment in different microhabitats. I manipulated predator access with various combinations of hardware cloth and bird netting in two old-fields in Minnesota. In each field, various combinations of fences and bird netting allowed access by no predators, all predators, just birds, or just lizards.

In a predator free environment, I expect grasshoppers to remain high in the vegetation to take advantage of better quality food resources and move freely to remain at optimal body temperatures. Significant bird predation may force grasshoppers lower in the vegetation at the cost of warmer thermal habitats and better food resources. Grasshopper may avoid lizards and small mammals by feeding where food resources are better and warmer thermal conditions exist. Grasshoppers may incur little fitness cost by avoiding ground dwelling predators unless grasshoppers need cooler thermal conditions or they are also attempting to avoid birds.

Methods

Study site

The research was conducted in successional grasslands at Cedar Creek Natural History Area (CCNHA), located approximately 60 km north of Minneapolis in east-central Minnesota (Tilman, 1987). I worked in two fields, one abandoned in 1968 (Field A), and the other in 1957 (Field B). Field A was dominated by cool-season grasses, *Poa pratensis* (19% cover) and *Agropyron repens* (15%), but also contained some warm-season grasses: *Schizachyrium scoparium* (8%) and *Panicum* spp. (6%) (Tilman, 1987). Field B was dominated by *Schizachyrium scoparium* (33%), *Poa pratensis* (6% cover), and a diverse assemblage of forbs, including *Lespedeza capitata*, *Solidago nemoralis*, and *Liatris aspera* (Tilman, 1987). Grasshoppers are the most dominant (by biomass) insect herbivores at CCNHA and *Melanoplus femurrubrum* is the most common species (Ritchie and Tilman, 1992, 1993). The northern prairie skink (*Eumeces septentrionalis*) and birds are potentially important predators of grasshoppers at CCNHA (Breckenridge, 1943). Skink abundance ranges from 58 to 206 adults per ha (W.C. Pitt, in press). Vesper sparrows (*Pooecetes gramineus*) and eastern kingbirds (*Tyrannus tyrannus*) are the most commonly observed birds feeding on grasshoppers in these fields. Combined densities of all insectivorous birds potentially preying on grasshoppers (e.g., sparrows, kingbirds, etc.) at CCNHA ranged from 2.9–3.5 individuals/ha (Davis *et al.*, 2000). Small mammals, including shrews (*Sorex* spp.) and the deer mouse (*Peromyscus maniculatus*), are also potential predators (Wovcha *et al.*, 1995), but are extremely rare in these fields (Huntly and Inouye, 1987).

I performed multiple experiments to determine the behavior of grasshoppers under different levels of predation risk. The risk of predation was manipulated by varying predator access with combinations of fencing and bird netting. First, I determined microhabitat selection (i.e., height of grasshoppers) and activity of grasshoppers by observing tethered and free-ranging grasshoppers. Second, I determined the consequences of changes in microhabitat selection by measuring the operative temperature and feeding rate of grasshoppers at various heights, as well as the amount of vegetation available and an index of plant quality.

Grasshopper behavior

In 1997 and 1998, I tested for predator effects on grasshopper behavior and microhabitat selection as part of a long-term experiment to measure predator impacts on arthropods. This experiment used 48 (6 replicates/treatment) predator exclosures established in two old-fields in 1996. The exclosures consisted of 5 × 5-m plots, which received one of four different predation treatments: (1) exclosures that excluded all predators with a 20 cm high window screen fence and 2.5 cm mesh bird netting at a height of 1 m, (2) exclosures that allowed lizards but not birds with a 20 cm high hardware cloth (12 mm mesh) fence and bird netting, (3) exclosures that allowed birds but not lizards with a 20 cm high window screen fence, and (4) exclosures that permitted all birds and lizards. The density of grasshoppers present in these plots varied; (1) 0.85 m⁻² in plots excluding all predators, (2) 0.71 m⁻² in plots allowing lizards but not birds, (3) 0.71 m⁻² in plots that allowed birds but not lizards, and (4) 0.87 m⁻² in plots that allowed birds and lizards (W.C. Pitt unpubl. data). For the behavioral study, I placed tethered grasshoppers in two experiments and observed free-ranging grasshoppers in one experiment within these plots.

For the tethering experiments, I measured behavioral responses of grasshoppers (adult *M. femurrubrum*) to the presence of predators. Male grasshoppers were chosen because they were more abundant than females, and they were similar in size compared to the larger females. I tethered grasshoppers with a 50 cm strand of 0.05 mm diameter monofilament similar to Belovsky *et al.* (1990). Grasshoppers were attached to the line with a noose around the pronotum, secured with cyanoacrylic glue. The line was tied to a fencing staple inserted in the ground. A meter stick was placed upright near each tethered grasshopper to facilitate quick visual height estimation without disturbing the grasshopper. All grasshoppers were captured with a sweep net from a nearby field each morning prior to tethering. Grasshoppers were allowed to acclimate from 5–30 min to the surrounding area before observations began. Observations lasted from 30–120 min from 0800–1900 h.

During July and August 1997, I selected two male grasshoppers at random from those captured that morning, secured their tethers, and placed them in plots 5 min prior to a 30 min observation period. One grasshopper was tethered under bird netting at least 75 cm from the plot edge, while the other was tethered in open vegetation 2 m outside the netting. I observed the grasshoppers from a distance of 1–3 m, and at 1 min intervals I recorded the vertical position of each grasshopper and whether the grasshopper was feeding, moving, or stationary. I excluded data for grasshoppers that escaped before the end of the session, those that attempted to leave the observation area (i.e., fully extended tether), or those that died. I evaluated the response of 27 pairs of tethered grasshoppers placed under bird netting vs. in the open. Observation periods were evenly spaced over the course of the day to include every hour between 0900–1900 h.

In the second tethering experiment during August 1998, I selected either male or female grasshoppers at random from those captured that morning. For each grasshopper, I secured their tethers, and placed five in each predator enclosure at random points at least 75 cm from the plot edge, and 1 m from an adjacent tethered grasshopper. Tethering experiments were conducted from 0800–1900 h on warm (>20 °C), sunny days. I recorded the height of grasshoppers. I checked grasshoppers every 2 h and excluded data for grasshoppers that escaped or were eaten between checks. I placed 180 grasshoppers (5 per treatment) in 36 of the 48 plots. Six plots in Field B were excluded because a previous fire removed most of the vegetation, and six plots were removed from the experiment in Field A to provide a similar number of plots between the two fields. The height of individual grasshoppers was averaged across time periods and the average heights of all grasshoppers within a plot were averaged to control for potential lack of independence.

I determined if free-ranging grasshoppers would exhibit similar behavior to tethered grasshoppers. On 15 August 1997 at 1000 h, I counted and measured the height of all (both male and female) grasshoppers found in different 0.5 m^2 permanent sampling quadrats (were marked with 10 cm high steel posts) within each of the 48 plots in the predator enclosure experiment. The heights of all grasshoppers within a quadrat were averaged to control for potential lack of independence among grasshoppers within a quadrat.

In August 1998, I tested whether grasshoppers responded to bird netting rather than predation risk by placing grasshoppers in areas that received novel protection from birds. I used novel protection from birds to determine if grasshoppers were responding to the presence of bird netting or a cue of past predator presence, such as chemical cues. Bird netting boxes would still contain these cues of past predator presence. I constructed a $1 \times 1 \times 1$ -m bird netting box and placed it in an open plot 30 min prior to the trial. I also placed one tethered grasshopper under the bird netting box and another in the open 2 m away and observed them in a manner similar to previously described experi-

ments. Observation periods evenly spaced over the course of the day to include every hour between 0800–1900 h. I evaluated the effect of novel bird netting boxes placed over 23 pairs of tethered grasshoppers. I expected grasshoppers to exhibit behavior similar to tethered grasshoppers under bird netting in the long-term experiment exclosures, if the grasshoppers were responding to an unintended effect of the bird netting (e.g., shading) rather than predation risk.

Grasshopper feeding rates

To estimate *M. femmurrubrum* potential feeding rates at different heights, I placed individual grasshoppers in 4 (height) \times 10 \times 18 cm window screen cages with a known fresh weight of quackgrass (*Agropyron repens*), whose base was inserted in a water vial to prevent rapid desiccation. Quackgrass is a high-quality plant readily eaten by *M. femmurrubrum* (Ritchie and Tilman, 1993). I set out 10 pairs of cages, with one cage of each pair on the ground at a height of 0–5 cm and the other perched at a height of 20–25 cm above the ground. Pairs of cages were placed randomly within 1 m of each other to control for the effects of spatial variation within a field. Grasshoppers in each pair of cages were the same sex. Trials lasted from 09.30–13.30 h, thus bracketing the peak time of grasshopper feeding (Chase, 1996). I also set out four cages containing vegetation but no grasshoppers so that I could estimate water loss of the plants presented during the trials. After each trial, the remaining grass in each vial was weighed and compared to estimate the fresh weight eaten. The fresh weight remaining was the corrected for desiccation using estimated water loss from plants in cages without grasshoppers.

Vegetation available

To examine the amount of green biomass useable as food for grasshoppers at different vegetation heights, I clipped a 10 cm \times 1 m strip of vegetation from 10 plots near (<10 m) the predator exclosure experiment in each field in August 1998. I sectioned each strip according to height (0–5 cm, 5–10 cm, 10–20 cm, >20 cm), separated live versus dead vegetation and weighed the live plant material after drying at 45 °C for 48 h. This dried plant material was ground through a 40-mesh screen, digested in a 2 g/l pepsin and 0.1 N HCL solution for 48 h at 37 °C, dried at 45 °C for 48 h, and weighed again (Terry and Tilley, 1964). I subtracted the postdigestion from the predigestion mass to determine the *in vitro* digestibility. This *in vitro* measure of plant solubility correlates well with grasshopper *in vivo* digestibility and is a good indicator of plant quality for grasshoppers (Heidorn and Joern, 1987; Belovsky and Slade, 1995). The *in vitro* digestibility was multiplied by the dry biomass to yield the amount of useable food.

I estimated average vegetation height in plots to determine if there was a difference in plots with and without bird netting. I measured the height of plants at 25 random points in each plot of the predator exclosure experiment.

Operative temperature

I measured operative temperatures of 'model' grasshoppers at 0 and 20 cm above the soil surface in plots with bird netting and in plots without netting (Chappell and Whitman, 1990). Operative temperature incorporates solar radiation, terrestrial radiation, convection, and conduction into a measure of the actual thermal environment experienced by organisms (Gates, 1980). I used live grasshoppers as 'models', inserted a needle probe into each, randomly placed in the plot, and recorded the model's temperature after 10 min using thermal data loggers (Hobo Temp, Onset Computer Corporation, Massachusetts). The grasshoppers were suspended at the appropriate height with the probe cord attached to a stick. I chose a 10 min interval because the 'model' grasshoppers had assumed a stable temperature after this time but were not desiccated.

Data analysis

For the detailed behavior observations, I used a paired *t*-test to compare the height of grasshoppers under bird netting and those in the open, and a single-factor ANOVA to compare the heights of free ranging tethered grasshoppers among predator treatments. I used compositional analysis to compare time budgets of grasshoppers between control and bird exclosure treatments to control for the lack of independence among behaviors (Aebischer *et al.*, 1993; Elston *et al.*, 1996). I calculated the ratio of proportion of time spent feeding or moving to that time spent stationary. As recommended, I added 0.0001 to any zero proportions, and log-transformed the ratios to yield normal distributions (Clark and Messina, 1998). These ratios were compared between treatments and time of day, using a multiple analysis of variance (MANOVA). I used a two-sample *t*-test to compare amount of vegetation eaten and operative temperatures at 0 and 20 cm. I used a simple linear regression to determine relationships between height vs. vegetation available and digestibility.

Results

Habitat conditions

Operative temperature did not vary between grasshoppers placed at a given height under bird netting and those in the open ($T = 0.47$, $df = 64$, $p = 0.639$). However, operative temperatures at 20 cm above the soil surface averaged

1.21 ± 0.29 °C warmer (29.66 ± 0.56 °C vs. 28.45 ± 0.51 °C) during daylight hours than those at the soil surface beneath the same plant ($T = 4.25$, $df = 33$, $p = 0.0002$).

In feeding trials with food provided at different heights, grasshoppers consumed 33% more vegetation at 20–25 cm vs. 0–5 cm (0.097 ± 0.022 g vs. 0.059 ± 0.013 g; $T = 3.14$, $df = 6$, $p = 0.008$).

In vitro digestibility increased as height increased (Table 1; $T = 2.25$, $df = 99$, $p = 0.026$). Digestible biomass was unimodally distributed across vegetation height with a median at approximately 17 cm (Table 1). The height of vegetation did not vary among treatments ($F = 0.01$, $df = 3.96$, $p = 0.997$).

Grasshopper behavior

Grasshoppers were found higher in the vegetation under bird netting (Fig. 1). During 1997, tethered grasshoppers were found higher in the vegetation under bird netting than grasshoppers in open plots ($\bar{x} = 11.09 \pm 1.09$ cm vs. 6.64 ± 1.25 cm, Fig. 1; $T = -2.72$, $df = 52$, $p = 0.006$).

During 1998, I evaluated the response of tethered grasshoppers placed in each of the four types of predator enclosures. Tethered grasshoppers remained higher in the vegetation under bird netting (total enclosure plots and plots allowing only lizards) and remained lower in the vegetation when only exposed to birds compared to plots allowing both birds and lizards (Fig. 1; $F = 16.3$, $df = 3.32$, $p < 0.0001$).

In the 1997 survey of free-roaming grasshoppers, I found grasshoppers in 29 of the 48 sampling quadrats. The effect of the treatments on the height of free-roaming grasshoppers was not statistically significant, but the pattern of heights was similar to that for tethered grasshoppers within these treatments (20.6 ± 1.96 cm vs. 14.0 ± 1.70 cm, Fig. 1; $F = 2.41$, $df = 3.25$, $p = 0.09$).

Grasshoppers under bird netting spent less time moving and feeding than grasshoppers in the open (Fig. 2; $F = 3.36$, $df = 2.27$, $p < 0.05$), with this effect being largely associated with decreased feeding time (Table 2). Grasshoppers under netting fed and were active at similar times of the day to grasshoppers in open plots (Table 2; $F = 0.80$, $df = 24.54$, $p = 0.73$).

Table 1. Analysis of vegetation sectioned according to height (0–5, 5–10, 10–20, > 20 cm)

Height (cm)	Biomass \pm SE	Digestibility \pm SE	Digestible biomass \pm SE
0–5	2.238 ± 0.203	0.317 ± 0.024	0.729 ± 0.107
5–10	3.157 ± 0.242	0.312 ± 0.016	0.988 ± 0.097
10–15	2.971 ± 0.261	0.335 ± 0.018	0.976 ± 0.092
15–20	2.490 ± 0.307	0.338 ± 0.018	0.827 ± 0.118
> 20	9.291 ± 1.920	0.367 ± 0.018	3.268 ± 0.633

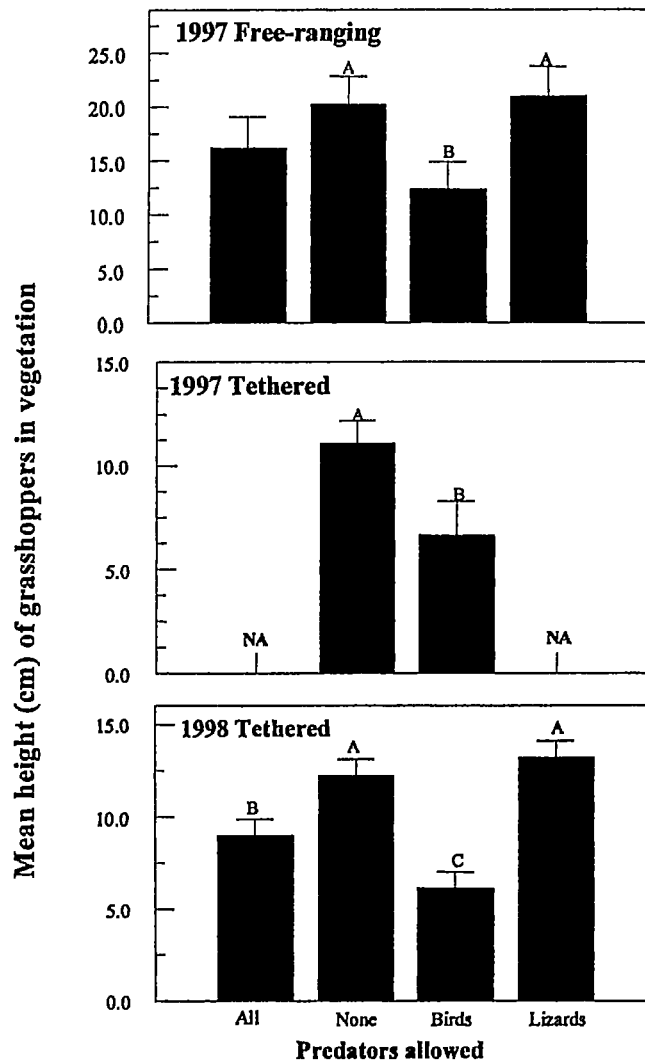


Figure 1. Average height above the ground at which tethered and free-ranging grasshoppers were found in vegetation in various predator treatments, at Cedar Creek Natural History Area, Minnesota. Predator treatments allowed all predators, no predators, just birds, or just lizards. Error bars represent 95% confidence interval. Means that do not share the same letter differ ($p > 0.05$) in height.

To determine if grasshoppers were responding to bird netting rather than risk, I evaluated the effect of novel bird netting boxes placed over 23 pairs of tethered grasshoppers. Bird netting boxes placed over grasshoppers did not result in grasshoppers remaining higher in vegetation ($T = 1.53$, $df = 21$, $p = 0.928$).

Discussion

My results suggest that grasshoppers modify their behavior in response to predation risk (Fig. 1), as grasshoppers were observed at higher positions in

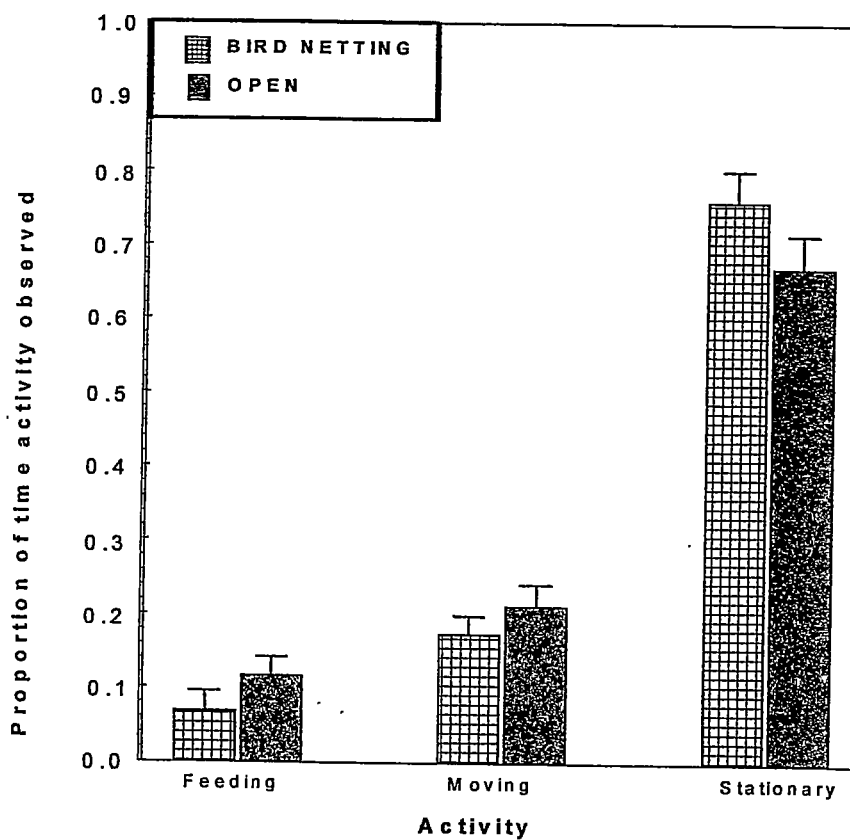


Figure 2. Proportion of time spent in each activity for 54 tethered grasshoppers under bird netting and in the open, at Cedar Creek Natural History Area, Minnesota. Error bars represent 95% confidence interval.

Table 2. Results of MANOVA of tethered grasshopper activity

Source of variation	df1	df2	F	p
Treatment	2	27	3.36	0.049
Treatment feeding	1	28	6.91	0.013
Treatment moving	1	28	0.10	0.757
Time	24	54	0.86	0.649
Treatment × time	24	54	0.80	0.725
Error	28	56		

the vegetation when all predators were excluded and when only birds were excluded (i.e., ground predators allowed). Grasshoppers used intermediate heights when no predators were excluded, and were found lower in the vegetation when ground predators were excluded (i.e., birds allowed). When faced with avian predators, the low vegetation positions used by grasshoppers were associated with reduced food resources and cooler thermal conditions. If grasshoppers were selecting positions based on food abundance (i.e., digestible biomass), they should have a similar distribution across heights as food

abundance. Free-ranging grasshoppers exposed to birds were found lower than the median of digestible biomass (14.0 ± 1.70 cm vs. 17 cm). If grasshoppers were selecting positions based on plant digestibility, they should select positions higher in the canopy. The most digestible plant parts occurred above 20 cm. If grasshoppers were selecting positions based on warmer temperatures, they would select positions higher in the canopy. Predators evidently force grasshoppers to select lower positions in the canopy than grasshoppers would occupy based on food resources or thermal conditions.

At lower heights, grasshoppers had less food of lower quality, were exposed to cooler thermal conditions, and fed at a slower rate when high quality food was available *ad libitum*. Thus, grasshoppers may experience a trade-off between reducing the risk of avian predation and consuming food, avoiding ground predators, and occupying optimal thermal habitats. Air temperatures at CCNHA (26.1 °C, average August maximum, Climatology Working Group 1999) are below the optimal body temperatures for temperate grasshopper growth, egg production, and fitness (~ 35 °C, Begon, 1983; Grant *et al.*, 1993; Willott and Hassall, 1998). Thus, grasshoppers may rely on direct solar radiation to increase body temperatures (Begon, 1983; Willott and Hassall, 1998). Average operative temperatures (29 °C) were higher than air temperatures. Due to the interception of direct solar radiation by leaves, higher levels of direct solar radiation are experienced higher in the vegetation (Rauner, 1977; Gates, 1980). As expected, operative temperatures were higher at 20 cm than at ground level. Higher body temperatures in the 25 – 35 °C range are often associated with faster development rates, higher egg production, and ultimately increased fitness (Gage and Mukerji, 1977; Grant *et al.*, 1993; Willott and Hassall, 1988). Although the optimal temperatures for grasshoppers at CCNHA are not known, optimal temperatures in similar climates are higher than CCNHA operative temperatures (Willott and Hassall, 1998). Hence, to avoid aerial predators, grasshoppers may be forced into less favorable microhabitats that prevent them from fully utilizing solar radiation lower in the canopy.

For equal food availability, grasshoppers consume fewer resources when they are lower in the vegetation. When the caged grasshoppers were provided with similar amounts of plants at different heights, grasshoppers consumed 33% more plant biomass at 20 cm than at ground level. This increase in feeding rate is likely the result of higher operative temperatures at 20 cm than at 0 cm (Rauner, 1977; Gates, 1980), because warmer grasshoppers may feed at a faster rate (Harrison and Fewell, 1995). In addition to changes in feeding rate, the amount and quality of food were much lower at lower positions in the vegetation.

The height of grasshoppers was strongly affected by birds, although the insectivorous bird densities at CCNHA were low (2.9–3.5 individuals/ha; Davis

et al., 2000). However, these densities were similar to bird densities in other grasslands where birds had a significant effect on grasshopper populations, such as Nebraska (1.25–2.25 individuals/ha; Joern, 1986) and Arizona (3.3 individuals/ha; Bock *et al.*, 1992). In addition, 4% ($n = 46$) of the grasshoppers placed in predator exclosures that allowed birds were taken by birds when grasshoppers were left in plots for 2 h. The height of grasshoppers was also influenced by the presence of ground predators (Fig. 1). In 1998, tethered grasshoppers were found lower when ground predators were excluded. Grasshoppers may respond to skinks because skinks are abundant in these fields (> 100 per ha, W.C. Pitt unpublished data) and grasshoppers are a major prey item in skink diets (Breckenridge, 1943). The difference in heights of tethered and free-ranging grasshoppers was likely the result of experimental protocol. All tethered grasshoppers were initially placed on the ground, and thus the average position of tethered grasshoppers was reduced by a low starting position.

I can only speculate as to how grasshoppers detect the presence of predators. Grasshoppers can only detect predators by visual, tactile, auditory, or olfactory cues. Because birds were not present when observations were made, naïve grasshoppers placed inside the predator exclosures were not likely responding to visual, tactile, or auditory cues of birds. These tethered grasshoppers responded in a similar manner to those (free-ranging) permanently occupying the exclosures. Grasshoppers may have been able to detect ground predators using visual or auditory cues, although ground predators were rarely detected by observers during the trials. Another possibility is that grasshoppers may have been able to visually detect the bird netting. However, grasshopper behavior did not change in response to novel protection from birds (i.e., the bird netting boxes), so grasshoppers appear to be responding to cues associated with predators and not the presence of bird netting. A likely possibility is that the grasshoppers were responding to volatile chemicals, such as chemical cues from the prior presence of predators or injured or dead conspecifics (Nault *et al.*, 1973; Losey and Denno, 1997; Wisenden *et al.*, 1997), which may have been absent without predators. Prey detection of predators by means of chemical cues is well documented in the literature (Soluk, 1993; Crowl and Covich, 1994; Feminella and Hawkins, 1994; McIntosh and Townsend, 1994; Tikkanen *et al.*, 1994; Wisenden *et al.*, 1997).

This study shows that predators may have significant effects on prey populations beyond simply reducing prey numbers through predation events. These changes in vertical position may ultimately affect individual grasshopper fitness (i.e., food resources and thermal conditions influencing survival and egg production) and ultimately population sizes. From this study, it is unclear if these predator avoidance behaviors would have a positive or negative effect on grasshopper populations. Potentially, predators may reduce grasshopper

survival and egg production by forcing grasshoppers into unfavorable microhabitats, thus reducing population sizes. However, predators may reduce nymph numbers early in the season, thus allowing more food resources for the remaining grasshoppers and eventually increasing populations. Consideration should be also given to behavioral changes and potential consequences when conducting predator removal experiments, because these effects may be stronger and more common in terrestrial environments than previously thought (Schmitz *et al.*, 1997; Schmitz, 1998).

To model the potential outcomes or optimal strategy would be a daunting task using traditional habitat or foraging models, but may be possible with multiobjective programming (Rothley *et al.*, 1997). Multiobjective programming, a promising new approach to model behavior, may determine the optimal strategy of these conflicting behavioral demands: avoiding multiple predators, occupying preferred thermal habitats, and foraging on high quality plants (Rothley *et al.*, 1997). However, a grasshopper's ability to avoid predators and forage is dependent on the thermal habitat (Whitman, 1988; Harrison and Fewell, 1995). Furthermore, the relationship between performance and temperature may not be linear and a simple theoretical solution is unlikely. Additional field and theoretical study is warranted to consider the fitness consequences of these behavioral changes resulting from avoiding multiple predators.

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