Grasshopper Susceptibility to Predation in Response to Vegetation Cover and Patch Area

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Abstract.—An individual's risk to predation is influenced by the foraging strategies of its predators, its own anti-predator mechanisms, and the physical characteristics of its habitat. In this study, three grasshopper species (*Amphitornus coloradus*, *Ageneotettix deorum*, and *Melanopus sanguinipes*) were tethered and placed in single grasshopper species patches of 10, 20, and 30 individuals in two different habitats to examine factors that affect grasshopper susceptibility to predation. Species tended to be less susceptible to vertebrate predation in areas most similar to their naturally chosen microhabitats. *M. sanguinipes* was less susceptible to vertebrate predation than either *A. deorum* or *A. coloradus*. [Key-words: anti-predator defense mechanisms, grasshoppers, patch size, predation]

Introduction

The success of prey defense is dependent on foraging characteristics and capabilities of predators, including how, when, and with what biases foragers search for prey and prey patches (Stephens & Krebs 1986). Habitat preferences by prey should figure significantly into the problem. Prey defenses and predator hunting tactics present a classic recursive relationship in which both parties must be considered for ecologists to understand either participant (Malcolm 1992).

Prey defenses should evolve that allow individuals to either avoid detection, prevent correct identification, thwart attack or allow escape from predators (Endler 1991, Malcolm 1992). For any particular prey, these mechanisms are often both habitat and predator specific. For example, the efficacy of cryptic color patterns is dependent on the resemblance to background colors and shapes as perceived by predators. This requires a consideration of both prey and background characteristics (Edmunds 1974, Endler 1978, Guilford 1992, Malcolm 1992). Habitat selection by the prey should affect the efficacy of such prey defenses (Rosenzweig 1991).

Prey patch characteristics may also affect predator foraging behavior and hence prey predation risk. The effect of prey density on predation risk is well studied, as this factor is critical for both ideal free distribution theory (Fretwell and Lucas 1970, Milinski and Parker 1991) and optimal foraging theory (Stephens and Krebs 1986). The role of patch area may also influence foraging behavior and predation risks but to date has received little consideration.

This study examined grasshopper susceptibility to predation in a naturally heterogeneous sandhills grassland in North America. Specifically, we considered the relative effects of habitat type, grasshopper species identity, and patch size to assess prey selection by predominant predators in an experimental setting in the field.

Study Site

Experiments were conducted at Arapaho Prairie (Arthur County, Nebraska, USA) a site representative of Nebraska Sandhills grassland (Barnes et al. 1984). Sandhills grassland consists of large vegetated dunes dominated by a mixture of short and tall grass species of several genera (*Andropogon*,

Bouteloua, *Calamovilfa*, *Schizachytium*, *Sporobolus*, and *Stipa*). While grasses comprise about 80% of total biomass, 200 plus forb species makeup about 80% of the total plant species diversity (Keeler et al. 1980). Vegetation is patchily distributed throughout the site providing a mosaic of open and closed habitats depending on grass cover and recent pocket gopher disturbances. The sandy substrate promotes the importance of disturbance in structuring this plant community resulting in variable structural microhabitats. As a result of this heterogeneity, grasshopper density and species composition vary dramatically among sites (Joern 1982a, Joern unpublished data).

The grasshopper species examined in this study were: *Ageneotettix deorum* (Scudder), *Amphitornus coloradus* (Thomas), and *Melanopus sanguinipes* (F.). Under natural conditions, these species differ somewhat in both microhabitat use and feeding preferences (Joern 1982a, 1985, 1986). *Ageneotettix deorum*, a grass feeder, is typically found in open, sandy patches moving to taller vegetation only to feed or avoid extreme temperatures. *Amphitornus coloradus*, also a grass feeder, is typically found at the base of grass clumps in close association to open sand and litter. *Melanopus sanguinipes* feeds on a variety of grasses and forbs and can be readily found up on vegetation. These generalities about species habitat preferences were further supported by our experience in collecting these animals. *M. sanguinipes* was most readily obtained from sites with high density vegetation. *A. deorum* and *A. coloradus* were most easily captured at sites with less dense vegetation (Fuller personal observation).

Bird species identity and diversity at Arapaho Prairie are typical of North American grasslands (Cody 1974; Wiens 1977). Common bird species at this site include: grasshopper sparrows, *Ammodramus savannarum*, and western meadowlarks, *Sturnella neglecta* (Joern 1992). Less abundant species were: lark sparrows, *Chondrestes grammacus*, and lark buntings, *Eremophila alpestris* (Joern 1992). Collectively, these bird species have been shown to significantly affect grasshopper species presence or absence and reduce grasshopper populations at Arapaho Prairie by 25-27% (Joern 1986, 1992). Common lizard species include: lesser earless lizard, *Holbrookia maculata*, fence lizard, *Sceloporus undulatus*, six-lined racerunner, *Cnemidophorus sexlineatus*, and many-lined skink, *Eumeces multivirgatus* (Ballinger et al. 1979).

Materials and Methods

Field experiments were designed to assess the importance of microhabitat differences, species identity, and patch size to predation of grasshoppers. Grasshopper species used in these experiments exhibited different patterns of microhabitat use as indicated.

Experimental patches of grasshoppers were constructed in closed areas of dense vegetation (mostly grass matrix) and open areas of sparse vegetation (mostly forbs, dead plant material, and bare ground). Predominant grass species in these patches were *Calamovilfa longifolia*, *Stipa comata*, and *Bouteloua gracilis* (Keeler et al. 1980). Vegetation cover was 80-85% in experimental sites designated as closed and 15-20% in those designated as open, as estimated by visual approximation using Daubenmeier's method (1974). Three replicate sites for both closed and open plots were chosen within areas of both dense and sparse vegetation, respectively. These six sites were reused throughout the study. The sites were distributed throughout Arapaho Prairie. Sites were separated by at least 200 m.

Within each patch, individual grasshoppers were arranged in a triangular pattern, separated from their nearest neighbor by 0.88 m (Fig. 1); overall grasshopper densities were invariably 3 individuals/m², similar to those previously observed at Arapaho Prairie (Joern 1992). Patch size, defined as the number of individuals present in a patch, varied only in area with density held constant (Fig. 1). Grasshoppers were placed in single-species patches of size 10, 20, and 30 individuals. All patches consisted of equal proportions of males and females. Each experimental replication required the construction of 18 patches in 4 experimental days. Four replicates (here after referred to as experimental blocks) were completed between July 6 and August 8, 1992. Within each block, the order of patch size and species treatments were randomized among days. The location of patch type treatments was randomized among the 3 representative sites.

Patches were constructed by tethering grasshoppers to a fixed point that protruded approximately 5 cm above the ground (see Belovsky et al. 1990). Fixed points were created by bending a 20 cm piece of wire into a U-shape and thrusting the wire into the ground. Wires were obtained from old field flags. Thirty fixed points were arranged in a triangular pattern (fig. 1) in June 1992 at each of the six sites. Grasshoppers were tethered by tying and gluing fine fishing string (monofilament line - diameter 0.05 mm) around the thorax and then attaching the other end to a fixed point with masking tape. Confining grasshoppers to known locations allowed them to be relocated and the predation risk to be evaluated throughout each day in which an experimental trial was conducted. Each piece of string was 0.50 m prior to tethering. Each plot was censused at 3 hour intervals from 0800 h to 2000 h. When a grasshopper was missing, the source of predation was determined, and the grasshopper was replaced. We concluded that vertebrate predation was responsible for missing individuals when tethers were found with no grasshopper. Ant predation was always detected in progress, because ants were unable to consume grasshoppers in the 3 hour interval between censuses.

The night before beginning a trial, grasshoppers were tethered. Each experimental trial lasted 24 hours. Grasshoppers were placed in their patches by taping the loose end of the string (i.e. the end of the string without the grasshopper) to the fixed point. Patches were set up at 0800-0900 h and censused every 3 hours until 2000 h. A final check was made and surviving grasshoppers were removed from patches the following morning between 0800-0900 h. During censuses, naturally occurring grasshoppers were removed from the patches, experimental grasshoppers caught in vegetation were untangled, and missing individuals were replaced. Periodical replacement kept patch densities roughly equal throughout each day. This allowed predation values to be calculated as the average number of grasshoppers eaten per patch per day.

An analysis of variance was performed on both vertebrate and ant predation values using SAS Proc GLM (SAS Institute, 1985) for a randomized block design. Time was used as the blocking factor. The model considered the following variables: experimental block, patch type, patch site, patch size, and species (Table 1). Multiple comparisons were conducted on adjusted t-values for all means.

Results

Predation values were measured as the number of grasshoppers eaten per patch per day. Considering both sources of predation, namely vertebrates and ants, comparisons of raw means indicated that ants often presented a higher predation risk to tethered grasshoppers than did vertebrates (ants: mean = 5.986±5.68 SE, n=72, vertebrates: mean = 4.583±0.532 SE, n=72). In open areas, ants represented 66% of predation while vertebrates were responsible for 59% of predation in closed areas (figure 2). Predation values were greater during the day (0800 - 2000h) than during the night (2000 - 0800 h) (figure 3). Vertebrate predation was 4X greater during the day than at night. Ant predation was 2.46X greater during the day than at night.

Vertebrate Predation

For a model of vertebrate predation, treatments accounted for a significant amount of the total variation in vertebrate predation values ($R^2 = 0.4616$, $P = 0.013$, Table 1). Residuals did not differ from a normal distribution (Kolmogorov-Smirnov Lilliefors N=72, maxdif = 0.073, $P = 0.425$). The main effects of patch size, patch type, species, and the interaction of patch type with species accounted for significant amounts of the total variation (Table 1).

Vertebrate predation increased in a linear fashion with patch size (Fig. 4a, orthogonal contrast, $P < 0.0048$). Per capita predation risks did not differ with patch size (Fig. 4b, one-way ANOVA $P > 0.90$). On average, patches were not depleted over 50% during the course of one day by vertebrates alone (Fig. 4a).

Overall, grasshoppers experienced higher predation from vertebrates in closed habitats (figure 2, $P = 0.020$). Predation values were 1.64X higher in closed habitats than in open habitats.

Species differed in their susceptibility to vertebrate predation. *M. sanguinipes* (mean = 2.708±0.609 SE, n=24) experienced significantly less predation than either *A. deorum* (mean = 5.667±0.902 SE, N=24, $P = 0.022$) or *A. coloradus* (mean = 5.375±1.098 SE, N=24, $P = 0.012$). *A. coloradus* and *A. deorum* did not differ in vertebrate predation values ($P = 0.797$).

Figure 5 presents vertebrate predation on species between closed and open habitats. *A. deorum* sustained a significantly higher predation value in closed plots than in open plots ($P =

0.002, Fig. 5a). Neither *A. coloradus*, nor *M. sanguinipes* experienced significant differences in predation risk between the two habitat types (*P* = 0.112, *P* = 0.500, Fig. 5a). These same data can be used to compare species predation values within habitat types. In closed plots, *M. sanguinipes* experienced significantly lower predation than either *A. deorum* or *A. coloradus* (*P* = 0.0004, *P* =0.0068, Fig. 5b). There were no significant differences in predation among species in open areas.

Ant Predation

The model of ant predation accounted for a significant amount of the total variation in ant predation values (R^2=0.677, *P* < 0.001, Table 2). Residuals did not differ from a normal distribution (Kolmogorov-Smirnov Lilliefors N=72, maxdif = 0.066, *P* = 0.569). The main effects of patch size, species, and the interaction between patch size and species accounted for significant amounts of the total variation (Table 2).

Ant predation increased linearly with patch size (Fig. 6a, orthogonal contrasts, *P* < 0.001). Per capita predation risks did not differ with patch size (figure 6b, one-way ANOVA *P* = 0.695).

Species differed significantly in their susceptibility to ant predation. *A. coloradus* (mean = 7.958±1.260 SE, N=24) was significantly more susceptible to ant predation than *M. sanguinipes* (mean = 4.167±0.701 SE, N=24, *P* = 0.0002) and tended to be more susceptible to ant predation than *A. deorum* (mean = 5.833±0.772 SE, N=24, *P* = 0.0622). *A. deorum* also experienced significantly greater predation than *M. sanguinipes* (*P* = 0.0486).

Figure 7 presents ant predation on species within each patch size. In patch size 30, *A. coloradus* suffered significantly greater predation than either *A. deorum* or *M. sanguinipes* (*P* = 0.0001, *P* = 0.0001 respectively). Species predation did not vary within patch sizes 10 or 20 (*P* > 0.120 for all cases). Per capita predation risk did not differ among patch sizes for any of the three species (one-way ANOVA, *P* > 0.160 for all tests).

Discussion

Vertebrate Predation

In this experiment, it was possible to attribute predation to either vertebrates or ants. Birds are most likely the predominant predators in the vertebrate group. Lizards typically have a much lower basal metabolism than birds and as a result do not require as many prey items as birds (Nagy 1983). Their contribution to daily predation values is probably minimal. This is supported by the fact that vertebrate predation was significantly lower in open habitats where lizards are most often found at Arapaho Prairie (Ballinger et al. 1979). Small mammals may also eat tethered grasshoppers. Grasshoppers suffered predation attacks throughout each experimental day, but small mammals at Arapaho Prairie forage mainly at night and probably ate grasshoppers between the evening (2000h) and morning checks (0800h). However, any vertebrate predation that occurred between the evening and morning checks may also be due to birds because birds begin foraging long before the 0800 h check each morning (Kaspari 1991). Also vertebrate predation was less at night (2000 - 0800 h) than during the day (0800 - 2000 h) indicating that small mammals are not the major predators in the vertebrate group. Although there is no reason why avian predation cannot explain most of the observed

patterns seen in vertebrate predation, we certainly recognize the potential for alternate predator influences.

The relationship between the predation values obtained in this study and natural predation rates is unclear. Vertebrate predation values might be artificially high due to tethers restricting grasshopper escape behaviors (i.e. hopping). Conversely, patch censuses may have disrupted foragers and lowered predation values. Other grasshopper studies using the tether method have found no significant differences in behavior between tethered and untethered grasshoppers (Belovsky et al. 1990). In this study there was no significant experimental block effect indicating that predators neither increased nor decreased their use of experimental patches over the course of this experiment. The predation values reported here are most likely an accurate reflection of predator/prey encounters, predator detection, and predator identification of prey types.

Species Predation

A. coloradus and *A. deorum* were more susceptible to predation than *M. sanguinipes*. Similar results have been found in other studies at Arapaho Prairie. In a predator removal experiment, both *A. deorum* and *A. coloradus* numbers increased significantly in plots where birds were excluded relative to control plots where birds were present (Joern 1986). In contrast, *M. sanguinipes* was not significantly affected by the presence or absence of birds. These studies taken together provide strong evidence that vertebrate predation has a larger impact on *A. coloradus* and *A. deorum* than *M. sanguinipes* at Arapaho Prairie. In contrast, *M. sanguinipes* was found to be more susceptible to predation than *A. coloradus* or *A. deorum* at a study site in Montana (Belovsky et al. 1990). At present, we have no explanation for this discrepancy.

From a behavior perspective, the results indicate that vertebrate predators prefer *A. coloradus* and *A. deorum* over *M. sanguinipes*. This finding can be explained within the context of optimal foraging theory. Foragers are expected to maximize their energy intake relative to the amount of time required to catch and handle a given prey item (Stephens and Krebs 1986). The grasshopper sparrow, a major grasshopper predator, is gape-limited and faces the decision whether to eat small grasshoppers whole or to forage upon large grasshoppers. Large grasshoppers must be handled (i.e. the wings and legs must be removed) before they can be swallowed (Kaspari 1990). Female *M. sanguinipes* exceed the gape of grasshopper sparrows and must be handled prior to consumption (Kaspari 1990). *A. deorum* and *A. coloradus* can be eaten whole. *M. sanguinipes* could be less profitable to grasshopper sparrows due to the extra handling time required for its consumption. It is unknown whether the handling times required to consume these grasshopper species vary in a similar manner for other vertebrate predators.

M. sanguinipes could possess anti-predator defenses that are effective against a wide variety of predators. We noticed while tethering the grasshoppers that *M. sanguinipes* was harder to handle than either *A. deorum* or *A. coloradus*. *M. sanguinipes* readily spat juice on us and frequently attempted to bite and jump away. Such behaviors may make handling and preparing *M. sanguinipes* more difficult for predators and further decrease its profitability.

Habitat Specific Predation

In this experiment, grasshopper species suffered the greatest predation risk in habitats least similar to those in which they are most frequently found. When compared with other species, *M. sanguinipes*, which is typically found in dense vegetation, experienced significantly lower predation than either *A. coloradus* or *A. deorum* in closed habitats. When compared between patches, *A. deorum* which is typically found in open, sandy areas, sustained lower predation in open areas than in closed areas. *A. coloradus* and *M. sanguinipes* also tended to be least susceptible to predation in patch types most similar to their naturally chosen habitats although these differences were not significant.

The differences detected between species predation values relative to patch types indicate that these prey species may possess traits that lower their predation risks in specific habitat types. A number of habitat-specific mechanisms may account for these results. Crypsis is generally defined as the condition in which animals resemble their background (Edmunds 1974). Although not well tested, the obvious similarity between grasshopper color patterns and their backgrounds can be adaptive (Isley 1938, Rowell 1971, Otte and Williams 1972, Gillis 1982, Dearn 1990). Grasshoppers often select microhabitats based on structural features (Mulkern 1969, Joern 1982b). Any fitness advantage that a color pattern may bestow on an individual is dependent on the microhabitat in which the individual resides (Endler 1978). If birds impact prey based on their ability to discern prey items, then the prey should avoid areas in which their coloration confers no crypsis. Alternatively, other habitat-specific defense mechanisms, such as motion detection, may be employed. Individuals may use the rustling of surrounding vegetation as a cue for a pursuing predator (Fleishman 1992). Such a mechanism may be dependent on specific types and densities of vegetation. Other behavioral defenses, such as sitting postures, may also be adapted to the habitat in which prey naturally occur. When performed in the wrong context, these behaviors may act to increase prey susceptibility to predation.

Patch Size

We found that patch area had no effect upon individual grasshopper susceptibility to predation. Vertebrate predation increased linearly with patch size (area). Patch productivity (prey density) was identical in all patches. Per capita predation did not vary with patch area. This is consistent with the expectation of an ideal free distribution of foragers (Milinski and Parker 1991). Our results indicate that area may have a linear effect on the ability of foragers to detect prey patches, but no effect upon grasshopper susceptibility to predation per se.

The probability that a random forager will locate a patch should increase with patch area. Simply stated, more birds should encounter and forage from large patches. Large patches could be easier to relocate for individuals that must frequently return to the nest to provision developing offspring. Dominant bird species at the site often forage outside breeding territories away from the nest. Given such, a large number of bird species may forage in the patches.

Conversely, vertebrate predators may not have perceived our experimental patches. In a heterogeneous, densely vegetated setting, complete knowledge of patch boundaries on the part of foragers would seem, at best, difficult. Naturally occurring grasshoppers located at the perimeters might also make patch boundaries ambiguous.

Vertebrate vs. Ant Predation

This experiment was designed to measure vertebrate predation, in particular avian predation, upon three grasshopper species. However, grasshoppers were found to suffer greater predation from ants than from birds. If genuine, this finding is important as it strengthens the view that both vertebrates and invertebrates can be important grasshopper predators. Previous considerations of grasshopper predators have mainly focused upon birds (Belovsky et al. 1990, Belovsky and Slade 1993; Joern 1986, 1992; Kaspari and Joern 1993). In a similar study, ants acted only as scavengers of dead adult grasshoppers (Belovsky et al. 1990). Extensive ant predation upon live grasshoppers has not been observed at Arapaho Prairie nor at the National Bison Range in Montana (Chase personal communication). In the present study, the prevalence of ant predation may only reflect an experimental artifact of tethering. Tethering and occasional tangling may restrict the range of motion needed to escape ants in the field. However, if ant predation upon tethered grasshoppers is an accurate reflection of natural ant predation patterns, then the results found in this study reveal important information on the interaction between grasshoppers and ants. The possible interpretations of ant predation patterns are discussed below.

Ant Predation

Species differed in susceptibility to ant predation. *M. sanguinipes* was least susceptible to ant predation. This supports our contention that *M. sanguinipes* may possess antipredator defenses that are effective against a wide array of predators. *A. coloradus* was most vulnerable to ant predation. We have no explanation for this finding. Ants' preference for *A. coloradus* could be due to either its energetic contents as a food source or its ease of locating, handling, and/or capturing.

Ants foraged more from large patches than from small. Specifically, predation increased linearly with patch size in a fashion similar to that of vertebrate predation. Per capita predation did not differ with patch size. Densities were identical in all patch sizes. Only the area of the patch differed. Increases in patch area should increase the probability of ants locating patches. Many ant species search systematically for food in large groups dispersing in highly branched trails (Mirenda et al. 1980, Ganeshaiah and Veena 1991). This strategy allows some ants to thoroughly search a given area efficiently without traveling unnecessarily long distances from the nest (Ganeshaiah and Veena 1991). Ants searching in this manner should encounter large patches sooner than small patches. Ants should forage longer and prey upon more grasshoppers from large patches than from small patches.

A. coloradus experienced greater predation than the other two species when located in large patches. Ant food searching behaviors and prey preferences may account for this pattern. Ant predation was greatest in patches that were most easily located and contained preferred prey. Similar foraging behavior has been demonstrated in some ant species. Foragers of *Formica schaufussi* tend to return to previously rewarding sites and search more vigorously in patches containing preferred foods (Fourcassie' and Traniello 1994). *Formica aquilonia* also returns repeatedly to forage from rewarding sites provided

that the food source is maintained (Cosens and Toussaint 1985). The ability of ants to differentiate among prey types and direct other foragers to rewarding sites makes preferred prey particularly susceptible when found in easily located patches.

In conclusion, grasshopper susceptibility to vertebrate predation was significantly affected by patch type and species identity. Greater vertebrate predation was found in closed habitats indicating that the major predators in the vertebrate group were birds. Species tended to be less susceptible to predation in areas most similar to their naturally chosen habitats. Habitat specific defenses, such as crypsis, may have evolved. *M. sanguinipes* was less susceptible to vertebrate predation than either *A. deorum* or *A. coloradus*. *M. sanguinipes* may have evolved anti-predator defenses which are effective against a wide variety of predators.

Acknowledgments

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Figure Legends

Table 1. Analysis of variance of factors affecting vertebrate predation.

Dependent Variable = Vertebrate Predation (individuals eaten per patch per day)

Source	DF	Sum of Squares	F	$P > F$
Model	20	668.110	2.19	0.0128
Error	51	779.389		

Source	Type III SS	DF	MS	F	P
Experimental Block	31.611	3	10.537	0.690	0.562
Patch Type	88.889	1	88.889	5.817	0.020
Patch Size	212.583	2	106.292	6.955	0.002
Species	127.583	2	63.792	4.174	0.021
Patch Type*Patch Size	18.861	2	9.431	0.617	0.543
Patch Type*Species	118.361	2	59.181	3.873	0.027
Patch Size*Species	22.333	4	5.583	0.365	0.832
Patch Type*Patch Size*Species	47.889	4	11.972	0.783	0.541

Table 2. Analysis of variance of factors affecting ant predation.

Dependent Variable = Ant Predation (individuals eaten per patch per day)

Source	DF	Sum of Squares	F	$P>F$
Model	20	1117.667	5.34	0.0001
Error	51	533.319		

Source	Type III SS	DF	MS	F	P
Experimental Block	51.931	3	17.310	1.655	0.1883
Patch Type	21.125	1	21.125	2.020	0.1613
Patch Size	563.111	2	281.556	26.924	0.0000
Species	173.361	2	86.681	8.289	0.0008
Patch Type*Patch Size	12.333	2	6.167	0.590	0.5582
Patch Type * Species	42.750	2	21.375	2.044	0.1400
Patch Size * Species	186.389	4	46.597	4.456	0.0036
Patch Type*Patch Size *Species	66.667	4	16.667	1.594	0.1902

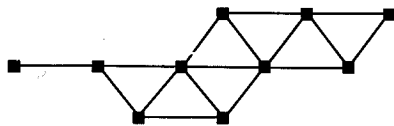**Patch Size 30**
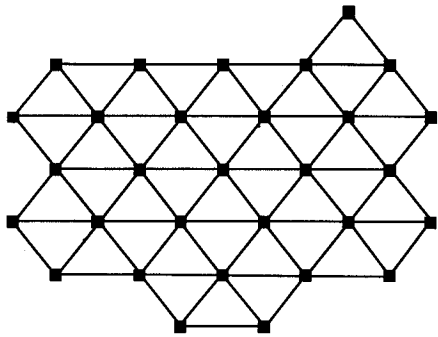
Patch Size 20
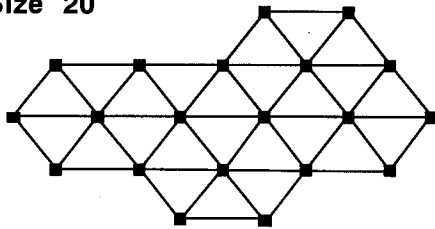
Patch Size 10

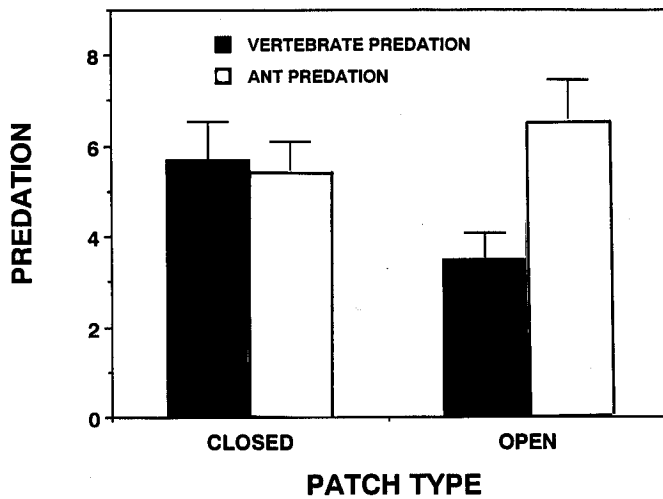**Fig. 1.** Grasshopper arrangements in patch sizes of 30, 20, and 10 individuals. Lines represent 0.88m between neighbors.
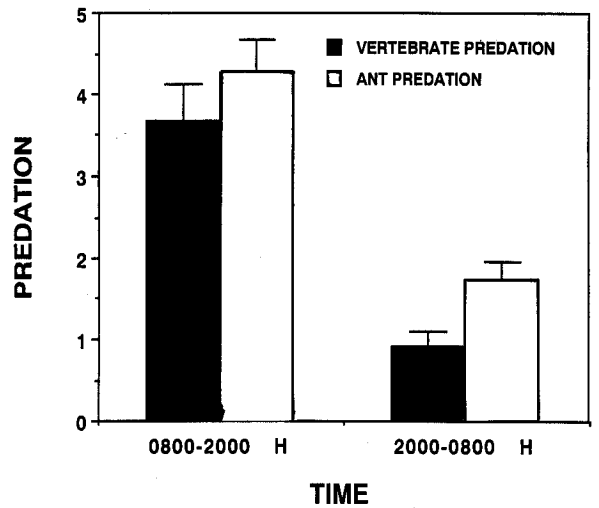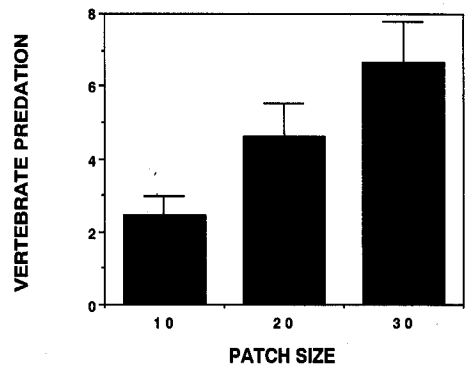
Fig. 3. Vertebrate and ant predation (individuals eaten per patch per 12 hours) during day (0800 - 2000 h) and night (2000 - 0800 h). Bars are standard errors. N=72 for all means. Day: Vertebrate mean = 3.667±0.457 SE, ant mean = 4.264±0.409 SE. Night: Vertebrate mean = 0.917±0.186 SE, ant mean= 1.736±0.223 SE.
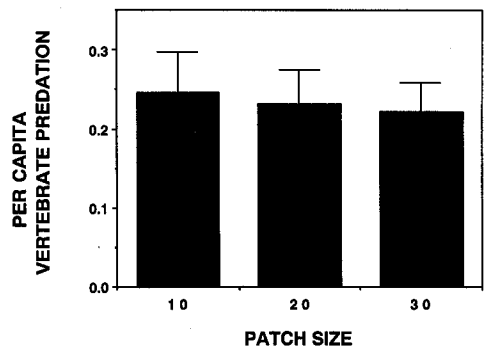
A.

B.

Fig. 4. **A:** Average vertebrate predation (individuals eaten per patch per day) in patch sizes 10, 20, and 30. Bars are standard errors. Patch size 10: mean = 2.458±0.511 SE, patch size 20: mean = 4.625±0.880 SE, patch size 30: mean = 6.667±1.096 SE. N=24 for all means. B: Average per capita predation (individuals eaten per patch per day per patch size) in patches 10, 20, and 30. Bars are standard errors. Patch size 10: mean = 0.246±0.051 SE, patch size 20: mean = 0.231±0.044 SE, patch size 30: mean = 0.222±0.037 SE. N=24 for all means.
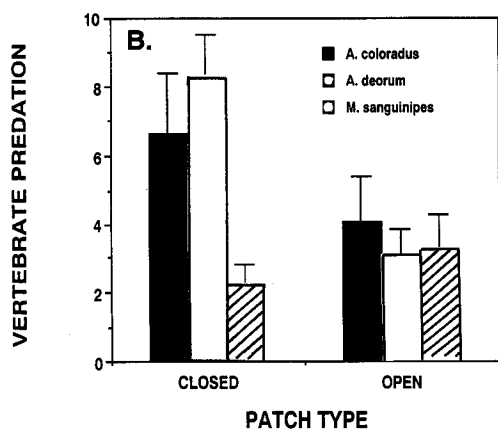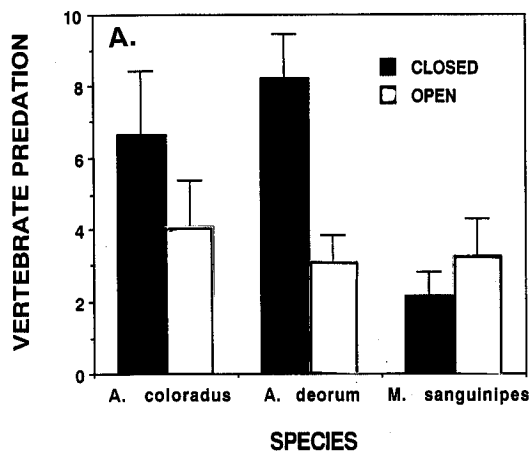
Fig. 2. Vertebrate and ant predation (individuals eaten per patch per day) in open and closed habitats. Bars are standard errors. N=36 for all means. Closed: vertebrate mean = 5.694± 0.851 SE, ant mean = 5.444±0.654 SE. Open: vertebrate mean = 3.472±0.596 SE, ant mean = 6.528±0.931 SE.

Fig. 5. Average species vertebrate predation (individuals eaten per patch per day) between closed and open patch types. Bars are standard errors. N = 12 for all means. Closed: *A. coloradus* mean = 6.667±1.755 SE, *A. deorum* mean = 8.250±1.268 SE, *M. sanguinipes* mean = 2.167±0.638 SE. Open: *A. coloradus* x = 4.083±1.288 SE, *A. deorum* mean = 3.083±0.763 SE, *M. sanguinipes* mean = 3.250±1.045. **A:** This graph compares predation between open and closed patches for each species. **B:** The same date from figure A is displayed here. This graph compares predation between species in each habitat type.
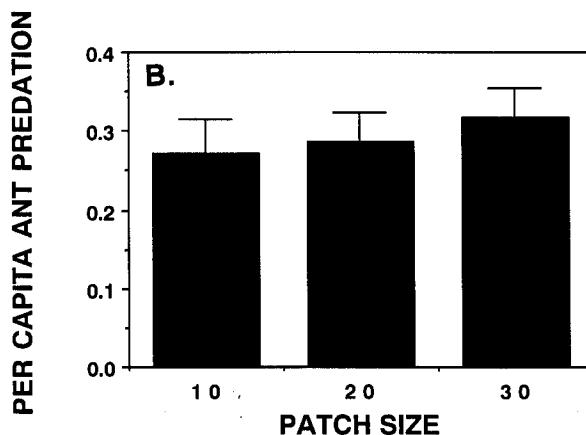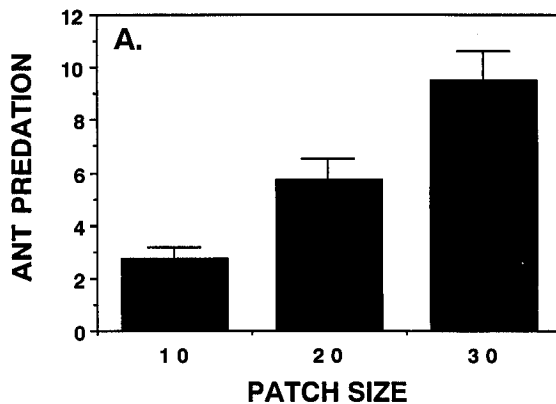
Fig. 6. A: Average ant predation (individuals eaten per patch per day) in patch sizes of 10, 20, and 30 individuals. Bars represent standard errors. N=24 for all means. Patch size 10: x = 2.708±0.448 SE, Patch size 20: x = 5.708±0.796 SE, Patch size 30: x = 9.542±1.085 SE.

B: Average per capita ant predation (individuals eaten per patch per day per patch size) in patch sizes of 10, 20, and 30 individuals. Bars represent standard errors. N=24 for all means. Patch size 10: x = 0.271±0.045, Patch size 20: x = 0.285±0.038 SE, Patch size 30: x = 0.318±0.036 SE.
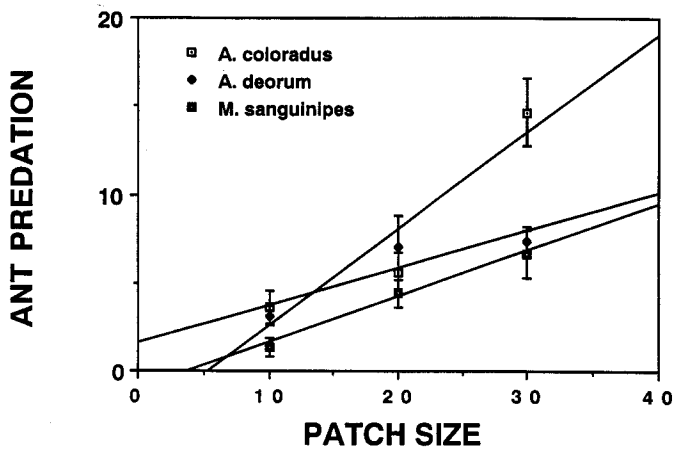
Fig. 7. Average species ant predation (individuals eaten per patch per day) within patch sizes 10, 20, and 30. Bars represent standard errors. N = 8 for all means. Patch size 10: *M. sanguinipes* mean = 1.375±0.532 SE, *A. deorum* mean = 3.125±0.581 SE, *A. coloradus* mean = 3.625±0.981 SE. Patch size 20: *M. sanguinipes* mean = 4.500±0.886 SE, *A. deorum* mean = 7.000±1.832 SE, *A. coloradus* mean = 5.625±1.117 SE. Patch size 30: *M. sanguinipes* mean = 6.625±1.335 SE, *A. deorum* mean = 7.375±0.778 SE, *A. coloradus* mean = 14.625±1.908