The role of vertebrate and invertebrate predators in a grasshopper community

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We conducted experiments at the National Bison Range, Montana to compare grasshopper densities in cages with and without spiders, and inside and outside avian exclosures to examine the impacts of the most common invertebrate and vertebrate predators. Spider predation did not reduce grasshopper populations. Avian predation reduced the abundance of large- and small-bodied grasshopper species, but total grasshopper abundance increased in the presence of birds, because medium-sized grasshopper species (250–500 mg adult size) became more abundant. The decrease in abundance of large-bodied grasshoppers was due to birds preferentially killing them; however, predation did not explain declines in small-bodied grasshoppers or increases in medium-sized grasshoppers. These changes in abundance may be due to avian predation modifying competitive interactions. Medium-sized species increase in abundance, when the competitively superior large-species are reduced; this in turn increases competition by the superior medium-sized species on the small species. Therefore, avian predation produced indirect effects on competitive interactions and acted in a "keystone" fashion.

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Community ecologists claim that terrestrial herbivores often are predator-limited and seldom food-limited, i.e., HSS (Slobodkin et al. 1967, Hairston et al. 1960, Hairston 1989). An alternative view is that herbivore populations are food-limited (Fretwell 1977), and predators only kill prey already destined to die from food-shortages (compensatory mortality sensu Errington 1946a, b, 1956). Another possible explanation integrates predation and food-limitation, claiming that the competitive allocation of food resources between different herbivore species is modified by selective predation. This is the classic "keystone" predator concept (Paine 1966, 1984). Because insect herbivores are not usually considered to be food-limited (Strong et al. 1984, Lawton and Strong 1981), these alternatives are less frequently invoked for them.

We examined the above three alternative hypotheses (strictly predator-limited, strictly food-limited, and a combination of both) using experimental manipulations of grasshopper populations and their principal invertebrate (spiders) and vertebrate (bird) predators.

Numerous studies argue that grasshopper densities are primarily controlled by predators (Dempster 1963, Greathead 1963, Lavigne and Pfadt 1966, Stower and Greathead 1969, Joern and Rudd 1982, Joern 1986, 1992, Kajak et al. 1968, Fowler et al. 1991, Hurd and Eisenberg 1990, Bock et al. 1992). These claims are based on qualitative observations, with the exception of a few experimental studies with avian predators (Joern 1986, 1992, Fowler et al. 1991, Bock et al. 1992) and spiders (Kajak et al. 1968, Hurd and Eisenberg 1990). However, Joern (1992) found that birds did not consistently reduce grasshopper densities across micro-habitats within a year and between years. Nonetheless, our results support the hypothesis that food-limitation in combination with predation structures the grasshopper

Table 1. Comparison of microclimate measures inside and outside the grasshopper cages. Measurements were made at 0200, 1000, and 1400 hours on five summer days. These times were used to represent the range of warmest and coolest conditions during day and night. Means and standard errors are presented.

Parameter	Ratio of inside to outside value	Effect on grashopper's thermal budget
Solar radiation (W m^{-2})	0.80±0.04	Decrease
Air Temperature (°C)	1.04±0.06	Increase
Wind (m s^{-1})	0.96±0.07	Increase
Ground Surface Temperature (°C)	0.97±0.03	Decrease
Humidity (mm Hg)	1.03±0.04	Increase

community, and the ability to observe simple predator-limitation will be restricted to environments where grasshoppers only attain low densities.

Study site

We studied predation on grasshoppers from 1985–1987 and 1989–1991 at a 4 ha Palouse prairie site at the National Bison Range, Montana, USA (Sanders and Lake Counties). The study site was fully described by Belovsky et al. (1990). The site is dominated by grasses (70–96% of dry mass in different years); *Poa pratensis* (L.) and *Elymus smithii* (Rybd.) are the most abundant grasses, while *Achillea millefolium* (L.), *Aster falcatus* (Lindl.), and *Erigeron* sp. are the most common forbs. Plant biomass in late September varied over the study from 53.5–98.2 g-dry m^{-2}.

Fifteen species of grasshoppers (Orthoptera, Acrididae) were observed at this site over 6 years; *Melanoplus femurrubrum* (DeGeer) and *M. sanguinipes* (Fabr.) were the most common (averaging 82% of all individuals). Peak grasshopper densities in patches of vegetation varied between 2–12 adults m^{-2} in August, and nymphal densities in early July were between 7–120 individuals m^{-2}. The most common spiders preying upon grasshoppers belong to the families Araneae, Lycosidae and Clubionidae. The major avian predators are the western meadowlark (*Sturnella neglecta*), the grasshopper sparrow (*Ammodrammus savannarum*) and the eastern and western kingbirds (*Tyrannus tyrannus* and *T. verticalis*).

Methods

1) *We studied the effects of spider predation on grasshopper populations* in the absence of birds using cages (0.01 m^2 basal area and 0.90 m height) made of aluminum insect screen. We buried the base of the cages into the ground over natural patches of vegetation and secured them with stakes to minimize wind damage; we folded and secured the tops of the cages using clips to permit easy access.

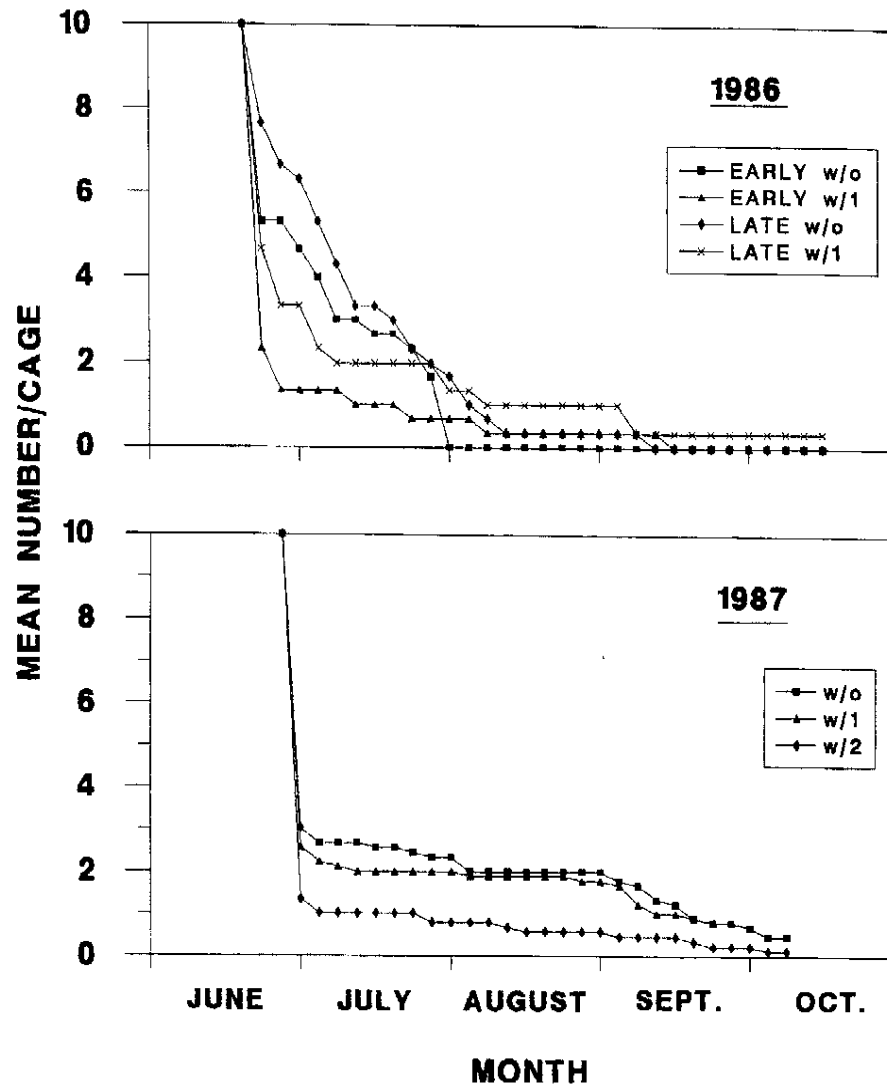We measured cage effects on abiotic conditions (Table 1) using five measures: 1) net radiation (Fritschen net radiometer), 2) air temperature, 3) wind speed (hot-wire anemometer), 4) ground temperature (infrared radiometer), and 5) vapor-pressure deficit (sling-psychrometer). Using a model of orthopteran thermal balance (Montcith 1973), these differences could lead to a 1.0°C average deviation in body temperature for grasshoppers (maximum deviation of 1.3°C) at each hour during a day. Based upon studies of the grasshopper's activity versus body temperature (Parker 1930, Brett 1947), we found that these differences would have little effect on the grasshoppers.

We placed the cages in a grid separated by at least 2 m and assigned predator-prey density treatments randomly to the cages. We stocked nymphs of the grasshopper, *M. femurrubrum*, as prey, because their small size made them more vulnerable at all age categories to spider predation. In 1986, the cages contained 10 early instar (1st-3rd instars) or late instar (4th-5th instars) nymphs. In 1987, cages contained 6, 10 and 16 early or late instar nymphs. These nymphal densities span the range of field densities measured for hatchlings in patches of vegetation (see Study site). We stocked spiders at 3 densities: zero, 1 (1986 and 1987), or 2 (1987 only) individuals/cage. In 1986, there were 4 combinations of grasshopper-spider densities: 10 early instar/0, 10 early instar/1, 10 late instar/0 and 10 late instar/1; in 1987, there were 9 combinations of grasshopper (early or late instar)-spider densities: 6/0, 6/1, 6/2, 10/0, 10/1, 10/2, 16/0, 16/1, 16/2. Each grasshopper-spider density combination was replicated with three cages/year. Stocking occurred in late-June, and censusing of the grasshoppers and spiders in the cages occurred every two days until early October when cold night-time temperatures killed grasshoppers.

We measured field densities of spiders during June, 1985, in six 100 m^2 areas by collecting, while crawling on the ground, all spiders observed that had an abdominal diameter >5 mm (smallest size observed to prey on grasshoppers).

2) *We studied the effects of bird predation on grasshopper populations* in 1985–1987 and 1989–1991, following the experimental design described by Joern (1986). Each year, we constructed three 100 m^2 exclosures at the site using nylon mesh (5 cm squares) to

Fig. 1. Average densities in experimental populations initiated with *Melanoplus femurrubrum* nymphs, with and without spiders, for the summers of 1986 and 1987. The densities reflect the number of grasshoppers at each time period regardless of their stage of development (i.e., early, late, or adult).

1986

- ■ EARLY w/o
- ▲ EARLY w/1
- ♦ LATE w/o
- ✕ LATE w/1

1987

- ● w/o
- ▲ w/1
- ♦ w/2

MEAN NUMBER/CAGE

JUNE   JULY   AUGUST   SEPT.   OCT.

MONTH

exclude birds. Each exclosure was contiguous on one side with a 100 m² area that was open (control). In late-September, we removed the nylon mesh, and placed insect netting (1.25 m-wide) around the exclosures and controls. The insect netting either contained escaping grasshoppers or forced them to fly high enough, so that we could observe their departure. Two individuals caught grasshoppers in each exclosure and control for 3–4 15 min consecutive periods, and preserved them in 70% ethyl alcohol for later identification to species and sex.

We estimated grasshopper density using a "catch-effort" technique (Southwood 1978: 230). The sum of all grasshoppers caught in the area prior to a 15 min catch period was the independent variable, and the number caught in that 15 min period was the dependent variable. We correlated these 3–4 values for an area using simple linear regression; the regression's x-intercept was an estimate of population size. The coefficient

of variation for these population estimates was 8–15%. Also, during the census, we counted all spiders that were observed to have an abdominal diameter >5 mm.

After censusing the grasshoppers in late-September, we measured the vegetation inside the exclosure and control areas by randomly sampling five 0.1 m² plots in patches of vegetation in each exclosure and control. We clipped the vegetation in each plot, separated it between grasses and forbs, and then dried, weighed, and chemically digested it (an index of digestibility to the grasshoppers: Belovsky and Slade submitted b). We estimated an index of food abundance for the grasshoppers in each area as the sum of the product of grass biomass and its chemical solubility and the product of forb biomass and its chemical solubility.

We recorded 25 toe-points (Daubenmire 1947) in each area as vegetated or bare ground to estimate the amount of the 100 m² area covered by vegetation. All grasshopper censuses were expressed in terms of num-

Table 2. Repeated measure unbalanced ANOVA results for the grasshopper population densities in cages over a summer related to year, initial density, initial age of individuals, and the presence/absence of spiders in experimental cages. Interaction terms were not significant.

Number of spiders	Variable	Between cages	Between days over a summer
1 spider	Year	F = 0.27 df = 1,24; P=0.61	F = 4.39 df = 23, 552; P < 0.001
	Age	F = 0.77 df = 1,24; P < 0.39	F = 1.14 df = 23, 552; P < 0.29
	Density	F = 3.71 df = 2, 24; P < 0.04	F = 1.85 df = 46, 552; P < 0.001
	With and without spiders	F = 0.58 df = 1, 24; P < 0.46	F = 4.39 df = 23, 552; P < 0.001
	Day		F = 23.22 df = 23, 552; P < 0.001
2 spiders	Density	F = 3.04 df = 2, 12; P < 0.08	F = 3.21 df = 46, 276; P < 0.001
	With and without spiders	F = 3.04 df = 1,12; P < 0.10	F = 1.21 df = 23, 276; P < 0.24
	Day		F = 7.29 df = 23, 276; P < 0.001

bers per area covered by vegetation (census per 100 m² and fraction of area covered by vegetation) to standardize for differences in vegetated areas.

In June, 1990 and 1991, we randomly placed five 0.25 m² rings in the exclosures and controls, so we could count the number of grasshoppers in the rings every 1-2 wk without having to enter the area. We estimated
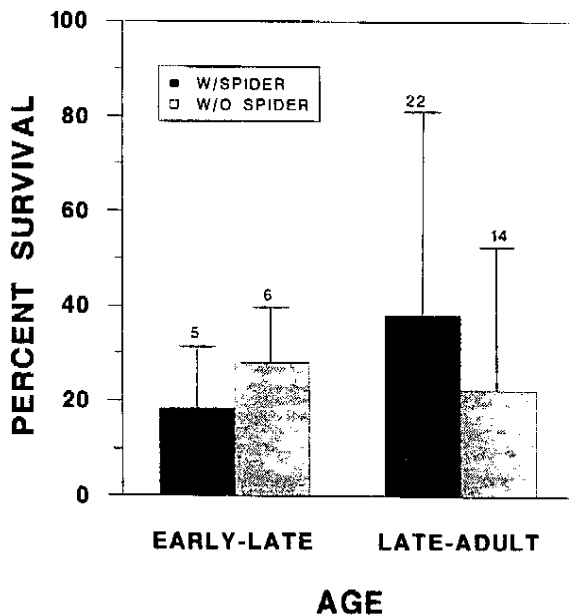

Fig. 2. The survival from early instars to late instars, and survival from late instars to adults of *Melanoplus femurrubrum* for experimental populations with and without spiders. Standard deviations and sample sizes are presented. The survival is presented for populations initiated with 10 individuals to control for density dependence (see Table 2).

population size for each 1-2 wk period as the number of individuals observed divided by the area encompassed by the rings (Onsager and Henry 1977). This allowed us to determine whether the more complete censuses in late-September provided representative results for the entire summer.

Joern (1986, 1992) reported that the nylon mesh had a minimal abiotic impact on the environment in the exclosures relative to the controls. However, to test whether the exclosures affected grasshopper movement, we conducted an experiment in the laboratory under uniform light. We placed an "exclosure" constructed of the nylon mesh (30 cm × 30 cm × 30 cm) within a box (45 cm × 45 cm × 30 cm), so that the area of floor and volume inside the "exclosure" equaled the area and volume outside the "exclosure". We then placed 10 grasshoppers inside the "exclosure" or outside, and recorded their distribution (inside vs outside) after 20 min. The experiment was conducted twice with grasshoppers initially outside the "exclosure" and twice initially inside the "exclosure". We detected no bias in grasshopper movement (χ^2 = 0.40, df = 1, P < 0.55). Joern (1992) conducted a longer term movement test on a larger scale with *Ageneotettix deorum* and found no effect of the mesh on their movement.

3) We measured annual changes in predation rates on grasshoppers during 1985–1987 and 1989–1991 using *M. sanguinipes* individuals that we placed in the field on monofilament tethers (Belovsky et al. 1990). Tethering was necessary because the exclosure experiments require unrealistic levels of replication to measure predation rates. We used *M. sanguinipes*, because it was abundant and survived well on tethers. Predation intensity was the number of tethered individuals killed by predators per 100 presentations (crude predation rate sensu Belovsky et al. 1990). A presentation was a 2 h

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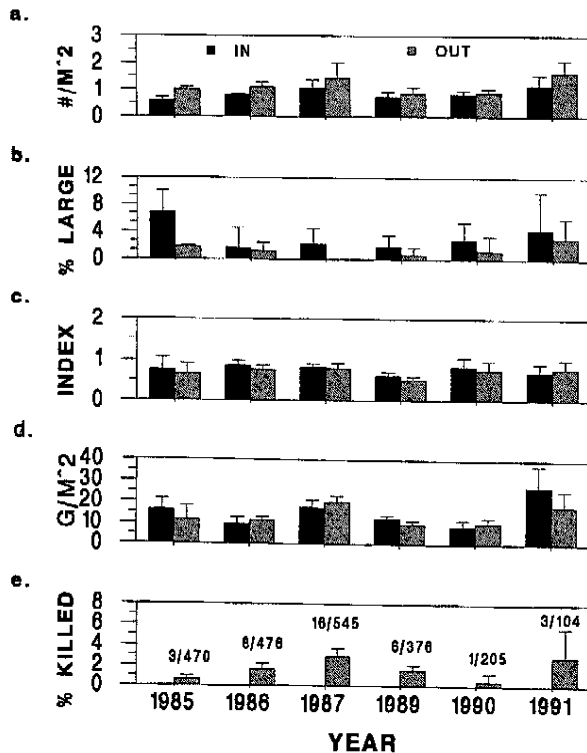
Fig. 3. Parameters measured in the avian exclosure and control compared over 6 years. Means and standard deviations are presented for the 3 replicate exclosures or controls in a year. Five parameters for late-September are presented: a) overall grasshopper density (# m^{-2} of vegetated area); b) the relative abundance of large grasshoppers (> 500 mg adult size); c) the Shannon-Weaver diversity index; d) food abundance for grasshoppers (g − soluble plant tissue m^{-2}); e) predation rates on tethered adult *Melanoplus sanguinipes* (% killed per 100 2 hr presentations in August; # of kills to presentations is also presented).

period during daylight hours. We conducted tethering experiments in August. Estimates of field densities at these times were available (Belovsky and Slade submitted a).

Statistical analyses employed the statistical package SYSTAT for the PC (Wilkinson 1990). Proportions were

always analyzed using arcsine transformations. ANOVA, ANCOVA and multiple linear regression were the principal statistical tests employed.

Results

Spider predation affected *M. femurrubrum* experimental populations over the summer (Fig. 1). Densities declined more rapidly over time with 1 spider/cage than with no spiders (Table 2, significant experimental effect between days). However, populations without spiders stabilized at the same or lower densities than those with 1 spider (Table 2, insignificant experimental effect between cages). When 2 spiders were present, populations were always less dense than those without spiders (Table 2, one-sided P < 0.05 for the experimental effect between cages). Finally, initial density had a significant or nearly significant negative effect on density (Table 2).

Spiders affected density in two ways. First, a lower proportion of grasshopper nymphs survived to become late instars when spiders were present (Fig. 2). Second, a greater proportion of late instar nymphs survived to become adults when spiders were present (Fig. 2). Early instar density and spiders had significant effects on survival (ANCOVA: spiders − F = 3.88; df = 1, 29; P < 0.05; initial density: F = 58.65; df = 1, 29; P < 0.001), but for late instars, only initial density had a significant effect on survival (ANCOVA: spiders − F = 0.78; df = 1, 31; P < 0.38; initial density − F = 3.87; df = 1, 31; P < 0.05).

Therefore, predation from 1 spider in the experiments was compensatory, or depensatory since the greater late instar survival at reduced densities "balanced" or exceeded the lower early instar survival due to spider predation. This permitted populations with 1 spider or none to stabilize at comparable adult densities. But, predation from 2 spiders reduced early instar survival below the level at which increased late instar survival at lower densities could compensate.

Table 3. The balanced design ANOVA results for the avian exclosure experiments (exclosure vs control).

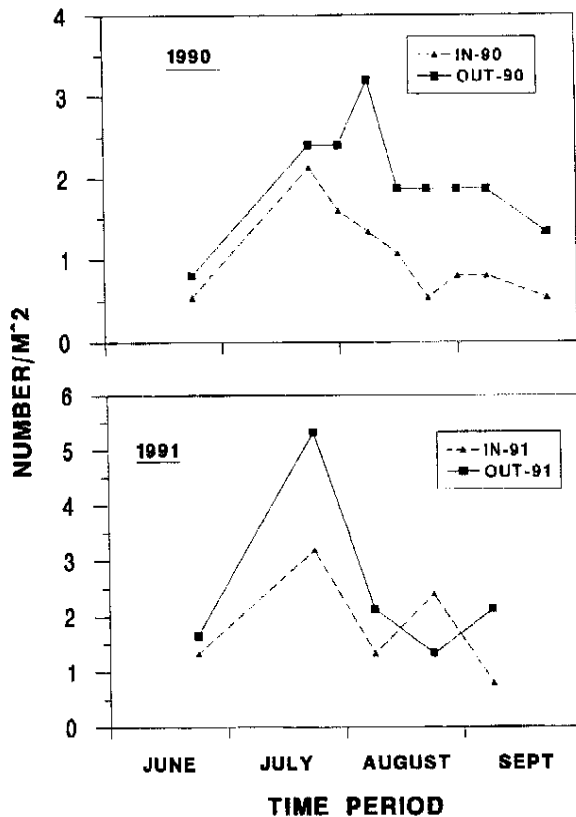| Dependent variable	Effect	F	df	P
Grasshopper density:	Year	4.84	5, 24	0.003
	Treatment	9.99	1, 24	0.004
	Year × treatment	0.57	5, 24	0.73
Percent large grasshoppers:	Year	1.79	5, 24	0.15
	Treatment	5.25	1, 24	0.03
	Year × treatment	0.59	5, 24	0.71
Food abundance:	Year	7.54	5, 24	0.001
	Treatment	1.15	1, 24	0.30
	Year × treatment	1.42	5, 24	0.25

Fig. 4. Grasshopper densities throughout the summers of 1990 and 1991 for the exclosure and control areas based upon ring-counts (see Methods).

controls were similar in early June as nymphs hatched, after this, densities were consistently greater in controls. This was counter to the expectation that predation should reduce densities.

While densities were greater in control areas, the effects of avian predation varied with the grasshopper species' body size. We used 3 body size categories: large species (>500 mg adult mass: *Dissosteira carolina* (L.), *Melanoplus bivittatus* (Say), *Arphia pseudonietana* (Thomas)); medium-sized species, which were most common (250-500 mg adult size: *M. femurrubrum* and *M. sanguinipes*); and small species (<250 mg: e.g., *Ageneottetix deorum* (Scudder), *Amphitornus coloradus* (Thomas), *Pseudopamala brachyptera* (Scudder)). Every year, the abundance of large grasshoppers was significantly lower in the controls (Fig. 3b, Table 2), averaging only 58.4% of exclosure densities. Small species also were significantly less abundant in control areas (median test = 11.90, df = 5, P < 0.05), averaging only 21.1% of exclosure densities. Therefore, the increase in overall grasshopper density in controls was solely due to medium-sized species, which was manifested at the community-level by a trend for grasshopper species diversity to decrease in controls (with birds) (Fig. 3c, sign test: P < 0.12). The greater overall density of grasshoppers in controls (with birds) did not reduce grasshopper food resources, since food abundance was not different for controls and exclosures (Fig. 3d, Table 3).

Using annual mean values, we examined the overall density of grasshoppers as a function of treatment (ex-

June spider densities averaged over 2 years in the field were 0.13 individuals m^{-2} ± 0.06 (N = 6) over the entire area, or 0.39 individuals m^{-2} in the vegetation, where grasshoppers occur. Since we placed cages over patches of vegetation, 1 spider/cage was 3X's the 2 year average June densities, and 2 spiders/cage was 6X's average. During early July, grasshopper nymphs at the site varied between 7-120 m^{-2} of vegetation in each year (Belovsky and Slade submitted a); this provided a ratio of grasshopper to spider numbers in the field between 18-311:1, while experimental ratios were 3-16:1. Therefore, spider predation in the field did not limit grasshopper densities, but was compensatory, since the spider density and ratio of grasshoppers to spiders in the experiments with 1 spider/cage were higher than in the field, but still produced a compensatory effect. It is unlikely that even a large between-year variability in spider densities would change this effect.

Bird predation produced a variety of effects that were not always expected. In mid-September, control (with birds) grasshopper densities always were greater than exclosure (without birds) densities (Fig. 3a, Table 3). This pattern did not depend upon the time of sampling during the summer (Fig. 4: paired t-test: t = 4.18, df = 17, P < 0.001): i.e., while densities in exclosures and
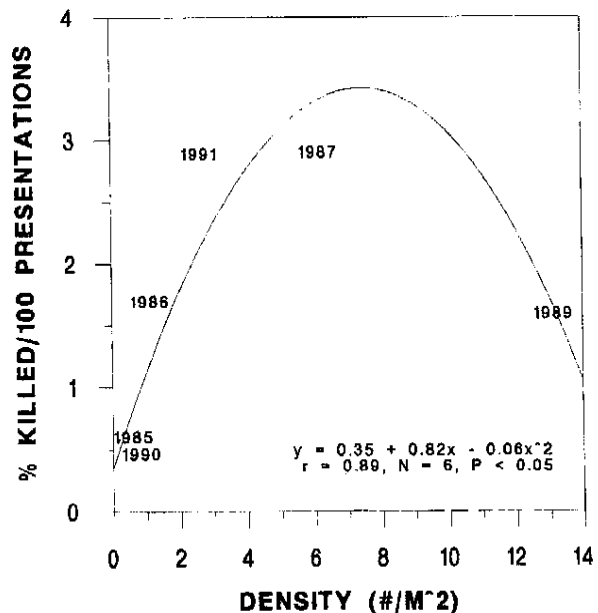

Fig. 5. Predation rates on tethered *M. sanguinipes* plotted with the overall grasshopper density in the field at the time of tethering during August. The quadratic regression fit to these data is presented.

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closure/control) and food abundance (ANCOVA: r = 0.98, N = 12, P < 0.001). Assuming that treatment effects would be primarily manifested through changes in the relative abundance of large species, we used a multiple linear regression (r = 0.74, N = 12, P < 0.03). The relative abundance of large grasshoppers had a negative effect (t = −2.25, P < 0.05), and food abundance had a positive effect (t = 2.93, P < 0.02). Therefore, food abundance and avian predation appeared to interact to structure the grasshopper community, with avian predation primarily acting to decrease the relative abundance of large species.

The number of spiders in the censuses was not related to the experimental treatment (exclosure/control) (sign test: P < 0.73). Therefore, birds did not seem to have an effect on the abundance of the grasshopper's major invertebrate predator; thus, avian effects were not operating indirectly through changes in spider predation.

Predation rates on tethered *M. sanguinipes*, primarily by birds (Belovsky et al. 1990), varied between years (χ^2 = 10.85, df = 5, P < 0.05). Predation rates increased as grasshopper density increased, but then decreased as density continued to increase (Fig. 5: quadratic regression - r = 0.90, N = 6, P < 0.09; density – P < 0.04; density^2 – P < 0.04). This is expected if predators had a Type II or III functional response, as was observed for one avian predator at this site (brown headed cowbird, *Molothrus ater*: Belovsky 1990, 1993).

We found that the large grasshopper species declined in relative abundance as the predation rate increased (r = −0.60, N = 12, P < 0.04). This relationship was unaffected by food abundance (P < 0.34).

Discussion

The experimental results indicate that the grasshopper community at this site is structured by both predation and food abundance. As expected from our other studies at this site (Belovsky and Slade submitted a), grasshopper densities increased with food abundance. Predation, on the other hand, had a much less straightforward role.

Spiders, the principal invertebrate predator, appeared to have little effect on grasshopper numbers at the spider densities and prey/predator ratios observed in the field. This predation was compensatory, if not depensatory (sensu Errington 1946a, b, 1956). Because bird predation did not appear to reduce spider densities, we concluded that the inability of spiders to reduce grasshopper densities was not an indirect effect of avian predation.

Compensatory predation requires density dependent responses in the prey population which were observed in this study and others (Belovsky and Slade submitted a). The increased survival of late instar nymphs at lower densities compensates for earlier spider predation; this

is possible, because late instar nymphs are large enough that they are less likely to be captured by spiders, and intraspecific competition for food is very intense among these grasshoppers (Belovsky and Slade submitted a).

Experimental studies, that have observed invertebrate predation reducing grasshopper densities (Kajak et al. 1968, Hurd and Eisenberg 1990) and potentially limiting their numbers, have used prey/predator ratios above those observed in the field. While our experiments indicated that spider predation could reduce grasshopper densities at lower prey/predator ratios, to achieve this, field ratios would have to be 19% of their observed values.

Birds, the principal vertebrate predator, did not produce the expected reduction in grasshopper numbers reported by others (Joern 1986, 1992, Fowler et al. 1991, Bock et al. 1992), but produced a mixture of effects. Birds decreased the absolute and relative abundances of large and small grasshoppers. We expected the decrease in the abundance of large species, since they were the preferred prey of birds (Belovsky 1990, Belovsky et al. 1990), but we did not expect the reduction in small species abundance, since they were not preferred. At our site, grasshopper vulnerability to avian predation increased with body size (Belovsky et al. 1990). Therefore, predation could not cause the decline in small species; this and the increase in medium-sized species must arise from an indirect effect of avian predation.

Avian predation's indirect effect might arise if the predation reduced the effects of intraspecific competition on a grasshopper species. As observed with spider predation, avian predators could reduce a grasshopper species' density, so that survival of those remaining could be increased. This would require intraspecific competition to depress survival more than predation, so that the predation was not only compensatory, but depensatory. While this might explain the increased density of medium-sized species, it would not explain the decline in small species densities. Therefore, we do not view this effect to be the principal reason for the observed results.

From other studies at this site, we know that when two grasshopper species compete, the larger species is a superior competitor, proportionally reducing the smaller species' numbers more than the smaller species reduces its numbers (Belovsky 1986, Belovsky and Slade submitted a, Krippner 1991, Moorehead 1993, Chase and Belovsky in press). However, as species become more different in size, the larger species is still a superior competitor, but the intensity of competition declines. This pattern would explain both the increase in abundance of medium-sized species, and the decline in small species. The decline in the abundance of larger species, as birds preferentially preyed upon them, might allow the medium-sized species to have greater survival increasing their numbers due to reduced competition with the large species. The increased densities of me-

dium-sized species might have an increased competitive effect on the small species, decreasing small species survival and abundance.

The studies reporting size-structured competition among grasshoppers at our site, also reported that this competition occurred for food (Belovsky 1986, Belovsky and Slade submitted a, Krippner 1991, Moorehead 1993, Chase and Belovsky in press). We found that overall grasshopper density was correlated with food abundance in the exclosures and controls, and increased grasshopper densities with bird predation did not reduce food abundance. This indicated that the increased overall grasshopper densities were a substitution of consumption by large and small species with an equivalent amount by the medium-sized species. Therefore, we believe that avian predation produced unexpected results for grasshopper populations by modifying their competitive interactions, making the birds "keystone" predators (sensu Paine 1966).

Avian predation appears to vary in importance for grasshopper communities. Several studies using the same experimental system of exclosures and controls have found avian predation to decrease the abundance of grasshoppers (Joern 1986, 1992, Fowler et al. 1991, Bock et al. 1992). While Joern (1992) reported that this pattern did not consistently emerge over 3 years and in different habitats, he never observed densities to increase with avian predation. However, our experiments conducted over 6 years have never produced a decline in overall grasshopper densities with avian predation (except for the large and small species), but have always resulted in an increase in density. Therefore, the effects of predation on grasshoppers cannot be considered to be uniform.

We believe that the variation observed in the effects of avian predation on grasshopper populations and communities may be explained by site differences in peak adult grasshopper densities observed over a summer and species composition. First, if large species are uncommon in an area, then birds' preferentially preying upon them will have little effect upon competitive interactions, and birds may predominantly prey upon the smaller species. Second, since we found predation intensity to vary with grasshopper density, increasing and then decreasing as density increased (Fig. 5), the ability of birds to impact grasshopper densities will be greatest at an intermediate density, that is relatively low (~ 2–3 individuals m^{-2}).

Based on reports of avian predation reducing grasshopper densities (Joern 1986, 1992, Fowler et al. 1991, Bock et al. 1992), we believe that these studies represent areas where large species were uncommon and/or peak summer adult densities were low (< 4 m^{-2}, where our site averaged > 4 m^{-2}). Furthermore, if grasshopper densities change with food abundance, as observed in our study, and food abundance varies annually by large amounts, 2 fold as observed in our study, the effects of predation could vary from year to year, only depressing overall densities when food abundance is low.

Conclusion

Neither spider nor avian predation decreased overall grasshopper densities, because predation was largely compensatory (sensu Errington 1946a, b, 1956). Avian predation actually increased overall grasshopper densities by playing a "keystone" role in the community (sensu Paine 1966, 1984); this occurred through its reducing the abundance of the competitively superior large grasshoppers, which allowed medium-sized grasshoppers to increase in abundance. Therefore, rather than simply depressing densities, avian predation interacted with food-limitation and interspecific competition to modify competitive interactions and structure the grasshopper community.

Our results indicate that predation in terrestrial herbivore communities can be important, but not necessarily in the simple density-limiting manner postulated by HSS (Hairston et al. 1960, Hairston 1989, Slobodkin et al. 1967). Rather the role of predation in terrestrial herbivore communities can be more complex, resembling the "size-efficiency" hypothesis (Hall et al. 1976) for zooplankton communities, where predation does not limit overall herbivore consumption of primary production, but changes herbivore species composition by modifying competitive interactions between herbivore species. Therefore, examining either for food- or predator-limitation in herbivore, even insect herbivore, communities may be too simplistic, and will require an approach that investigates the integration of these mechanisms' direct and indirect effects.

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