

# Direct and Indirect Effects of Avian Predation on Grasshopper Communities in Northern Mixed-grass Prairie

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**ABSTRACT** The ecological interactions between grasshoppers, predators, and resources that can limit the population growth of grasshoppers are poorly understood. A number of field experiments have shown that top-down control by avian predators can limit grasshopper populations, but the effects of avian predators on grasshopper populations can differ between years and between sites in the same habitat. I conducted experiments examining grasshopper populations in avian exclosures and control plots for 3 yr at two locations in eastern Montana. Avian predation had variable direct and indirect effects on grasshopper communities at the two locations. Grasshopper population densities, species richness, and diversity at the two sites were not consistently significantly affected by avian predation, indicative of weaker top-down effects. The effects of predation varied among years and between the two sites. Avian predators modified body size composition of grasshopper populations through size-selective predation on medium-bodied grasshoppers. Even in years when avian predators did not limit grasshopper populations, selective predation seemed to indirectly mediate competitive interactions among grasshoppers. Birds reduced the proportion of presumably competitively superior medium-bodied grasshoppers, and small-bodied grasshoppers increased in abundance.

**KEY WORDS** predation, Acrididae, birds, grasshopper populations, grasslands

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THE COMPLEX ECOLOGICAL INTERACTIONS between grasshoppers, predators, climate conditions, and host plants that can limit the population growth of grasshoppers remain poorly understood (Joern 2000). Although fluctuations in grasshopper densities have often been assumed to be related to weather conditions (Andrewartha and Birch 1954), correlations with abiotic conditions often explain <30% of the variation in grasshopper densities (Joern 2000). Both predation and competition can play important roles in regulating grasshopper populations; however, the relative importance of those biotic factors can change with environmental conditions, locations, and between years (Belovsky and Joern 1995, Joern 2000). A number of field experiments, mostly in mixed-grass prairie or semiarid grasslands, have generally shown decreased grasshoppers densities in the presence of avian predation, indicating that top-down control by avian predators can regulate grasshopper populations in these systems (Joern 1986, 1992, Fowler et al. 1991, Bock et al. 1992, Gardner and Thompson 1998). Similar experiments by Belovsky and Slade (1993) in Palouse prairie showed an increase in overall grasshopper populations in the presence of avian predation, with a decreased percentage of larger bodied grasshoppers. However, the effects of avian predation and competition on local grasshopper population dynamics can

differ between years and sites in the same habitat (Joern 1992, 2000, Belovsky and Joern 1995). Given the observed temporal and spatial variation in the importance of natural biotic controls, additional studies examining the direct and indirect effects of avian predation need to be conducted across a variety of grassland types to allow increased generalizations regarding the importance of avian predation on rangeland grasshopper populations. Furthermore, an increased understanding of when natural biotic agents exert a limit on grasshopper populations is important because of the potential for range managers to use natural biotic agents in managing grasshoppers when they play a significant role (Joern 2000).

Belovsky and Joern (1995) conducted a literature review and concluded that avian predation limited sites typically had relatively low grasshopper densities with a greater proportion of smaller-bodied grasshoppers. These sites were typically dominated by C<sub>4</sub> grasses and Gomphocerine grasshoppers. In contrast, food limited sites where avian predation either had no effect or a positive effect on grasshopper populations typically had high grasshopper population densities with a higher proportion of large-bodied grasshoppers and were dominated by C<sub>3</sub> grasses (Belovsky and Joern 1995). Belovsky and Joern (1995) also concluded that predator limitation would occur more frequently when food quality was poor. In addition to the direct top-down effects of bird predation on grass-

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hopper densities, birds can indirectly reduce or mediate competition among grasshoppers. Insectivorous birds typically select larger body size grasshopper species (Belovsky et al. 1990). Belovsky and Slade (1993) showed that selective predation by birds on competitively dominant large-bodied grasshoppers mediated interspecific competitive interactions. The objectives of this study were to determine if avian predation limited grasshopper populations, affected community composition or size class distribution, and mediated interspecific competition at two northern mixed-grass prairie sites in eastern Montana. An additional objective was to examine how the experimental results fit the patterns noted by Belovsky and Joern (1995).

### Materials and Methods

I studied the effects of bird predation on grasshopper populations at two sites in eastern Montana, closely following the approach of Joern (1986, 1992) and Belovsky and Slade (1993) to enable direct comparison of results with those studies. Whited was located in eastern Richland County, MT (47°28' N 104°4' W), and Miles City was located on the USDA-ARS Fort Keogh Livestock and Range Research Laboratory near Miles City, MT (46°22' N 105°5' W). I conducted avian enclosure experiments from 1999 to 2001 at the Miles City site and from 2000 to 2002 at the Whited site. The northern mixed-grass prairie sites were located ≈200 km apart. Greater than 90% of the vegetative biomass was typically composed of grasses and sedges. Vegetation at Whited was dominated by western wheatgrass (*Pascopyrum smithii*, also called *Agropyron smithii*), blue grama (*Bouteloua gracilis*), needle and thread (*Stipa comata*), prairie junegrass (*Koeleria pyramidata*), and threadleaf sedge (*Carex filifolia*). Vegetation at Miles City was highly dominated by western wheatgrass. The only common C<sub>4</sub> grass at either site was blue grama, a low growing bunchgrass that was more abundant at Whited. Common forbs included *Artemisia frigida* and *Sphaeralcea coccinea*.

At each site, I chose a homogeneous area that was free of cattle grazing and large enough to include three replicate pairs of avian enclosures and controls. Plot size was 10 by 10 m at Miles City and 9.1 by 9.1 m at Whited. Each avian enclosure shared one side with a control plot of equal dimensions. I used fence posts to mark the corners of all enclosures and controls and randomly assigned treatments to paired plots. Four replicates were sampled at Miles City in 1999. Avian enclosures were constructed of nylon mesh with 2.5-cm square openings (J.A. Cissel, Lakewood, NJ). No birds were observed in enclosures at either site. Common bird species in the area of the sites include western meadowlark [*Sturnella neglecta* (Audubon)], vesper sparrow [*Poocetes gramineus* (Baird)], horned lark (*Eremophila alpestris* L.), and grasshopper sparrow [*Ammodramus savannarum* (Gmelin)] (George et al. 1992, 1995). Each year in early June, I erected avian enclosures over a wire frame supported by 1-m-high corner posts and secured the bottom of the mesh onto the soil surface using landscape staples. The

movement of marked *Ageneotettix deorum* in the field was unaffected by similar mesh enclosures (Joern 1992). Similar avian enclosures had small effects on microclimate conditions (Joern 1986). I counted the number of grasshoppers within a series of 40 0.1-m<sup>2</sup> aluminum wire rings each July to determine peak grasshopper population densities in areas near the enclosures and controls (Onsager and Henry 1977).

I estimated total grasshopper density in enclosures and controls yearly in mid- to late August using a catch-effort removal technique (Belovsky and Slade 1993, Greenwood 1996). Fiberglass window screening (1.2 m high) was stretched around the perimeter of an enclosure or control to eliminate or minimize grasshoppers moving in or out of plots. The window screening was secured with small sandbags along the bottom. Individual enclosure nets were removed immediately before grasshopper removal. Two individuals systematically caught grasshoppers with an insect net in a given plot for three or four consecutive 15-min periods, with a 5-min rest period in between each catch. Grasshoppers escaping by flying over the screen were counted and identified to species when possible. Spiders capable of killing adults grasshoppers were noted. Grasshoppers were killed in 70% ethanol and frozen for later identification to species and sex. The catch in a given 15-min time period was used as the dependent variable in a regression, whereas the accumulated catch of grasshoppers before that catch period was the independent variable (Greenwood 1996). I used simple linear regression with the estimate of total population density in a control or enclosure equal to the x intercept of the regression line (Belovsky and Slade 1993). Nymph-overwintering grasshopper species, which hatch in late summer and are early instar nymphs in August, were excluded from all analyses.

Grasshopper species were grouped into three body size categories of small (<250-mg adult size, e.g., *Ageneotettix deorum* Scudder, *Opeia obscura* Thomas), medium (250- to 500-mg adult size, e.g., *Melanoplus femurrubrum* DeGeer, *M. gladstoni* Scudder, *M. sanguinipes* Fabricius, *Phoetaliotes nebrascensis* Thomas), and large (>500-mg adult size, e.g., *Arphia pseudonietana* Thomas, *M. differentialis* Thomas, *M. packardii* Scudder), following the categorization of Belovsky and Slade (1993). In order of abundance, common species at Whited included *M. gladstoni*, *O. obscura*, *P. nebrascensis*, *M. sanguinipes*, *M. femurrubrum*, *Hypochlora alba* (Dodge), and *A. deorum*. The most abundant species at Miles City in 2000 and 2001 were *M. sanguinipes*, *P. nebrascensis*, *O. obscura*, and *A. deorum*. In 1999, *P. nebrascensis* comprised 60% of grasshoppers caught at Miles City. Too few large-bodied grasshoppers were consistently present at either site for statistical analysis. I examined treatment differences in body size composition using medium-bodied grasshoppers. The arcsine transformation was used for statistical analysis of proportional data, although untransformed data are presented in figures. The effects of avian predation on community composition were analyzed using species richness, Shannon diversity index and Margalef's diversity index, which adjusts

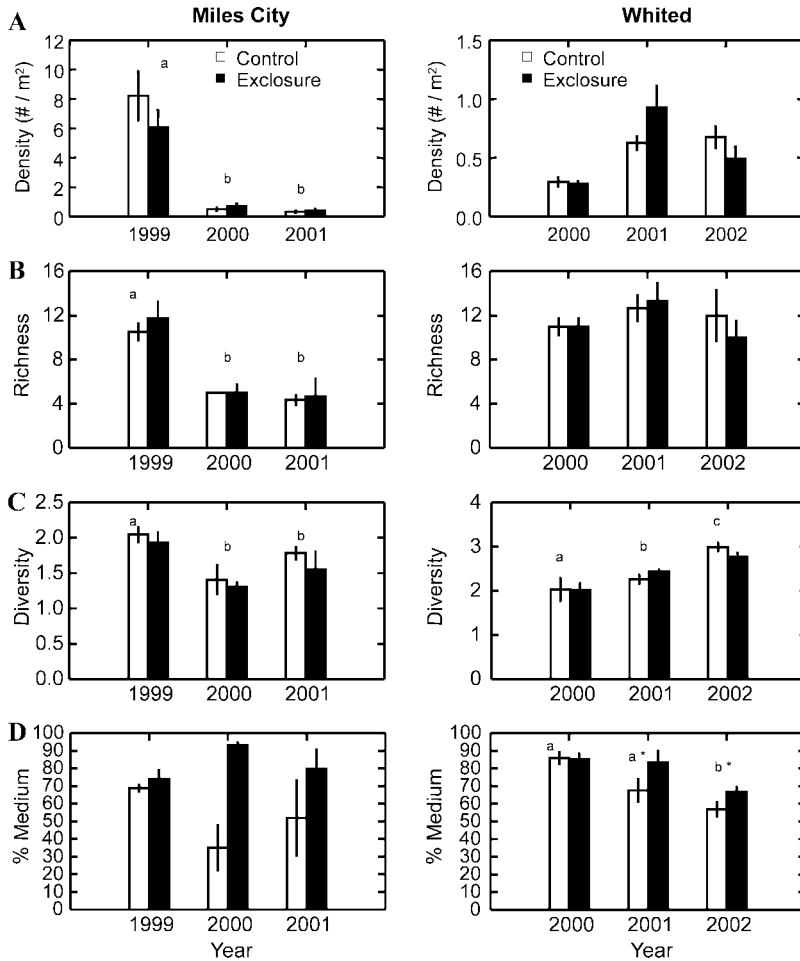


Fig. 1. Grasshopper density ( $\#/m^2$ ) (A), numerical species richness (B), Shannon-Weaver species diversity index (C), and percentage medium-bodied grasshoppers (D) in controls and exclosures at Miles City and Whited. Values are means  $\pm$  SE. Treatment means with different letters are significantly different between years (Bonferroni,  $P < 0.05$ ). \*Significant differences between exclosures and controls within a year (Bonferroni,  $P < 0.05$ ).

species richness for sample size (Magurran 2004). I used analysis of variance (ANOVA) models to examine the effect of year and avian treatment on grasshopper density, species richness, Margalef's diversity index ( $[\text{species no.} - 1]/\ln N$ ), Shannon diversity index, the number of small-bodied grasshoppers, and the percentage of medium-bodied grasshoppers.

I assessed green vegetative biomass and percentage nitrogen content of grasses at the end of the summer to determine if host plant availability differed significantly between exclosure and control plots and to examine if the effects of predation varied with plant quality (Belovsky and Joern 1995). After grasshoppers were removed, five  $0.1\text{-m}^2$  plots were clipped in each exclosure or control by randomly tossing a  $0.1\text{-m}^2$  ring and clipping the green vegetation inside the ring. Vegetation was separated by grasses and forbs and dried, weighed, and ground using a Wiley mill (Belovsky and Slade 1995). Total nitrogen content was determined using a dry combustion C/N analyzer

(Mastejovic 1997). Nitrogen content of grass samples was used as an index of host plant quality. Nitrogen content is frequently positively correlated with demographic attributes of grasshoppers (Joern and Behmer 1997, 1998). Treatment effects on forb biomass at Miles City and on total nitrogen content of forbs at both sites were not examined because of limited forb biomass in many samples. Mean values were used for vegetation analyses. ANOVA models were used to examine the effect of year and avian treatment on plant biomass and nitrogen content. Systat 10.2 (Systat Software 2002) was used for all statistical analyses.

## Results

Grasshopper densities in exclosures and controls varied between years at both sites (Fig. 1A; Table 1). At Miles City, grasshoppers were significantly more abundant in 1999 (Fig. 1A). Grasshopper densities at

**Table 1.** ANOVA results for grasshopper density per plot, species richness, Shannon species diversity index, Margalef diversity, percentage medium-bodied grasshoppers, and no. small-bodied grasshoppers for Miles City and Whited

Site	Dependent	Source	df	SS	F	P
Miles City	Grasshopper density	Avian	1,14	19278	0.75	
		Year	2,14	2129863	41.76	<0.001
		Interaction	2,14	62640	1.228	0.32
	Species richness	Avian	1,14	1.37	0.55	0.47
		Year	2,14	195.83	39.07	<0.001
		Interaction	2,14	1.49	0.29	0.75
	Shannon diversity	Avian	1,14	0.109	2.32	0.15
		Year	2,14	1.385	14.74	<0.001
		Interaction	2,14	0.015	0.16	0.85
	Margalef diversity	Avian	1,14	1.605	10.46	<0.001
		Year	2,14	0.023	0.30	0.59
		Interaction	2,14	0.108	0.71	0.51
	Percent medium-bodied	Avian	1,14	0.620	25.22	<0.001
		Year	2,14	0.010	0.19	0.83
		Interaction	2,14	0.329	6.68	<0.01
	Small-bodied	Avian	1,14	5230	4.65	<0.001
		Year	2,14	99315	44.16	0.049
		Interaction	2,14	4345	1.93	0.182
Whited	Grasshopper density	Avian	1,12	31.7	0.28	0.61
		Year	2,12	4976.6	21.58	<0.001
		Interaction	2,12	1251.8	5.43	0.02
	Species richness	Avian	1,12	0.89	0.25	0.63
		Year	2,12	16.00	2.21	0.15
		Interaction	2,12	5.78	0.80	0.47
	Shannon diversity	Avian	1,12	0.002	0.06	0.81
		Year	2,12	2.28	31.68	<0.001
		Interaction	2,12	0.11	1.58	0.24
	Margalef diversity	Avian	1,12	0.971	1.82	0.20
		Year	2,12	0.062	0.23	0.64
		Interaction	2,12	0.093	0.17	0.84
	Percent medium-bodied	Avian	1,12	0.040	7.28	0.02
		Year	2,12	0.232	20.93	<0.001
		Interaction	2,12	0.031	2.78	0.1
	Small-bodied	Avian	1,12	88.89	6.75	0.023
		Year	2,12	582.11	22.10	<0.001
		Interaction	2,12	68.11	2.58	0.116

Miles City were not affected by presence of avian predation, and the treatment by year interaction was not significant (Fig. 1A; Table 1). There was a significant treatment by year interaction at Whited (Fig. 1A; Table 1), indicating that grasshopper density did not differ in the same manner between exclosures and controls in each year. The interaction resulted from lower grasshopper densities in control plots exposed to avian predators in 2001, but not in 2000 or 2002 (Fig. 1A). Peak grasshopper densities at the Miles City site ranged from a high of 120/m<sup>2</sup> in 2000 to 15/m<sup>2</sup> in 2001 (Fig. 2). A population crash occurred at Miles City in 2000, with densities falling from a peak of 120/m<sup>2</sup> (Fig. 2) to <1/m<sup>2</sup> in mid-August (Fig. 1A) because of severe food limitation (D. Branson and M. Haferkamp, unpublished data). Peak grasshopper population densities at Whited were much lower and less variable than at Miles City, averaging between 7 and 10/m<sup>2</sup> (Fig. 2).

Species richness was similar in exclosures and controls at both locations, but varied significantly between years at Miles City (Fig. 1B; Table 1). Although grasshopper densities varied significantly between years at both sites, the results for Margalef's species diversity index, which corrects for differences in sample size, were similar to those of numerical species richness (Table 1). While Shannon species diversity

index was higher in control plots exposed to bird predation at Miles City in each year (Fig. 1C), Shannon diversity was not significantly affected by avian predation at either site (Fig. 1C; Table 1). Shannon diversity varied significantly between years at both sites (Fig. 1C; Table 1). Both Shannon diversity and species richness were significantly higher in 1999 at Miles City (Fig. 1), when final densities were also highest (Fig. 1A). Year and avian treatment did not significantly interact to affect species richness, Margalef's diversity, or Shannon species diversity at either site (Table 1).

The percentage of medium-bodied grasshoppers was significantly lower in control plots at both sites (Fig. 1D; Table 1). There was a significant treatment by year interaction on the percentage of medium-bodied grasshoppers at Miles City (Table 1). The interaction resulted from a large reduction in the percentage of medium-bodied grasshoppers in control plots in 2000 (Fig. 1D; Table 1), because medium-bodied grasshoppers were numerically 80% less abundant in controls in 2000. At Whited, control plots had a lower percentage of medium-bodied grasshoppers in both 2001 and 2002 (Fig. 1D), and the interaction was not significant (Table 1). In 2001, when avian predators appeared to reduce overall grasshopper densities, medium-bodied grasshoppers were 47% less abundant

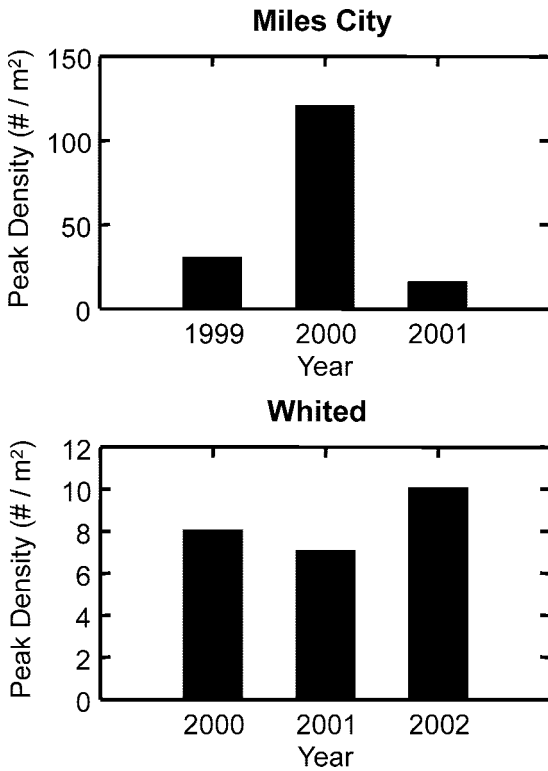


Fig. 2. Peak grasshopper densities at Miles City and Whited.

on average in controls. No significant differences were evident at Whited in 2000, when final population densities were low in both exclosures and controls (Fig. 1A). Small-bodied grasshoppers were numerically more abundant in controls in all years at both Miles City (Table 1; control =  $87.2 \pm 29.5$ , exclosure =  $50.7 \pm 21.3$ ) and Whited (Table 1; control =  $13.0 \pm 2.7$ , exclosure =  $8.6 \pm 1.9$ ). Few large-bodied grasshopper species were consistently present at either site. No large-bodied grasshoppers were caught at Miles City in 2000 or 2001. At Whited, only one large-bodied grasshopper was caught on average in each plot ( $x = 1.16 \pm 1.48$ ).

At both sites, grass biomass differed significantly between years but did not differ between exclosures and controls (Fig. 3A; Table 2). Very little green grass biomass remained at Miles City in 2000 (Fig. 3A), when peak grasshopper densities were very high (Fig. 2). Nitrogen content of grass differed significantly between years at Miles City, but did not differ between exclosures and controls at either site (Fig. 3B; Table 2). Nitrogen content of grass did not differ between years at Whited (Table 2). Forbs were not consistently present in clipped plots at Miles City, and no forbs were present in 2000 (Fig. 3C). At Whited, forb biomass varied significantly between years, but not between exclosures or controls (Fig. 3C; Table 2). There were no significant interactions on vegetation characteristics at either site.

## Discussion

Avian predation did not consistently reduce overall grasshopper numbers at the two northern mixed-grass prairie sites, as frequently observed in studies on mixed-grass or semiarid grasslands (Joern 1986, Fowler et al. 1991, Bock et al. 1992, Gardner et al. 1998). At Miles City, predation may have operated in a compensatory fashion by removing individuals that would have otherwise died from food limitation (Joern 2000, Oedekoven and Joern 2000), particularly in 1999 and 2000 when exploitative competition and food limited mortality was apparent (unpublished data). Belovsky and Slade (1993) and Belovsky and Joern (1995) predicted birds would have the greatest ability to impact grasshopper densities at relatively low densities of 2–4/m<sup>2</sup>, because avian predation intensity declines when grasshopper densities are either very low or high. Peak densities in all years at both sites were >6/m<sup>2</sup> (Fig. 2), higher than in studies showing more consistent effects of avian predation (Fowler et al. 1991, Bock et al. 1992, Joern 1992). Midsummer grasshopper densities were much higher at Miles City than Whited in all years (Fig. 2), which would also likely result in proportionally lower predation rates (Belovsky and Joern 1995). Belovsky and Joern (1995) also noted that food limited sites where avian predation either had limited or positive effects on grasshopper densities typically had high densities of large-bodied grasshoppers with exploitative competition. Medium-bodied grasshoppers were dominant at all sites, but exploitative resource based competition was evident at Miles City in 1999 and 2000 (unpublished data).

The effects of avian predation at Whited were variable (Table 1), with avian predation reducing grasshopper densities by 32% in 2001 (Fig. 1). In a 2-yr study of avian predation at sites located 5–50 km from the Whited site, Fowler et al. (1991) found birds reduced grasshopper densities by 26 and 37%, similar to Whited in 2001. Peak densities during the study of Fowler et al. were lower than at Whited, averaging 1–4/m<sup>2</sup>. The combined results from this study and Fowler et al. show that avian predation has variable importance in northern mixed-grass prairie. The effects of predation on grasshopper populations have been shown to vary temporally and spatially in Palouse and sandhills prairie, regardless of whether top-down or bottom-up control was generally dominant (Joern 1992, Belovsky and Joern 1995). Therefore, this study is allied with others in a range of ecosystems in showing that avian predation plays a variable role in the regulation of grasshopper populations (Joern 1992, Belovsky and Joern 1995, Ritchie 2000).

Belovsky and Joern (1995) predicted that populations are more likely to be predator-limited with poor quality food resources, but it is not possible to directly examine this prediction with data from two sites. Grass biomass was more abundant at Whited in 2001, when avian predation seemed to reduce grasshopper numbers (Fig. 3C). Grass nitrogen levels averaged 1% or less in all but 1 yr; as a result, vegetation sampling

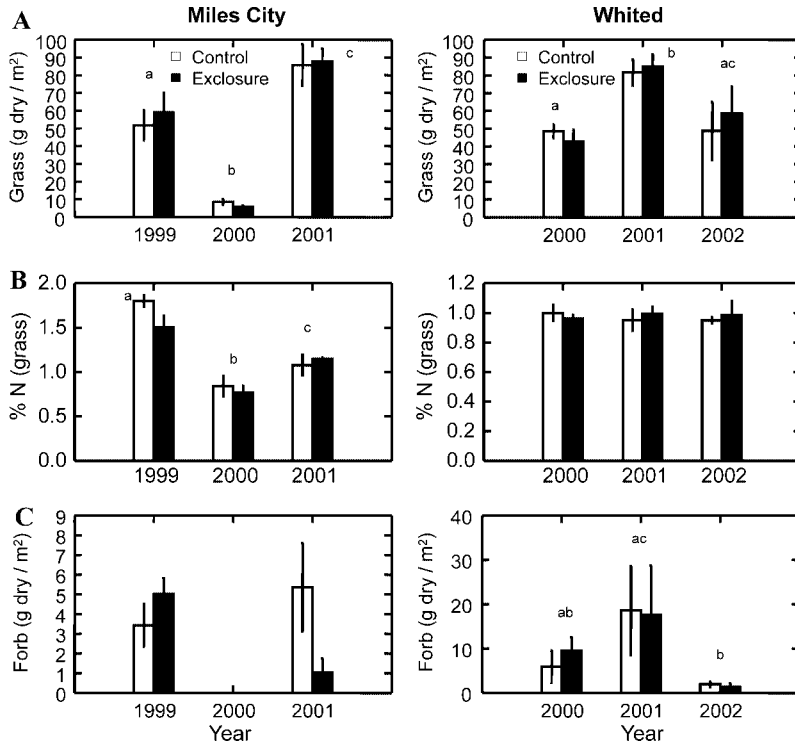


Fig. 3. Grass biomass (A), percentage nitrogen content of grass (B), and forb biomass (C) in controls and exclosures at Miles City and Whited. Values are means  $\pm$  SE.

earlier in the summer might have more accurately assessed host plant availability for grasshoppers. Host plant availability did not differ between exclosures and controls at either site (Table 2). Belovsky and Joern (1995) made the additional prediction that predator limitation would be less common at sites dominated by C<sub>3</sub> grasses. Although Whited had a higher proportion of C<sub>4</sub> grasses, biomass production at both sites was dominated by C<sub>3</sub> grasses.

Selective predation by birds caused a shift in body size composition, because the percentage of medium-bodied grasshoppers was lower in control plots during several years at Whited and Miles City (Fig. 1D).

Large-bodied grasshoppers, which were proportionally reduced by avian predators in the Palouse prairie (Belovsky and Slade 1993), were not abundant at either site. Because of lower predation intensity, avian predation is likely to have smaller effects on body size distribution when final grasshopper densities were high, as at Miles City in 1999. No differences in medium size grasshoppers were apparent at Whited in 2000, but <25 grasshoppers were caught on average in each plot. Fowler et al. (1991) found little evidence for size-selective predation at nearby sites, but their methodology differed from this study. In this study, avian predators modified the body size composition of

Table 2. ANOVA results for grass biomass, percentage nitrogen of grass, and forb biomass for Miles City and Whited

Site	Dependent	Source	df	SS	F	P
Miles City	Grass biomass	Avian	1,14	25.4	0.15	0.70
		Year	2,14	19334.0	58.05	<0.001
		Interaction	2,14	86.2	0.26	0.78
	Percent nitrogen (grass)	Avian	1,14	8.25 $\times 10^{-4}$	1.91	0.19
		Year	2,14	0.005	62.31	<0.001
		Interaction	2,14	2.01 $\times 10^{-4}$	2.33	0.13
Whited	Grass biomass	Avian	1,12	25.4	0.13	0.72
		Year	2,12	4757.0	12.59	0.001
		Interaction	2,12	186.6	0.49	0.62
	Percent nitrogen (grass)	Avian	1,12	1.85 $\times 10^{-6}$	0.12	0.74
		Year	2,12	1.37 $\times 10^{-6}$	0.04	0.96
		Interaction	2,12	1.53 $\times 10^{-5}$	0.49	0.62
	Forb biomass	Avian	1,12	2.0	0.03	0.87
		Year	2,12	833.7	5.89	0.02
		Interaction	2,12	19.1	0.14	0.88

grasshopper populations through size-selective predation on medium-bodied grasshoppers, even in years when they did not reduce overall grasshopper densities.

Belovsky and Slade (1993) showed that size-selective predation on larger-bodied grasshoppers also had indirect effects on competitive interactions. Birds reduced the proportion of competitively dominant larger bodied grasshoppers, resulting in increased densities of medium-bodied grasshoppers and higher overall population densities (Belovsky and Slade 1993). A larger grasshopper species is typically the superior competitor when two grasshopper species exploitatively compete for similar resources (Joern 1986, Belovsky and Slade 1993, 1995). Belovsky and Slade (1993) attributed the decrease in small-bodied grasshoppers in controls to increased competition from higher numbers of medium-bodied grasshoppers, because the intensity of exploitative competition typically declines with larger differences in body size (Belovsky and Slade 1993, Belovsky and Slade 1995). The combined results of reduced proportions of medium-bodied grasshoppers and increased densities of small-bodied grasshoppers in controls was consistent with birds indirectly mediating interspecific competition at Whited and Miles City. Smaller bodied grasshoppers averaged 72% more abundant in controls at Miles City and 51% more abundant at Whited. The results provide evidence that birds released small-bodied grasshoppers from competition, because small-bodied grasshoppers increased in abundance when birds reduced the proportion of medium-bodied grasshoppers in controls. Reduced interspecific competition from medium-bodied grasshoppers could result in higher survival and population densities of small-bodied grasshoppers in controls than would occur without avian predation. Belovsky and Slade (1993) attributed increased overall population densities to the substitution of equivalent resource consumption by a greater number of medium-bodied species in their highly food limited system. Both in this study and in Palouse prairie, birds seemed to function as keystone predators by limiting the abundance of larger-bodied competitively superior grasshopper species.

Species richness and diversity of grasshopper assemblages were not significantly affected by avian predation in this study. Although Joern (1986, 1992) found avian predation reduced species richness in western Nebraska in years when birds reduced grasshopper densities, Fowler et al. (1991) found no effect of bird predation on species richness in western North Dakota even when birds reduced grasshopper numbers. Food limitation may have larger effects on species diversity at Whited and Miles City, because Kemp and Cigliano (1994) showed that species richness declined with drought intensity. Effects of avian predation on Shannon species diversity in previous studies are likewise mixed, with Joern (1986) finding a positive effect, Belovsky and Slade (1993) finding a negative trend, and Fowler et al. (1991) finding no effect. Despite the significant effect of bird predation on body size composition in this study, birds did not

significantly affect grasshopper community composition.

A range of other vertebrate and invertebrate predators also prey on grasshoppers (Bock et al. 1992, Belovsky and Slade 1993, Pitt 1999). If birds directly or indirectly reduced the abundance of other predators in control plots, or if avian exclosures excluded other predators, the effects of avian predation on grasshopper population densities and body size composition could be obscured. Ritchie (2000) showed that spider predation was higher in exclosures, but spiders capable of eating large instar or adult grasshoppers were not abundant in exclosures at either site. Robber flies (Asilidae) can also affect grasshopper densities (Joern and Rudd 1982) but were not conspicuous at either site. A number of factors not measured in this study, including abiotic conditions, insectivorous vertebrate abundance, avian nesting habitat, avian abundance, and predator efficiency, could play significant roles in whether predators limit grasshopper populations at a given site (Bock et al. 1992, Joern 1992, Belovsky and Joern 1995, Ritchie 2000).

Increasing evidence indicates that no single factor appears to control insect herbivore populations (Joern 2000) and that either competition or predation may be more important in different years at a given location (Belovsky and Joern 1995). The results of this study, in combination with Fowler et al. (1991), indicate that avian predation can directly and indirectly impact grasshopper populations in northern mixed-grass prairie sites and that the direct effects vary spatially and temporally. Predation appeared to predominately operate in a compensatory manner at the two sites (Oedekoven and Joern 2000). In this study, avian predators did not exert a limit on grasshopper population densities in most years. However, intermittent strong top-down effects could play an important role in determining local grasshopper population dynamics over longer timer periods than were examined in this study, especially when predation acts in a compensatory fashion (Joern 2000, Oedekoven and Joern 2000). Belovsky and Joern (1995) also showed that avian predation could have significant effects on grasshopper population dynamics even when direct reducing effects of avian predation were not apparent. Importantly, even in years when avian predators did exert a limit on grasshopper populations, birds had important indirect effects on grasshopper assemblages. Selective predation by birds reduced the proportion of medium-bodied grasshoppers, and small-bodied grasshoppers increased in abundance. As a result, bird predation seemed to mediate the effects of competitively superior medium-bodied grasshoppers on small-bodied grasshopper species and reduce the effects of exploitative competition on smaller bodied grasshoppers.

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