

## EFFECTS OF BIRD PREDATION ON GRASSHOPPER DENSITIES IN AN ARIZONA GRASSLAND<sup>1</sup>

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**Abstract.** In a 4-yr field experiment, we tested the hypotheses that insectivorous birds (1) controlled densities of herbivorous grasshoppers in an ungrazed semiarid grassland in southeastern Arizona, and (2) functioned as keystone predators, by limiting abundances of grasshoppers that otherwise might change vegetation cover and species composition, and/or by mediating the effects of otherwise competitively superior members of the grasshopper assemblage.

We measured grasshopper densities and vegetation on 32 464-m<sup>2</sup> grassland plots for 1 yr, then enclosed 16 of these plots with bird exclosures and continued data collection for 3 yr. Eight of the 16 experimental plots were further modified in the last 2 yr of the study by installing fine-mesh 1 m high barriers designed to retard grasshopper dispersal. Microclimates of caged plots differed only slightly from open plots. Lizards and rodents increased inside the exclosures, but they were removed and released elsewhere such that their average abundances did not differ among treatments.

By the final year of the study, mean annual adult grasshopper density was >2.2 times higher on plots from which birds were excluded, and where grasshoppers were enclosed by dispersal barriers, than on unmanipulated control plots. Mean nymph density was >3.0 times higher in the same comparison. Grasshoppers were significantly more abundant in bird exclosures with insect dispersal barriers, indicating that experimental plots were dispersal sources rather than sinks. Seven of 12 common grasshopper species were more abundant inside the bird exclosures, while none was less abundant. Among the more abundant taxa, those responding most positively were grass feeders: *Eritettix simplex*, *Opeia obscura*, *Paropomala wyomingensis*, and *Phoetaliotes nebrascensis*.

We found no evidence that grasshoppers competed with one another under increased densities inside the bird exclosures. Although the amount of insect herbivory was somewhat higher inside the bird exclosures, and was positively correlated with grasshopper density across all 32 plots ( $r = 0.87$ ), overall vegetation cover and species composition did not differ among treatments by the end of the study. *Dactylotum variegatum*, an aposematic species apparently immune to avian predation, showed no significant responses to the experiment.

Birds clearly limited grasshoppers in this grassland ecosystem, but they failed to qualify as keystone predators, at least in the short term, for two reasons: (1) in their absence, increased grasshopper densities had no appreciable impact on vegetation cover or species composition; and (2) there was no evidence that birds mediated competition among grasshoppers.

**Key words:** *Acrididae*; Arizona; birds; competition; grassland; herbivory; keystone species; *Orthoptera*; predation.

### INTRODUCTION

An important issue in community ecology is the relative importance of competition, predation, and environmental variability in determining abundances of herbivorous animals (Andrewartha and Birch 1954, 1987, Hairston et al. 1960, Wiens 1977, Schoener 1982, Strong et al. 1984, Wilbur 1987, Stiling 1988, Price 1991). The physical environment permitting, all herbivore populations can grow to the point where resources become limiting, and competitive exclusion becomes likely (Paine 1984). However, predators po-

tentially can reduce herbivore numbers and eliminate competition among them (e.g., Oksanen 1988). A number of field experiments have demonstrated the importance of such "keystone predators" (sensu Paine 1966, 1974), although the great majority of studies have centered on marine or freshwater ecosystems (Sih et al. 1985, Wilbur 1987, Batzer and Resh 1991).

Birds are significant insectivores in forest ecosystems (e.g., Holmes et al. 1979, Loyn et al. 1983, Atlegrim 1989, Crawford and Jennings 1989), and may function there as keystone predators. However, their role in reducing competition among insects, or in preventing insect outbreaks, is not clear, especially in ecosystems other than forests.

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Grasshoppers (Orthoptera: Acrididae) are dominant invertebrate herbivores in grassland ecosystems (Otte 1981). Grasshopper population dynamics traditionally have been attributed largely to physical environmental variables (Dempster 1963, Uvarov 1977), and outbreaks of these insects frequently have been related to weather, especially precipitation (e.g., Capinera and Horton 1989). However, some recent field experimental evidence suggests that biotic interactions also can be important to grasshoppers (Joern and Gaines 1990). For example, interspecific competition for food may occur in some, but apparently not all, grasshopper assemblages (Belovsky 1986, Evans 1989). Other field experiments suggest that bird predation can have substantial (Joern 1986, Fowler et al. 1991), or only minor (Belovsky et al. 1990), impacts on grasshopper populations. Clearly, there is a need for more field experiments examining the importance and potential interactions among these biotic factors in determining grasshopper population dynamics and community structure (Joern and Gaines 1990).

Can avian insectivores mediate competition among grasshoppers, and in turn function as keystone predators in grassland ecosystems? We examined this question by excluding birds for 3 yr from experimental plots in a semiarid grassland in Arizona. One of the three most abundant grasshoppers in our study area was *Dactylotum variegatum*, an ecologically generalized species (Joern and Lawlor 1981) that also is aposematic and apparently immune to avian predation (Whitman 1990). This circumstance permitted a potentially powerful test of the competition hypothesis. We could measure the fate of *Dactylotum* in bird exclosures where all grasshoppers were protected from avian predation. We predicted that *Dactylotum* would decline inside bird exclosures if edible species increased, and if density compensation (Crowell 1962, MacArthur 1972) was occurring. The objectives of our study were to determine: (1) if densities of apparently edible grasshoppers increased in bird exclosures; (2) if *Dactylotum* or any other species declined in exclosures vs. control plots over the same period; and (3) if increased grasshopper abundances overall had a measurable impact on vegetation.

## METHODS

### *Study system*

The study area was part of the Appleton-Whittell Research Ranch, a 3160-ha sanctuary of the National Audubon Society on the Sonoita Plain, Santa Cruz County, Arizona. The sanctuary includes a mixture of private land and public land administered by the U.S. Forest Service and U.S. Bureau of Land Management. Elevation ranges from 1400 to 1500 m. Temperatures vary from a mean January daily minimum of  $-1.7^{\circ}\text{C}$  to a mean June daily maximum of  $32.4^{\circ}\text{C}$ . Twenty-year mean annual precipitation, calculated as a sum-

mer rainy season and its preceding winter, has been 43 cm;  $\approx 57\%$  falls between July and early September. Precipitation declined during the first three summers of the present study, from 45.4 cm in 1987, to 42.8 cm in 1988, and 34.5 cm in 1989; it then rose to 54.6 cm in 1990, due to an unusually wet summer.

The sanctuary has been free of livestock since 1968. We chose an upland mesa for the present study that supports a diverse native perennial grassland, and where we had conducted earlier work on vegetation, birds, and grasshoppers (Bock et al. 1984, Jepson-Innes and Bock 1989, Bock and Bock 1991, 1992). Dominant grasses were *Bouteloua gracilis*, *Lycurus phleoides*, and *Aristida* spp. A large variety of native dicotyledonous herbs was present, but none dominated the landscape. Scattered woody plants were mostly the low shrubs *Haplopappus tenuisectus* and *Baccharis pteronioides*, and a few small mesquite (*Prosopis juliflora*).

Combined density of all insectivorous birds at the study site in 1981–1982 was  $\approx 3.3$  individuals/ha (Bock et al. 1984). The most abundant species were Grasshopper Sparrow (*Ammodramus savannarum*), Cassin's Sparrow (*Aimophila cassinii*), and Eastern Meadowlark (*Sturnella magna*). In recent years, Botteri's Sparrow (*Aimophila botterii*) also has become common in the study area (Bock and Bock 1992). Each of these four species is largely insectivorous in summer (Bent 1965, 1968). Grasshopper and Botteri's Sparrows are known to feed extensively on grasshoppers (Joern 1988, Webb and Bock 1990). Observation of a Cassin's Sparrow nest at our study site for 18 h in 1984 showed that, of 208 insects delivered to nestlings, 197 (95%) were acridid grasshoppers (K. Jepson-Innes, unpublished data).

### *Experimental procedures*

In June 1987, we established a 75-m interval grid on the study mesa that included 48 grid intersection points (Fig. 1). We then measured grasshopper densities from June through mid-October, on 464-m<sup>2</sup> plots centered on each of the 48 grid intersections. Vegetation cover was measured by species on each of the plots in mid-August. We next ordinated the 48 plots based on principal components analysis of the grasshopper and vegetation data, and selected 32 plots that were most similar based on the first three components. Only these 32 plots were used for subsequent comparisons and experimental manipulations. We next divided these 32 into 16 experimental and 16 control plots, based on the 1987 (pretreatment) grasshopper and vegetation data. Assignment of plots to the experimental vs. control groups was not done randomly. Rather, we divided plots such that the experimental and control groups differed as little as possible, and in no cases significantly, in mean 1987 abundances of any common grasshopper or plant species.

In winter 1987–1988, we constructed bird exclosures over the 16 experimental plots. Each was 2 m high,

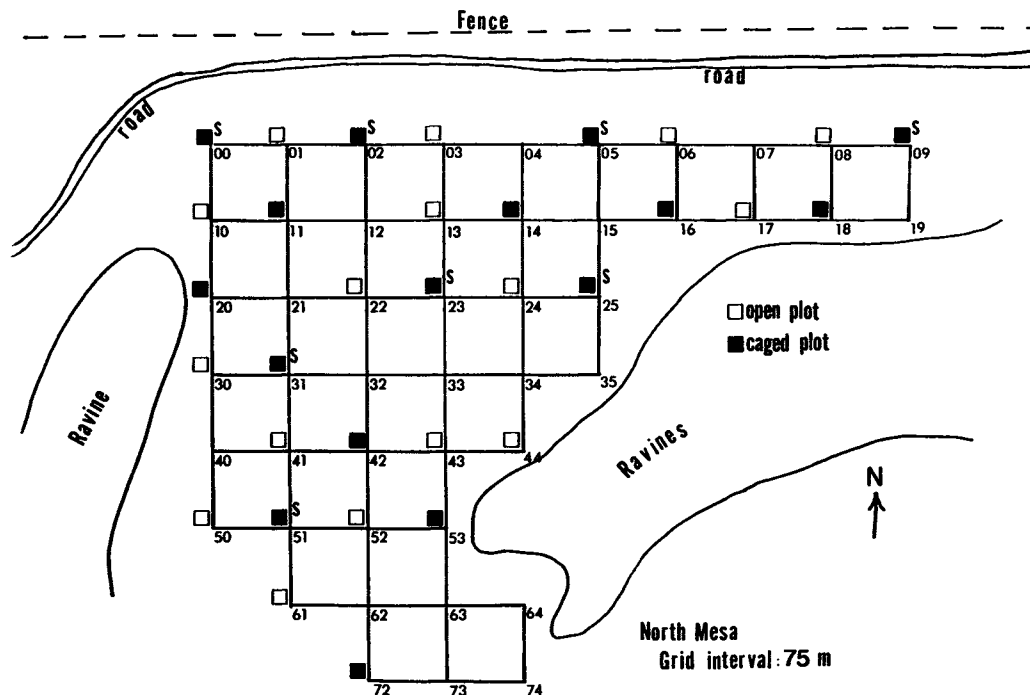


FIG. 1. Map of the study area in an ungrazed semiarid grassland in Arizona. □ = control plots. ■ = plots covered with cages excluding birds, 1988–1990. Large numbered squares are locations of plots on latitude-longitude grid. Cages shown with “S” were fitted with fine-mesh insect dispersal barriers, 1989–1990. See *Methods* for details of experimental procedures and sampling design.

30.5 m long, and 15.2 m wide ( $\approx 464 \text{ m}^2$ ). Walls were 2.5-cm mesh chicken wire, while roofs were black polypropylene 2.5-cm mesh netting. Roofs were removed each year in November, and replaced the following March. We did this to prevent cages from collapsing under the mass of occasional snows, but it also allowed granivorous birds access to the plots in winter.

There was one additional experimental manipulation. In spring 1989, we further modified 8 of the 16 caged plots (Fig. 1) by attaching a 1 m high nylon window screen barrier to the chicken wire walls, at ground level, around the plot perimeters. This screen was pinned to the ground at 0.5-m intervals, using 20 cm spikes. The objective of this manipulation was to retard movement of grasshoppers, to determine if densities inside the bird enclosures were a function of colonization. As with the previous plot selection, division of the caged plots into groups with and without screen was done selectively, such that the two groups did not differ significantly in their 1988 grasshopper densities or vegetation characteristics.

#### *Grasshopper densities*

Grasshoppers were counted and identified to species if adults, or as unidentified nymphs, as they were flushed from inside wire hoops enclosing  $0.5 \text{ m}^2$ , following procedures in Onsager and Henry (1978). This method is well suited to generally sparse and low vegetation such as occurred at our study site. In 1987 there were

nine hoops on each of the original 48 plots. Only adults were counted that year. From 1988 to 1990 there were 28 hoops on each of the 32 plots; both adults and nymphs were counted. Sampling began in early June of 1987, in late May of 1988–1990, and continued at approximately even intervals through early October of each year. All plots were sampled on the same dates within years, but the numbers of samples differed among years: 9 in 1987, 18 in 1988, 15 in 1989, and 12 in 1990. Samples were averaged to generate mean yearly densities per count per plot. Over the 4-yr duration of the study, we counted grasshoppers in individual hoops 44 208 times. Annual estimates of grasshopper densities should have been comparable among years, though based on different sample sizes, because counting continued over similar time spans each year. Because May count results were similar to those for June in 1988–1990, their absence from the 1987 data set should have had only minor impacts on 1987 estimates of mean yearly densities. In any event, our statistical analyses, and interpretation of the results of the experiment, did not depend on between-year comparisons of grasshopper density data (see *Data analysis* below).

#### *Vegetation*

We visually estimated canopy cover to the nearest 10% for each plant species inside each grasshopper hoop in mid-August of each year, and combined these

to generate vegetation cover values for each plot in each summer. In 1990, we also estimated the percentages of various plant species showing any evidence of insect herbivory on the 32 plots. We laid a tape centrally down the long axis of each plot, and examined all the leaves on each plant stem (identified to species) in contact with the tape at 0.5-m intervals. Only leaves showing signs of chewing along their lateral edges were considered evidence of insect herbivory, because leaves with fully severed tips could have been the result of rodent activity.

#### *Cage microclimates*

We placed four cylindrical plastic rain gauges at ground level in two pairs of caged and adjacent open plots in 1990. Gauges were read and emptied 12 times during the summer, with intervals ranging from 1 to 14 d ( $n = 24$  paired comparisons). Temperatures were recorded in cages using a thermometer hand-held  $\approx 2$  cm above the soil surface and allowed to equilibrate in full sun or in the shade of vegetation. Each recording was paired with a reading taken outside the cage either just before or just after the reading inside ( $n = 27$  pairs of full sun and 16 pairs of shade readings).

#### *Other vertebrates*

Mammals and reptiles could have influenced the results of our experiments by feeding on grasshoppers or vegetation. Pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and black-tailed jackrabbits (*Lepus californicus*) occurred on the study mesa, and were of necessity excluded from the caged plots. However, these herbivores were uncommon, and we have no indication that vegetation inside the cages increased in their absence. While these species are largely nocturnal in summer, we expected to flush them all, and especially rabbits, from resting sites on the study area during our other activities. In  $\approx 130$  field-days at the site over four summers, we saw pronghorn only 3 times, deer on  $< 1$  d in 20, and jackrabbits on  $< 1$  d in 10.

Rodents and reptiles could have colonized the caged plots. We monitored their populations on all plots, and prepared to remove them from enclosures if their numbers began to increase. The only abundant reptile was the bunchgrass lizard, *Sceloporus scalaris* (Bock et al. 1990). We made visual counts of these insectivores during each grasshopper census. Their numbers did not differ between control and experimental plots in 1988 or 1989. However, counts of bunchgrass lizards began to increase substantially in caged plots in June–July 1990. We hand-captured and removed 128 lizards from the 16 caged plots between 12 and 19 July, and count results did not differ for the remainder of the study.

Rodents can negatively affect both insect density and vegetation cover (e.g., Brown and Hejske 1990, Churchfield et al. 1991). We established a grid of 12 live traps on each of the 16 caged plots and on 9 ran-

domly selected open plots, beginning in June 1988. Traps were open for 26 nights over the following three summers. Trapping success was low ( $\approx 1$  capture per 20 trap-nights overall). *Reithrodontomys megalotis*, *Sigmodon fulviventer*, and *Baiomys taylori* were the only species captured with any frequency. All three approximately doubled on caged plots relative to open plots each summer. Rodents were removed from cages and released elsewhere on the sanctuary, such that total annual captures of *Reithrodontomys* and *Baiomys* did not differ between treatments in any year (C. E. Bock and J. H. Bock, unpublished data). However, *Sigmodon* continued to be trapped more often inside cages, despite ongoing removals. Because *Sigmodon* are largely grazing rodents (Randolph et al. 1991), it is unlikely they had a direct impact on grasshoppers. They could have reduced vegetation in the cages, but there was no evidence that this occurred. We suspect that increased rodent numbers in the cages were not related to grasshopper densities or vegetation, but were a response to the necessary exclusion of rodent predators from the experimental plots (C. E. Bock and J. H. Bock, unpublished data).

#### *Data analysis*

Our study was designed to determine if, and in what ways, three groups of study plots would come to differ from one another, in terms of grasshopper densities and vegetation cover, after 3 yr of experimental manipulation. The three groups of plots were selected such that they did not differ in their pretreatment (1987) grasshopper densities or vegetation characteristics. Therefore, subsequent differences among plot types could be attributed to effects of the experiment. Because the same plots were sampled repeatedly over 4 yr, annual density or cover estimates could not be considered statistically independent. Repeated-measures ANOVA would have been appropriate under this circumstance (Milliken and Johnson 1984), except that the three groups of plots were subject to different sequences of manipulations. Therefore, it was not possible to consider repeated-measures (year) effects and treatment effects simultaneously. Plot group 1 ( $n = 16$ ) was open in 1987–1990. Plot group 2 ( $n = 8$ ) was open in 1987, and then caged to exclude birds in 1988–1990. Plot group 3 ( $n = 8$ ) was open in 1987, caged to exclude birds in 1988, and screened to retard insect dispersal, as well as caged to exclude birds, in 1989 and 1990. Our solution was to restrict statistical analyses to 1990 data, and test hypotheses about the full 3-yr consequences of the experiment, while presenting results for the preceding years for comparative purposes only. For grasshopper densities, we used repeated-measures ANOVA, with 1990 sampling dates as a within-subjects (repeated-measures) factor, and plot type as a between-subjects (treatment) factor. Significant sample date  $\times$  treatment interactions would indicate circumstances where grasshopper densities differed among plot

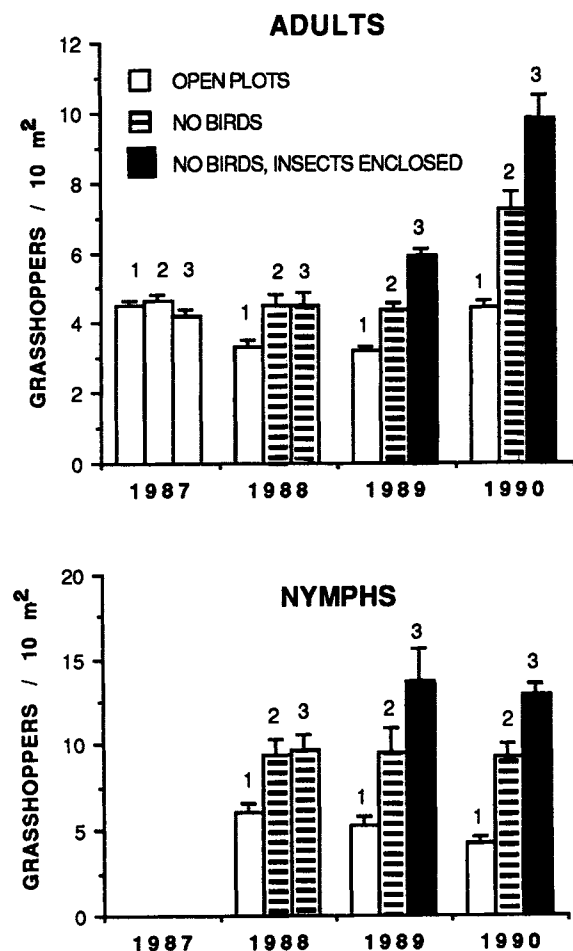


FIG. 2. Annual densities (mean and 1 SE) of adult and nymphal grasshoppers on 32 semiarid grassland plots in Arizona subject to three treatments over 4 yr. Numbers over error bars indicate the three plot groups in each year. Plots in group 1 ( $n = 16$ ) were open and unmanipulated from 1987 to 1990. Plots in group 2 ( $n = 8$ ) were open in 1987, and caged to exclude birds in 1988–1990. Plots in group 3 ( $n = 8$ ) were open in 1987, caged to exclude birds in 1988–1990, and also enclosed to retard insect dispersal in 1989–1990. Repeated-measures ANOVA, 1990 adults: treatment effect ( $F = 44.45$ ,  $df = 2$ ,  $P < .0001$ ), sample date effect ( $F = 58.62$ ,  $df = 11$ ,  $P < .0001$ ), interaction ( $F = 0.91$ ,  $df = 22$ ,  $P = .58$ ). Repeated-measures ANOVA, 1990 nymphs: treatment effect ( $F = 70.55$ ,  $df = 2$ ,  $P < .0001$ ), sample date effect ( $F = 158.98$ ,  $df = 11$ ,  $P < .0001$ ), interaction ( $F = 2.03$ ,  $df = 22$ ,  $P < .005$ ).

types in different ways, depending upon time of year. Grasshopper count data were transformed using  $\log_{10}(x + 1)$  to meet normality and homogeneous variance assumptions of parametric statistics. We used the Tukey multiple-comparison procedure (Zar 1984) to look for significant ( $P < .05$ ) pairwise differences between mean 1990 densities on plots of the three treatments. For percent vegetation cover, sampled only once in mid-August, we compared 1990 arcsine-transformed data among treatments using one-way ANOVA. Numbers of insect-grazed and ungrazed plants inside vs.

outside bird enclosures were analyzed with the chi-square contingency statistic. A product-moment correlation coefficient was computed to determine if the percentage of plants showing evidence of insect herbivory was related to 1990 mean annual grasshopper density on the various plots.

## RESULTS

### Cage microclimate

We measured a seasonal total of 56.99 cm precipitation in the two caged rain gauges, compared to 56.78 cm on the open plots ( $n = 24$  paired comparisons,  $t = 0.23$ ,  $P = .82$ ). Full sun temperatures averaged  $0.12^{\circ}\text{C}$  higher outside than inside cages ( $n = 27$ ,  $t = 0.23$ ,  $P = .82$ ), while shaded temperatures were identical to the nearest  $0.01^{\circ}\text{C}$  ( $n = 16$ ).

### Grasshopper densities

By the final year of the study (1990), mean annual adult grasshopper density was  $>2.2$  times higher on plots from which birds were excluded, and where grasshoppers were enclosed by dispersal barriers, than on unmanipulated control plots (Fig. 2). Mean nymph density was  $>3.0$  times higher in the same comparison. Densities in bird enclosures without insect dispersal barriers were  $>1.6$  and  $>2.1$  times higher than on unmanipulated plots for adults and nymphs, respectively. Repeated-measures ANOVA revealed highly significant ( $P < .0001$ ) 1990 treatment effects for both adults and nymphs (see legend to Fig. 2 for statistics). All pairwise comparisons of treatment means were highly significant (Tukey's multiple-comparison tests,  $P < .01$ ).

Twelve grasshopper species comprised  $>95\%$  of all adult individuals counted, and 7 of these responded significantly and positively to the experiment by 1990 (Table 1). Common taxa showing the strongest response were *Eritettix simplex*, *Opeia obscura*, *Paropomala wyomingensis*, and *Phoetaliotes nebrascensis*. Other species responding positively were *Amphitornus coloradus*, *Syrbula montezuma*, and *Melanoplus gladstoni*. No species was significantly less abundant on experimental plots vs. control plots. *Arphia pseudonietana* and *Psoloessa texana* apparently were much more abundant in the wet summer of 1990 than in preceding years, but they did not differ among treatments. *Dactylotum variegatum*, the aposematic species apparently immune to predation, was counted in somewhat higher numbers in open plots vs. caged plots in 1990, but these differences did not approach statistical significance (Table 1).

Yearly mean abundance data mask important seasonal shifts in densities of nymphs vs. adults, and among the different adult taxa, that are reflected in the highly significant sample date effect ( $P < .0001$ ) revealed by each repeated-measures ANOVA (Fig. 2, Table 1). In 1990, nymphs were maximally abundant in August,

while adults were most common from September to early October (Fig. 3). This pattern was similar throughout the study. The fall peak in adults (and probably much of the August peak in nymphs) was due largely to *Phoetaliotes nebrascensis*, by far the most abundant species in the study area (Fig. 4). Among the more abundant taxa, other late-season species were *Melanoplus gladstoni* and *Opeia obscura*. By contrast, *Eritettix simplex* was abundant as soon as we were able to begin annual sampling in May (Fig. 4). *Paropomala* was a midsummer species that declined sharply after the end of August. *Dactylotum* was present throughout the sampling period, but it was most common from June through early August. In no case did the experimental exclusion of birds, or enclosure of grasshoppers by dispersal barriers, appear to change a grasshopper species' phenology, whether or not there were major changes in its abundance.

### Vegetation

There was a strong positive correlation between grasshopper density and the percentage of plants showing some signs of insect herbivory on the 32 plots in 1990 (Fig. 5;  $r = 0.87$ ). While we made no effort to quantify the actual percentage of each leaf consumed on the stems sampled, on most stems most leaves showed no damage at all, and affected leaves rarely were  $> 25\%$  consumed. Signs of insect herbivory were more common on herbs than on grasses overall, but the increase in leaf damage related to our experiment was more striking among grasses, particularly *Bothriochloa barbinodis*, *Bouteloua gracilis*, and *Bouteloua curtipendula* (Table 2).

While increased densities of grasshoppers resulted in somewhat higher levels of herbivory (Fig. 5), there is no evidence that this had any major impact on overall vegetation cover or species composition by the end of the experiment. Grass and especially herb canopy cover apparently were higher in the very wet summer of 1990 than in the preceding 3 yr. However, we found no significant differences in total grass or herb canopy cover among treatments in 1990 (Fig. 6), nor did cover of any individual plant species differ between caged and open plots. Admittedly, we sampled plant cover in mid-August, before adult grasshoppers reached peak densities (Fig. 3). However, by 1990 the experimental plots had been subject to three summers of increased herbivory, and still there were no significant differences in plant cover among plot types (Fig. 6).

### DISCUSSION

Bird predation limited densities of 7 of the 12 most abundant grasshopper species, and of the grasshopper assemblage as a whole. Because populations reached highest densities in cages fitted with screen insect dispersal barriers, we conclude that the bird enclosures became sources for grasshopper emigration rather than recipients of immigration. Previous experiments sim-

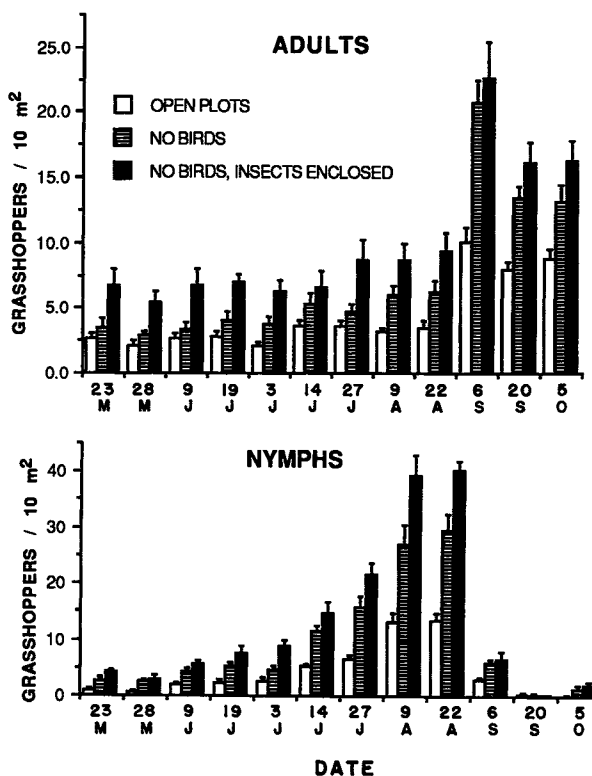


FIG. 3. Densities of combined adult and combined nymphal grasshoppers on semiarid grassland plots of three treatments, as measured on 12 sampling dates from 23 May 1990 to 5 October 1990. Data were means and 1 SE.

ilar to ours (Joern 1986, Fowler et al. 1991) may have underestimated the impacts of avian predators on grasshoppers, because bird enclosures were in place only for 1 yr, and they also lacked insect dispersal barriers.

We do not believe differences other than the absence of birds are sufficient to explain the increased grasshopper densities inside our experimental plots. Vegetation did not change as a result of our experiment. No other common insectivorous vertebrates differed in abundance between open and caged plots. Invertebrate predators, especially robber flies (Asilidae), can affect grasshopper densities, at least in some situations (Joern and Rudd 1982, Joern and Gaines 1990). We did not quantify invertebrate predators in the present study, but robber flies were conspicuous both inside and outside the bird enclosures. Temperature and precipitation did not differ between our open and caged plots. Joern (1986) also found only slight differences in microclimate between open plots and bird enclosures constructed of mesh netting identical to our cage roofs: a 5% reduction of net radiation inside cages, and no significant differences in ground-level wind speed. Fowler et al. (1991) reached similar conclusions about microclimates of their bird enclosures in North Dakota.

Birds are generalized grasshopper predators in this

Taxon	Year	Grasshopper density (individuals/10 m <sup>2</sup> )					
		Plot group 1		Plot group 2		Plot group 3	
		$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
<b>Subfamily Gomphocerinae</b>							
<i>Ageneotettix deorum</i>	1987	0.33	0.05	0.27	0.05	0.45	0.07
	1988	0.26	0.03	0.40	0.04	0.36	0.05
	1989	0.07	0.01	0.11	0.03	0.15	0.03
	1990	0.16	0.04	0.19	0.03	0.32	0.06
Repeated-measures 1990*—treatment: $F = 2.27$ , $P = .12$ —date: $F = 28.81$ , $P < .0001$ —interaction: $F = 1.38$ , $P = .12$							
<i>Amphitornus coloradus</i>	1987	0.12	0.03	0.12	0.03	0.08	0.03
	1988	0.08	0.01	0.13	0.04	0.11	0.01
	1989	0.04	0.01	0.08	0.02	0.11	0.02
	1990	0.06 <sup>a</sup>	0.02	0.14 <sup>b</sup>	0.02	0.21 <sup>c</sup>	0.03
Repeated-measures 1990*—treatment: $F = 10.06$ , $P = .0005$ —date: $F = 4.55$ , $P < .0001$ —interaction: $F = 1.25$ , $P = .21$							
<i>Eritettix simplex</i>	1987	0.81	0.09	1.13	0.09	0.84	0.20
	1988	0.36	0.04	0.51	0.08	0.52	0.04
	1989	0.76	0.05	1.29	0.09	1.66	0.19
	1990	0.74 <sup>a</sup>	0.09	1.45 <sup>b</sup>	0.20	2.32 <sup>c</sup>	0.21
Repeated-measures 1990*—treatment: $F = 24.62$ , $P < .0001$ —date: $F = 88.49$ , $P < .0001$ —interaction: $F = 4.66$ , $P < .0001$							
<i>Opeia obscura</i>	1987	0.17	0.04	0.11	0.04	0.07	0.04
	1988	0.13	0.02	0.15	0.04	0.22	0.04
	1989	0.07	0.01	0.10	0.02	0.14	0.03
	1990	0.22 <sup>a</sup>	0.02	0.51 <sup>b</sup>	0.06	0.78 <sup>b</sup>	0.14
Repeated-measures 1990*—treatment: $F = 24.48$ , $P < .0001$ —date: $F = 59.94$ , $P < .0001$ —interaction: $F = 5.07$ , $P < .0001$							
<i>Paropomala wyomingensis</i>	1987	0.48	0.08	0.37	0.08	0.33	0.12
	1988	0.29	0.04	0.44	0.08	0.44	0.08
	1989	0.13	0.02	0.21	0.04	0.25	0.08
	1990	0.20 <sup>a</sup>	0.04	0.39 <sup>b</sup>	0.09	0.92 <sup>c</sup>	0.21
Repeated-measures 1990*—treatment: $F = 13.09$ , $P < .0001$ —date: $F = 37.36$ , $P < .0001$ —interaction: $F = 6.06$ , $P < .0001$							
<i>Psoloessa texana</i>	1987	0.04	0.01	0.04	0.03	0.07	0.04
	1988	0.03	0.01	0.01	0.01	0	
	1989	0.10	0.02	0.08	0.03	0.06	0.03
	1990	0.22	0.03	0.21	0.08	0.42	0.14
Repeated-measures 1990*—treatment: $F = 2.38$ , $P = .11$ —date: $F = 10.95$ , $P < .0001$ —interaction: $F = 1.57$ , $P = .051$							
<i>Syrbula montezuma</i>	1987	0.01	0.01	0.04	0.03	0.01	0.01
	1988	0.06	0.01	0.06	0.02	0.08	0.02
	1989	0.03	0.01	0.04	0.02	0.08	0.03
	1990	0.04 <sup>a</sup>	0.01	0.18 <sup>b</sup>	0.04	0.18 <sup>b</sup>	0.05
Repeated-measures 1990*—treatment: $F = 13.39$ , $P < .0001$ —date: $F = 14.55$ , $P < .0001$ —interaction: $F = 3.22$ , $P = .0001$							
<b>Subfamily Oedipodinae</b>							
<i>Arphia pseudonietana</i>	1987	0					

caged to exclude birds in 1988–1990, and also fitted with insect dispersal barriers in 1989–1990. For species showing a significant treatment effect in 1990, treatment means with different superscript letters were significantly different ( $P < .05$ ) using Tukey's multiple-comparison tests.

		Grasshopper density (individuals/10 m <sup>2</sup> )					
Taxon	Year	Plot group 1		Plot group 2		Plot group 3	
		$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Subfamily Melanoplinae							
<i>Dacylotum</i>	1987	1.05	0.08	1.19	0.11	1.27	0.09
<i>variegatum</i>	1988	0.63	0.04	0.64	0.10	0.52	0.06
	1989	0.63	0.06	0.41	0.09	0.54	0.07
	1990	0.62	0.06	0.52	0.06	0.51	0.10
Repeated-measures 1990*—treatment: $F = 0.83$ , $P = .45$ —date: $F = 11.75$ , $P < .0001$ —interaction: $F = 1.05$ , $P = .40$							
<i>Melanoplus</i>	1987	0.39	0.08	0.35	0.09	0.20	0.07
<i>desultorius</i>	1988	0.44	0.05	0.69	0.09	0.67	0.11
	1989	0.22	0.03	0.24	0.04	0.26	0.02
	1990	0.40	0.06	0.61	0.11	0.35	0.08
Repeated-measures 1990*—treatment: $F = 2.36$ , $P = .11$ —date: $F = 49.62$ , $P < .0001$ —interaction: $F = 1.23$ , $P = .21$							
<i>Melanoplus</i>	1987	0.12	0.03	0.12	0.05	0.12	0.05
<i>gladstoni</i>	1988	0.14	0.02	0.21	0.04	0.19	0.04
	1989	0.13	0.02	0.18	0.05	0.31	0.04
	1990	0.34 <sup>a</sup>	0.04	0.67 <sup>b</sup>	0.14	0.75 <sup>b</sup>	0.14
Repeated-measures 1990*—treatment: $F = 5.09$ , $P = .013$ —date: $F = 110.80$ , $P < .0001$ —interaction: $F = 2.68$ , $P < .0001$							
<i>Phoetaliotes</i>	1987	0.71	0.09	0.79	0.15	0.80	0.15
<i>nebrascensis</i>	1988	0.88	0.14	1.15	0.23	1.33	0.26
	1989	0.87	0.11	1.57	0.20	2.24	0.14
	1990	1.10 <sup>a</sup>	0.15	2.21 <sup>b</sup>	0.29	3.09 <sup>c</sup>	0.26
Repeated-measures 1990*—treatment: $F = 18.20$ , $P < .0001$ —date: $F = 690.81$ , $P < .0001$ —interaction: $F = 13.59$ , $P < .0001$							

\* Results of repeated-measures ANOVA of 1990 density data for all tests, with date of sample as a within-subjects factor ( $df = 11$ ), and plot group (treatment) as a between-subjects factor ( $df = 2$ ).

TABLE 2. Percentages of stems of all grasses and herbs, plus percentages of stems of the most abundant species, that showed any evidence of insect herbivory, on open plots vs. caged plots with birds excluded and higher densities of grasshoppers. Data were collected 9–10 September 1990.

Taxon	Open plots		Caged plots		$\chi^2$	$P^\dagger$
	%	$n^*$	%	$n$		
<i>Aristida</i> sp.	5.6	198	10.3	223	3.21	NS
<i>Bothriochloa barbinodis</i>	39.3	28	70.0	30	5.40	<.025
<i>Bouteloua gracilis</i>	12.6	373	35.7	364	53.98	<.0001
<i>B. chondrosioides</i>	19.4	67	34.0	47	3.11	NS
<i>B. curtipendula</i>	15.0	20	57.9	19	7.87	<.01
<i>Eragrostis intermedia</i>	26.5	34	47.8	23	2.69	NS
<i>Lycurus phleoides</i>	23.4	111	40.7	108	7.58	<.01
Total grasses	14.7	844	32.8	848	123.68	<.0001
<i>Croton corymbulosus</i>	64.3	14	76.9	13	0.54	NS
<i>Desmanthes cooleyi</i>	50.0	10	93.8	16	6.68	<.01
<i>Evolvulus arizonica</i>	35.3	17	57.1	21	1.79	NS
<i>Portulaca coronata</i>	54.6	11	60.9	23	0.12	NS
<i>Sida procumbens</i>	51.9	81	70.5	61	5.05	<.025
Total herbs	48.5	196	67.8	205	15.46	<.001

\*  $n$  = the number of stems of each plant species sampled for signs of insect herbivory in each treatment.

† Chi-square contingency tests for independence of treatment vs. the number of plants with and without signs of insect herbivory ( $df = 1$ ).



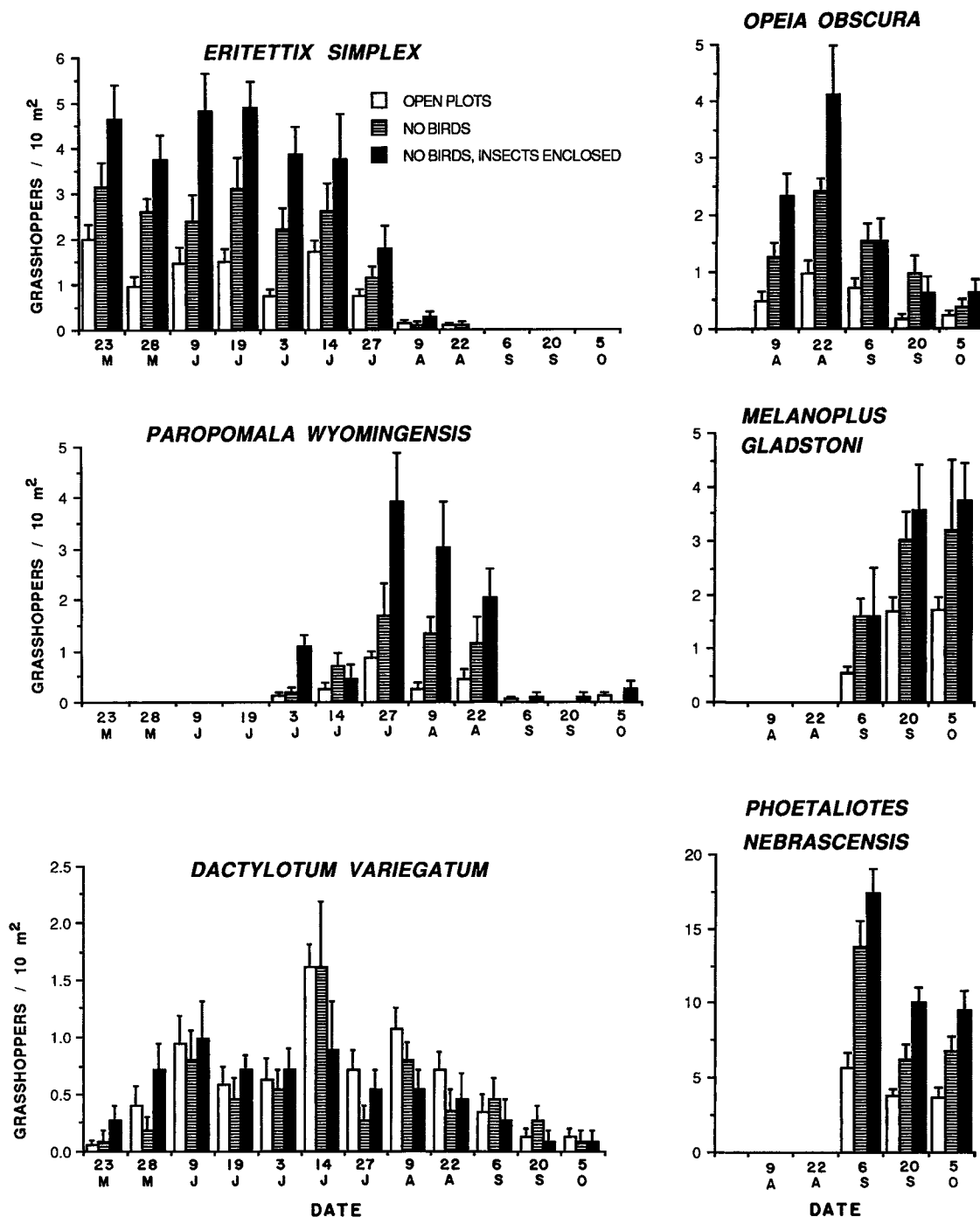


FIG. 4. Same as Fig. 3, for adults of the six most abundant grasshopper species in the study area. Note that species on the right side of the figure were not present until 9 August or later.

Arizona grassland, as they apparently are in Nebraska sandhills prairie (Joern 1986). However, avian insectivores may play a very different role in a Palouse prairie in western Montana (G. E. Belovsky et al. 1990; *personal communication*). At the Montana site, birds preyed mostly on a few relatively large-bodied grass-

hoppers, with the result that overall grasshopper densities increased in the presence of birds, due to compensatory increases in populations of smaller bodied species. Grasshoppers apparently are much more abundant in Montana than in the Arizona or Nebraska sites, and competition for food appears to be the most

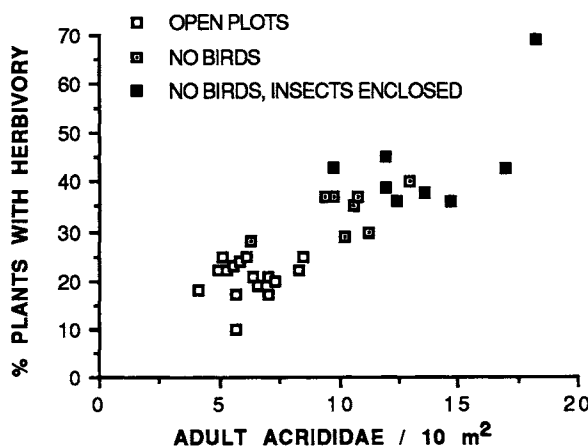


FIG. 5. Percentage of plant stems with at least one leaf showing evidence of insect herbivory, plotted against mean adult grasshopper density on 32 plots in a semiarid grassland treated as described in the legend to Fig. 2. Data were from 1990;  $r = 0.87$ .

important factor limiting the grasshopper community as a whole (Belovsky 1986).

We were particularly interested if the aposematic *Dactylotum variegatum* decreased in our bird enclosures, since all species were afforded equal immunity to avian predation. However, *Dactylotum* densities did not differ among the treatments. There probably were only limited possibilities for competition between *Dactylotum* and the grasshoppers that responded positively to our experiment. Five of these species are in the acridid subfamily Gomphocerinae (Table 1), whose members are almost entirely grass feeding (Otte 1981). *Dactylotum* feeds on *Baccharis* shrubs as nymphs in the spring (Parker 1982), and, like most members of its subfamily (Melanoplinae), mainly on dicotyledonous herbs as adults (Joern 1979a, b). While *Dactylotum* adults were most abundant in early- to midsummer, other common melanoplines in the study area (the two *Melanoplus* and *Phoetaliotes*) were present as adults mainly in fall. Even among these, the most abundant (*Phoetaliotes*) is primarily a grass-feeder (Evans 1989).

We found no evidence that competition occurred among any grasshoppers in our study area, because no species showed significant compensatory declines as a result of the experiment. Increased herbivory was detectable, especially on grasses that probably were the predominant food of most grasshoppers that responded positively to the experiment. However, this increased herbivory had no major impacts on overall vegetation cover or species composition after 3 yr. Tall-grass prairie in Kansas appears similar, insofar as field experiments revealed no competition among grasshoppers, other invertebrates, and rodents, or that their herbivory had any major effects on vegetation (Evans 1989, Gibson et al. 1990).

Under outbreak conditions, grasshopper densities in

North American grasslands can reach 30–40 animals/m<sup>2</sup>, at which point their impacts on vegetation can be severe (Hewitt and Onsager 1983). Even at more moderate densities, grasshoppers are capable of significantly affecting grassland production (Mitchell and Pfadt 1974). However, grasshopper densities in our study area were very low. Even after 3 yr of protection from birds, peak adult densities were <2.5/m<sup>2</sup>. Increased herbivory did occur in the absence of birds, and this likely would have long-term ecological and evolutionary significance (Holmes et al. 1979). However, birds in our study area failed to qualify as key-stone predators. At least in the short term, grasshoppers protected from avian predators did not achieve densities where they competed for limited resources, or where they significantly influenced grassland cover or species composition. Other unknown factors apparently prevented grasshoppers in our enclosures from reaching these higher densities.

Grasshopper population dynamics appear to be affected by many variables, including precipitation (Dempster 1963, Capinera and Horton 1989), grazing by ungulate mammals (Capinera and Sechrist 1982,

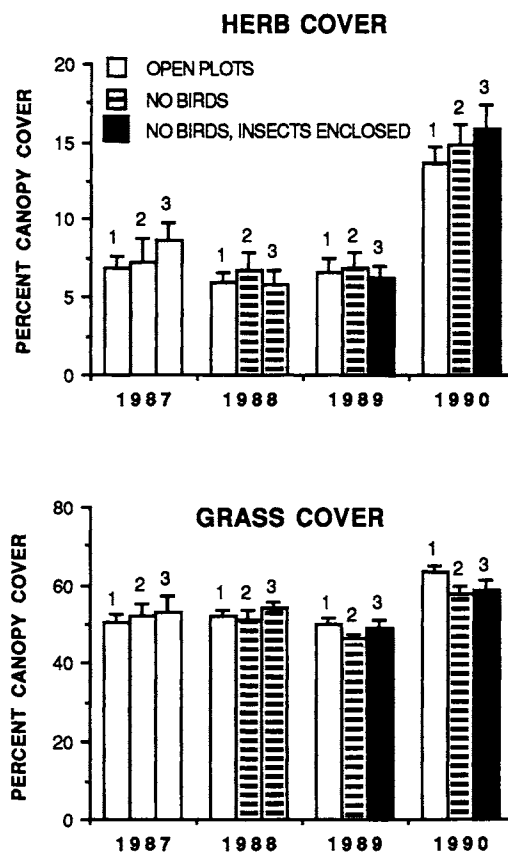


FIG. 6. Mid-August canopy cover of grasses and herbs on three groups of plots in a semiarid grassland treated as described in the legend to Fig. 2 (means and 1 se). ANOVA results for 1990 herb cover:  $F = 0.79$ ,  $df = 2$ ,  $P = .46$ . ANOVA results for 1990 grass cover:  $F = 2.63$ ,  $df = 2$ ,  $P = .089$ .

Jepson-Innes and Bock 1989, Quinn and Walgenbach 1990), and intra- and interspecific competition (Belovsky 1986). Results of the present field experiment in Arizona, and of similar studies in Nebraska (Joern 1986) and North Dakota (Fowler et al. 1991), indicate that avian predation also can limit grasshopper densities in a variety of ecosystems. However, it is not clear if, or under what circumstances, grasshopper populations released from avian predation might reach outbreak densities. Insect herbivores generally may be more influenced by predators in relatively undisturbed, late-successional communities (Price 1987, 1991), such as the ungrazed grassland we studied in Arizona (Bock et al. 1984). Higher densities of grasshoppers frequently are associated with disturbances such as drought (Capinera and Horton 1989) or ungulate grazing (Jepson-Innes and Bock 1989), but field experiments have not yet been conducted to evaluate the importance of avian predation under these circumstances.

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