Variable impact of avian predation on grasshopper assemblies in sandhills grassland

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Spatial and temporal variability in the impact of avian predation on total grasshopper density and species diversity in a sandhills grassland was evaluated with field experiments. Experiments were run for 3 years at two locations along a topographic gradient created by a large sand dune system which supports a mixed-grass prairie. Overall average grasshopper densities at the site were approximately 3–4 individuals/m², considered low to moderate densities in the long-term record, and densities were about the same for all years within sites. I eliminated avian predation from plots at each site through the use of large, wide-mesh exclosures set up in early July each year. I sampled 5–6 weeks later and compared grasshopper densities and number of species from the enclosure cages with control plots. When significant differences were observed, grasshopper densities were depressed about 25% and the number of species usually decreased by two. Variability in the impact of avian predators was observed among years and among sites for both total grasshopper density and number of grasshopper species. Assessment of the impact of avian predation on population or community dynamics of grasshoppers must include spatial and temporal variability.

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Avian predators may affect the ecological dynamics of their insect prey at individual, population and community levels (Hassell 1978, Lawton and McNeill 1979, Strong et al. 1984, Berryman et al. 1987). Experimental and observational studies in forest and grassland systems (Holmes et al. 1979, Otvos 1979, Berryman et al. 1987) have previously documented a clear negative effect of avian predation on insect prey populations. Examples include: the depression of population sizes in understory Lepidoptera larvae (Holmes et al. 1979), forest spiders (Askenmo et al. 1977, Rypstra 1984), overwintering populations of the corn borer in agricultural systems (Black et al. 1970), arthropods in litter of tropical forest understory (Gradwohl and Greenberg 1982), grasshoppers in mixed grasslands (Joern 1986, Fowler et al. 1991, Bock et al. 1992), overwintering Lepidoptera pupae (Solomon et al. 1977), psyllid outbreaks in eucalyptus forests (Loyn et al. 1983) and

bilberry damage by lepidoptera and sawfly larvae when birds were excluded (Atlegrim 1989). Such results are not always observed, as documented by the relatively low risk to avian predation by some grasshopper species in Palouse grassland from Montana (U.S.) (Belovsky et al. 1990). Sometimes observed complex and compensating responses occur as when vespulid wasps aggregate in prey patches created by exclosures designed to prevent bird foraging on forest lepidoptera larvae resulting in no difference between treatment and control samples (Steward et al. 1988).

Several lines of evidence suggest that predation can be ecologically important to grasshoppers: (1) a significant number of predators on grasshoppers exist (Dempster 1963, Greathead 1963, Lavigne and Pfadt 1966, Joern and Rudd 1982, Joern and Gaines 1990), (2) significant behavioral and color adaptation to avoid predators has been described (Isley 1938, Rowell 1971,
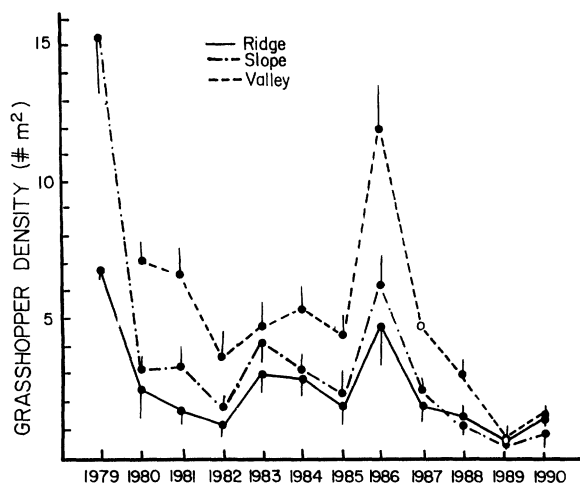
Fig. 1. Annual variation in adult grasshopper densities at Arapaho Prairie. Densities were estimated from 4 transects each consisting of 50 0.1 m² rings set out randomly along the transect. Points for each year represent means and 2 SE of the 4 transects for each site. Estimates were made in each year in early August. The three sites represent the three major areas in the Nebraska sandhills dune field, each consisting of differences in soil characteristics, vegetation and harshness of the physical environment.

Schultz 1981, Gillis 1982) and (3) field experiments have documented increases in grasshopper densities when predators are removed (Kajak et al. 1968, Joern 1986, 1988, Fowler et al. 1991, Bock et al. 1992, Belovsky and Slade, pers. comm.). Here, I document spatial and temporal variation in the impact of avian predation to entire adult grasshopper assemblages with regard to both densities and species diversity. This study is a follow-up to a previous report (Joern 1986). Susceptibility of individual species or attributes influencing susceptibility are not directly assessed.

Methods

Study site

I performed this study from 1983–1985 at Arapaho Prairie located in the southwestern portion of the Nebraska (Arthur Co., USA) sandhills grassland, an area comprised of upland dune systems (Barnes et al. 1984). Dunes with steep slopes grading into flat valleys predominate and are vegetated with a mixture of ca. 200 species from both tallgrass and shortgrass prairie systems (Keeler et al. 1980). Typical vegetation structure is a heterogeneous mosaic of vegetation and patches of open sand.

Nebraska sandhills grassland supports a diverse grasshopper assembly which exhibits a variety of phenological patterns. To date, approximately 60 species have been collected from the site, although only ca. 30–35

species are typically found in single years (Joern 1982, unpubl.). While often patchily distributed, most grasshopper species are widely distributed throughout the site. Overall total grasshopper densities varied among years and between valley and slope sites along a topographic gradient but were relatively constant for the duration of this study (Fig. 1) with average densities (all species combined) of ca. 3–4 individuals/ m².

Bird species regularly found at this sandhills site are typical of North American grasslands of this type (as in Cody 1974, Wiens 1977, Risser et al. 1982). Dominant species are the ubiquitous grasshopper sparrows (*Ammodramus savannarum*) and western meadowlarks (*Sturnella neglecta*). Other common species include: lark sparrows (*Chondestes grammacus*) and lark buntings (*Calamospiza melanocorys*). Breeding seasons begin in late April with first clutches typically completed by mid-June. About a third of the breeding pairs attempt a second clutch depending on conditions (Kaspari, unpubl.). Juveniles usually fledge from mid-June to mid-July and greatly inflate the foraging bird population after fledging. Family groups and small flocks tend to range widely in late summer. Birds remain at the site until early September at which time they mass for seasonal southerly migration. The large increase in avian densities in July and August coincides with the period of peak adult grasshopper densities (Joern 1982). Bird densities also vary among years. Grasshopper sparrow population densities on a 1.0×0.5 km plot censused using the spot-flush technique varied between 14–16 breeding pairs from 1981–1984 and nearly tripled in density in 1985 (Kaspari 1991).

Experimental treatments

In each of three years, I excluded birds from some areas and compared results with equally sized plots in which birds were free to forage unencumbered. Techniques followed those of Joern (1986). Seven randomly placed replicates of each treatment (predator exclusion and control) from each of two areas along a dune topographic transect (slope and valley) were employed (total of 28). Exclosures were constructed as a series of 10m × 10m × 1m structures covered with 2.5 cm plastic mesh (Cissel Inc., Farmington, NJ), the same as that used by Holmes et al. (1979) in a study of avian predation on forest insects. I firmly staked edges against the ground surface to prevent entry into the exclosure in this manner. For control plots (10m × 10m), I marked the corners but otherwise did not manipulate these areas except for initially disturbing the area to approximate disturbance associated with setting up the mesh exclosures. I erected the treatment plots in early July of each year of the study (1983, 1984, 1985) and then sampled in mid-August. The experiment was run for approximately 40 days in each year. Treatments were set up only on the dune slope in 1983 (previously re-
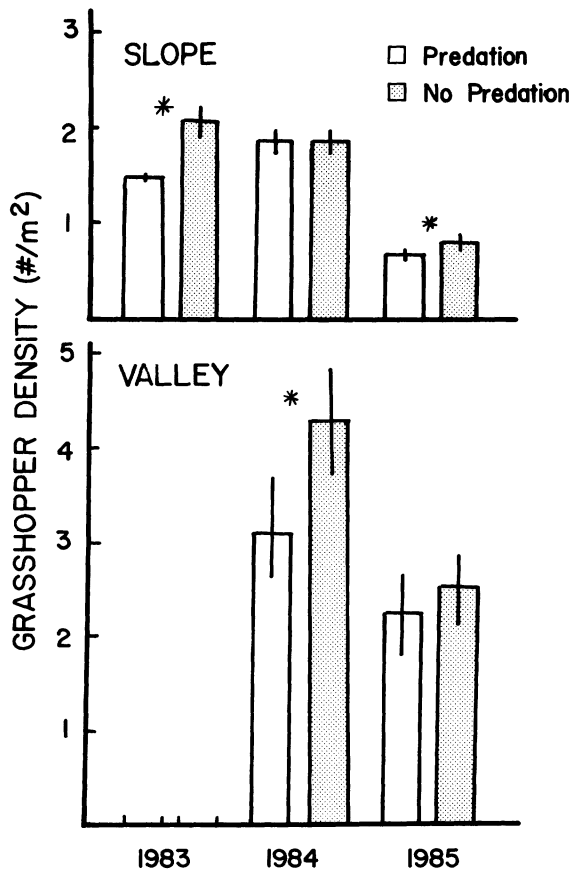
Fig. 2. Impact of avian predation on total grasshopper densities over time and space. Average densities of grasshoppers in plots with and without predation are compared; means and 2 SE are shown. The asterisk indicates a statistically significant difference at the 0.05 level for the specific comparison.

throughout the entire plot. At this point, one additional, complete systematic pass was made through the entire sample area.

Results and discussion

Overall grasshopper density

Spatial and temporal variation in the overall impact of avian predation to grasshopper densities at this site was observed when birds were excluded (Fig. 2). When statistically significant drops in grasshopper density were observed, the average difference was on the order of a 25% difference after the ca. 5–6 week period of the experiment. Based on repeated measure, single-factor ANOVAs (to account for repeated sampling of the same plots among years), statistically significant increases in density differences were observed in exclosure plots ($P < 0.05$) and site differences were also detected ($P = 0.06$). Comparisons between predation treatments within years at each site (Mann Whitney U)

ported in Joern 1986) and at both slope and valley sites in 1984 and 1985. I added these additional sites after the first year since overall grasshopper densities are consistently greater in the valley versus the slope over a ten year census period (Fig. 1). Furthermore, I felt that unique site-specific differences might exist as suggested in several comprehensive models of insect population dynamics (Peterman et al. 1979, Berryman et al. 1987, Joern and Gaines 1990).

I censused grasshoppers in mid-August, ca. 5–6 weeks from the start of the experiment, as described in Joern (1986). After securing the plot perimeter with fiberglass window screen to inhibit escape of grasshoppers within plots, I collected grasshoppers with an insect net while systematically searching the area. The screen barrier served to minimize or eliminate movement of grasshoppers into or out of the plot during sampling and grasshoppers which did move to the boundaries of the sample plots typically jumped up onto the screen and were easily captured. I sampled each plot until 10 or fewer individuals were collected on a single, systematic search
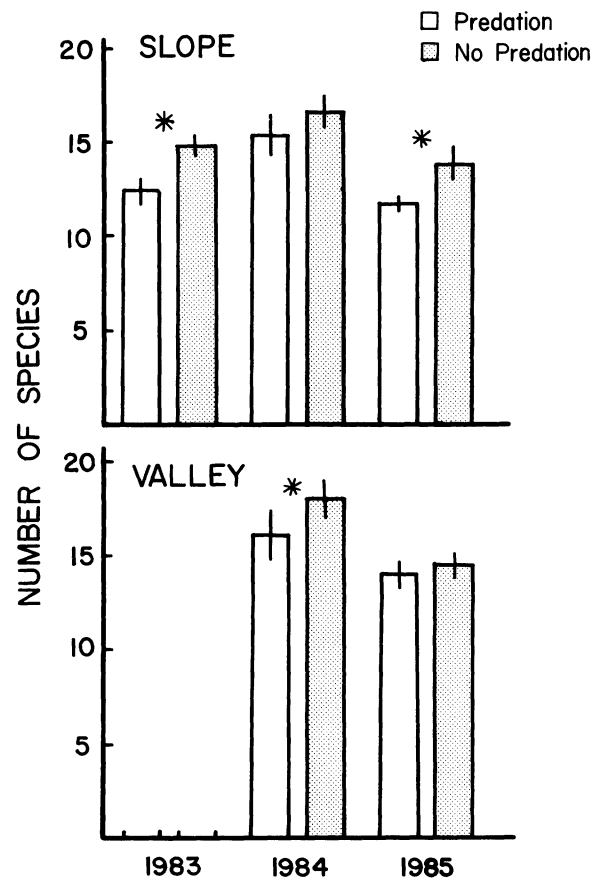

Fig. 3. Impact of avian predation on average number of grasshopper species over time and space. Average numbers of grasshopper species per plot and 2 SE are shown. The asterisk indicates a statistically significant difference at the 0.05 level for the specific comparison.

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indicated important differences among years. For the slope, significant density differences (P<0.05) between treatments were recorded in 1983 and 1985 but not 1984. For the valley sites, a significant difference in overall grasshopper densities was observed in 1984 (P<0.05) but not 1985.

Species density

On average, approximately two more species were typically found in exclosure plots with no avian predation (Fig. 3), *if* there was a significantly detectable impact upon overall density from this treatment (Fig. 2). Overall, the same approximate number and taxonomic identity of species were encountered at both slope and valley sites. Loss of uncommon species in control plots relative to exclosures was largely responsible for significant differences in species number. Avian predation appears to exert its effect on the number of species by removing rarer species although densities of all grasshopper species are lowered.

Effect of exclosure cage

The extent to which mesh exclosures contribute directly to treatment differences by altering microclimate or grasshopper movement patterns, in addition to altering predation pressure, was also addressed in this and previous studies. Microclimate was altered to some degree though not extensively given the large mesh size of the exclosures (Joern 1986). As previously reported (Joern 1986), wind speed at the top of the vegetation canopy was reduced 18%, net radiation was reduced 5% and total radiation was reduced 8% inside the exclosure. Note that grasshoppers spend most of their time *below* the grass canopy top and that wind speed is typically near zero in this microhabitat most of the time – except under high wind conditions. As a result, differences in wind speed within and outside exclosures are in reality much less to a grasshopper than the observed 18% measured difference and are unlikely to be significantly different. Overall, these differences in microclimate are very small and seem unlikely to account for the large differences in numbers of grasshoppers between treatments.

The explicit effect of the mesh sides and top to grasshopper movement was also experimentally examined. Observations indicated that grasshoppers readily moved through the netting with no obvious hindrance and behaved as if the mesh netting was a normally encountered part of the microhabitat structure. As a partial test, marked individuals of *Ageneotettix deorum* (140 individuals, equal sex ratio) were released in equal numbers in four quadrats of a 10m × 10m plot which were either completely separated by mesh netting or completely unhindered by netting and then recaptured 3 days later. Movement into different quadrats was readily monitored and transitions of recovered grasshoppers among quadrats based on whether a mesh barrier existed or not were not significantly different (Fisher's Exact Test, P=0.4). This result again indicates that individual movement is not hindered by the mesh netting, at least for *Ageneotettix deorum* at Arapaho Prairie. I consider the small-scale movement of *A. deorum* to be representative of within-habitat movement observed in other grasshopper species (Joern 1983, Gaines 1989).

Consequences

Detectable effects of avian predation on grasshopper assemblies are clearly evident and it is also clear that the responses vary in both time and space. Overall density and species diversity often decrease from the predation pressure, but not in all years nor is the response among sites in synchrony. Keeping such variability in mind is important for understanding basic population and community processes in this group of insect herbivores. It is also worth noting that the directions of the responses, even when statistically non-significant, were always in the direction expected for significant predation effects.

Typically, significant spatial heterogeneity is seen in vegetational and topographic attributes which, in turn, affect grasshopper distributions (Joern 1982, Heidorn and Joern 1987). At Arapaho Prairie, grasshopper densities are usually greater in the valleys and steadily decrease toward the ridges of the dunes, with additional differences, dictated by plant quality or other recent localized activities such as pocket gopher activity, that affect spatial vegetation structure (Heidorn and Joern 1987). Such spatial differences in grasshopper density provide a template which effectively defines the state of the system against which predation operates. Birds are most likely to forage in patches with the highest prey densities (Stephens and Krebs 1986) as seemed to be the case in 1984 when birds foraged in the valleys but not on the slopes resulting in noticeable differences in impact to grasshopper assemblies from predation in the two areas.

The likelihood that avian predation will have a significant effect on prey assemblages also varies with temporal variability in overall grasshopper densities, which vary greatly among years at Arapaho Prairie (Fig. 1). Other important site attributes such as climate and primary productivity also exhibit much temporal variability and can also influence grasshopper densities (Joern and Gaines 1990, Belovsky and Slade 1992). However, a significant difference in prey densities is not the only factor which influences the importance of predation. While the overall densities of the grasshoppers were approximately the same during the course of this study, the impact of avian predation on either overall grasshopper density or species density was not constant among the three years of this study. 1984 was very dry

and much of the vegetation dried up, especially on the slope. As grasshopper numbers declined, birds moved from the slope to the valley to forage, a site which already supports a higher grasshopper density under almost all conditions. This shift in foraging location is supported by anecdotal observation but no quantitative estimates were made. A consequence of such a shift in foraging activity is that there was no measurable effect due to the avian exclosures on the slope in this year. Fowler et al. (1991) also found no effect from avian predation on grasshopper density during a drought year but a significant depression in grasshopper densities (40%) the following year when climatic conditions were typical.

Similarly, as suggested by recent population models incorporating multiple equilibria (Peterman et al 1979, Berryman et al. 1987), avian predation is most likely to be an important density- and frequency-dependent force when prey densities are relatively low. This expectation is met in a variety of forest (Holmes et al. 1979, Otvos 1979, Takekawa et al. 1982) and grassland (Joern 1986, Fowler et al. 1991, Bock et al. 1992) studies of the impact of avian predation on prey populations. Frequency-dependent selection and switching has been documented for grasshopper sparrows foraging for prey at a density of 3–4 individuals/ m², approximately the same as in the present study (Joern 1988). Unfortunately, high grasshopper densities were not observed during the course of this study to determine when, if ever, grasshoppers escape the impact of predation. Tests at a range of higher densities are desirable to fully describe this response. The escape threshold is likely contingent on a variety of other state variables other than overall grasshopper density. For example, the degree of spatial heterogeneity in grasshopper distribution which will affect the pattern of avian foraging, the specific taxonomic mix of grasshopper species which will alter search rate (Joern unpubl.), and nesting and breeding success of birds independent of prey availability.

In this study, spatial heterogeneity of grasshopper distribution in particular defines those areas for which the impact of avian predation (at the assembly level) will be important. This very reasonable expectation deserves careful empirical testing.

Indirect analyses of the impact of avian predation on prey populations in grasslands using energetics models (Wiens 1973, 1974, Wiens and Dyer 1975) concluded that avian predation had little impact on arthropod standing crop. Wiens (1973) did suggest that population oscillations in some arthropod groups (e.g., grasshoppers) may be damped. Both my study and that of Fowler et al. (1991) indicate that the impact of avian predation is often significant but does vary in time and space. In both of these studies, however, foraging behavior of the birds was significantly altered by the effect of drought on prey distributions which then influenced which patches the birds foraged, if they even remained at the

site. Under such conditions, predation pressure was often not detectable as the birds did not forage in certain patches. These results suggest that there is a very interesting interplay between external forces delimiting prey patches, especially extreme conditions such as drought, and the dynamics of the predators with their prey. Spatially explicit patterns of foraging coupled with how and why these change are probably the most important aspects of the problem for further study, at least initially.

While it is not possible to readily interpret the mechanistic reasons for temporal variation in the impact of avian predation for the present study, it is important to recognize such variability. Models of population or community dynamics must factor such variation into the picture.

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