

INTERSPECIFIC INTERACTIONS AMONG PHYTOPHAGOUS INSECTS OF TALLGRASS PRAIRIE: AN EXPERIMENTAL TEST¹

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Abstract. Densities of the grasshopper *Phoetaliotes nebrascensis* (Acrididae) were manipulated in native tallgrass prairie at Konza Prairie, Kansas, to measure competitive and facilitative effects on densities of co-occurring phytophagous insects. In late June 1987, *P. nebrascensis* nymphs were transferred among enclosed plots (each 550–900 m²) to produce three pairs of plots with grasshoppers either removed or added. Pretransfer densities in the six plots were estimated at ≈ 5 nymphs/m²; 2–2.5 nymphs/m² were then removed or added. Densities of the manipulated species and other abundant phytophagous insects were subsequently monitored (by sweep net) through mid-August.

The manipulations in late June resulted in mean densities of *P. nebrascensis* nymphs 1.5–4 times as large on addition plots as on removal plots; these differences persisted through mid-August. No significant differences between treatments were found, however, in the numbers of individuals of other Acrididae or Tettigoniidae on four post-transfer sampling dates (July to mid-August). Significant differences were also not found in the numbers of individuals of Phasmatidae, Homoptera, or phytophagous Hemiptera and Coleoptera, or in the biomasses of live grass, dead grass, or forbs present in mid-August.

1987 was a year of moderate primary production on Konza Prairie. The manipulations produced experimental treatments that mimicked intermediate vs. relatively high natural densities of *P. nebrascensis*. The results indicate that under these conditions, changes in *P. nebrascensis* density have little net short-term impact, competitive or otherwise, on the population dynamics of co-occurring grasshoppers or other phytophagous insects.

Key words: *Acrididae*; *competition*; *facilitation*; *grasshoppers*; *grassland*; *herbivory*; *interspecific interactions*; *phytophagy*; *Phoetaliotes nebrascensis*; *tallgrass prairie*.

INTRODUCTION

One of the longstanding questions in community ecology is: how much does interspecific competition influence natural communities (e.g., Schoener 1982, Conner and Simberloff 1986, May and Seger 1986). Widespread dissatisfaction with previous, largely indirect and observational, approaches to addressing this issue has led to a recent emphasis on field experiments wherein the densities of one or more potentially competitive species are manipulated in otherwise natural settings (e.g., Connell 1983, Schoener 1983). The presence of significant interspecific competition is generally inferred when these manipulations lead to clearcut responses of coexisting species, e.g., the density of a second species increases when individuals of a given species are removed.

While many such field experiments have now been performed for many groups of organisms, few experiments have been undertaken for folivorous insects (Connell 1983, Schoener 1983, Fritz et al. 1986). Hairston et al. (1960) and Slobodkin et al. (1967) proposed

on general grounds that folivorous insects rarely compete for resources. Andrewartha and Birch (1954) also argued strongly in favor of this position, although for different reasons. Field observations and pattern analyses were offered by others as demonstrating the importance of interspecific competition among folivorous insects, but these indirect approaches were found wanting (Lawton and Strong 1981).

In the absence of much field experimentation (but see, e.g., Strong 1982a, b), Strong et al. (1984) tentatively concluded from a variety of published studies that interspecific competition is generally not an important factor among folivorous insects. Karban (1986) challenged this conclusion, arguing convincingly that more field experiments are needed to build robust generalizations. In this spirit, I present here a field experiment involving folivorous insects of tallgrass prairie.

My manipulation of densities of the most abundant grasshopper inhabiting the prairie (*Phoetaliotes nebrascensis* [Thomas] [Orthoptera: Acrididae]) permits evaluation of both competitive effects and other potential interactions, including facilitation of other insect folivores' numbers. One plausible such facilitative (indirect) interaction, for example, is that activities of the grass-feeding *P. nebrascensis* enhance numbers of forb-feeding grasshopper species: by feeding on grasses,

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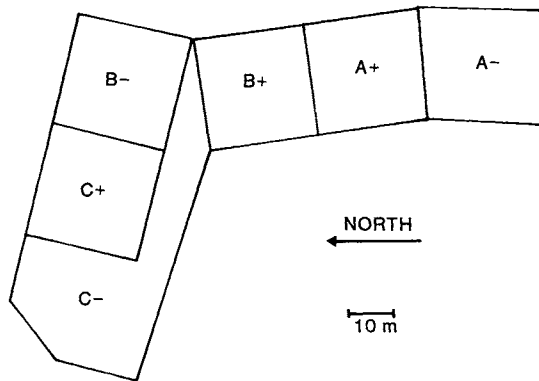


FIG. 1. Physical layout (drawn approximately to scale) of the three pairs of plots (A, B, C) with nymphs of *Phoetaliotes nebrascensis* removed (-) or added (+).

P. nebrascensis might promote growth of forbs, thereby benefiting forb feeders. Thus I consider the net effect of density manipulation of one common folivore on the densities of other folivores of varying degrees of dietary overlap.

THE STUDY SITE AND ORGANISMS

The study was conducted at the Konza Prairie Research Natural Area, a preserve of The Nature Conservancy, operated by the Division of Biology at Kansas State University. Konza Prairie is a 3500-ha tract of native tallgrass prairie in the Flint Hills of Kansas, 15 km south of Manhattan, Kansas. Dominant grasses include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*A. scoparius* Michx.), and Indian grass (*Sorghastrum nutans* [L.]), among which grow a diversity of other grasses and forbs (see Freeman and Hulbert 1985).

Local densities of the univoltine *Phoetaliotes nebrascensis* were manipulated in early summer when this and most other grasshopper species (also univoltine) that inhabit the prairie had developed to the second and third of five nymphal instars. Population densities of co-occurring grasshopper species and other phytophagous insects (listed below) were measured thereafter over the next 6 wk (until the appearance of flowering grass stems made sampling infeasible). During this time, most grasshopper species (including *P. nebrascensis*) matured to the fourth and fifth (final) nymphal instar, or to the adult stage.

As the most abundant short-horned (acridid) grasshopper occurring on Konza Prairie, *P. nebrascensis* constitutes 20–80% of the individuals of Acrididae present in local assemblages (Evans et al. 1983, Evans 1984, 1988a, b). It feeds almost exclusively on grasses (especially *A. gerardii*, *A. scoparius*, and *Poa pratensis* L.), and overlaps extensively in diet as well as space with a second abundant species, *Orphulella speciosa* (Scudder) (see Mulkern et al. 1969, Campbell et al. 1974, Evans 1988a). Several other commonly co-

curing and grass-feeding acridid species overlap less extensively in diet with *P. nebrascensis*, while a second group overlaps relatively little, feeding instead solely or to a large degree upon forbs (these are hereafter referred to as forb and mixed feeders). The study focused especially on the impact of manipulating *P. nebrascensis* density on the population dynamics of these confamilial species.

METHODS

Study plots

Experimental manipulations of grasshopper densities were performed in 1987 using six large enclosed plots (each enclosing 550–900 m²; Fig. 1) on an upland ridge. The plots were enclosed within sheet metal fencing sunk 0.2 m into the ground and extending 0.8 m above the ground. They had been used previously (1983–1986) to study invertebrate and small-mammal herbivory in tallgrass prairie (see Seastedt et al. 1987). Adjacent plots were blocked as pairs A, B, and C for analysis in the present study. Data collected throughout the 1986 growing season revealed minimal (and statistically nonsignificant) differences in biomass and nitrogen content of grasses and forbs between paired plots (T. R. Seastedt, *personal communication*). Plant species composition also was similar in paired plots (Table 1). One plot of each pair was chosen randomly to have grasshoppers removed (A-, B-, C-) and the other plot to have grasshoppers added (A+, B+, C+). All plots were burned in April 1987.

The experiment was designed to study large plots as treatment replicates. The six pre-existing plots therefore were not modified at the outset to increase sample size (e.g., split in half with additional fencing). Large plot size minimized the tendency of manipulated grasshopper densities to equilibrate across plots during the experiment through differential rates of emigration/immigration (preliminary observations indicated that the metal fencing slowed net migration by often deterring would-be migrant grasshoppers, but the fencing did not eliminate fully such movement among plots). To enhance the effectiveness of the fencing as a barrier to dispersal, a 1-m strip just inside the fencing around each plot was mowed weekly during the summer of 1987.

Experimental manipulations

Sweep samples for grasshoppers were taken in early summer 1987 prior to manipulations (see Sampling, below). From these samples, the densities of *P. nebrascensis* in the plots were estimated at ≈ 5 grasshoppers/m² (conversion from numbers per sweep to numbers per square metre was made using Tables 3 and 4 in Evans et al. 1983). Therefore, in an effort to make *P. nebrascensis* densities in addition plots ≈ 3 times those in removal plots, 2–2.5 nymphs/m² were removed from the removal plots and added to the addition plots. In particular, between 23 June and 1 July,

TABLE 1. Percentage of occurrence of abundant plant species in 1-m² samples taken within the study plots in September 1986 ($N = 16$ samples per plot; all plant species are listed that occurred in at least 50% of samples in at least one plot). Nomenclature taken from Freeman and Hulbert (1985).

Plant species	Plot*					
	A-	A+	B-	B+	C-	C+
Percentage of occurrence						
Grasses:						
<i>Andropogon gerardii</i> Vitman	100	100	100	100	94	100
<i>A. scoparius</i> Michx.	94	100	100	100	94	94
<i>Bouteloua curtipendula</i> (Michx.)	50	56	63	63	88	100
<i>Dichanthelium oligosanthos</i> (Shult.)	100	94	94	100	100	100
<i>Koeleria pyramidata</i> (Lam.)	69	69	88	69	50	50
<i>Poa pratensis</i> L.	88	100	94	88	88	100
<i>Sorghastrum nutans</i> (L.)	94	94	75	100	38	50
<i>Sporobolus asper</i> (Michx.)	94	94	88	100	100	81
Forbs:						
<i>Amorpha canescens</i> Pursh.	12	44	69	94	100	100
<i>Ambrosia psilostachya</i> DC.	81	44	69	63	31	81
<i>Artemisia ludoviciana</i> Nutt.	88	88	56	56	12	6
<i>Aster ericoides</i> L.	75	75	88	81	63	88
<i>Kuhnia eupatorioides</i> L.	50	38	31	38	12	12
<i>Solidago missouriensis</i> Nutt.	25	12	50	31	0	19
Sedges:						
<i>Carex</i> or <i>Cyperus</i> spp.†	100	100	100	94	100	100

* Paired plots A, B, and C had *Phoetaliotes* grasshoppers either added (+) or removed (-).

† Species in these genera were not distinguished.

4300 nymphs of *P. nebrascensis* were collected by sweeping and removed from plots A- (1200), B- (1100), and C- (2000), and transferred to plots A+ (1400), B+ (1400), and C+ (1500). During this period, 975 nymphs of *Orphulella speciosa* were collected elsewhere on the prairie and released into the plots (150 to each plot except C-, which received 225; C- was ≈ 1.5 times as large in area as C+). On 8 July, an additional 1000 nymphs of *P. nebrascensis* were transferred from plot C- to C+.

Sampling

Plots were sampled for insects by sweeping. Sweep sampling can vary greatly in effectiveness depending on many factors, including the nature of the insects (e.g., species and age), the vegetation swept, and the weather (e.g., see Southwood 1978). In tallgrass prairie, however, sweeping provides an effective means of measuring the relative abundances of grasshopper species present at any one place and time (Evans et al. 1983). Because paired plots were of similar vegetation structure and composition and were sampled within minutes of each other, sweeping yielded reliable estimates of the relative abundances of individual species (e.g., *P. nebrascensis*) in these plots.

All six plots were sampled nondestructively for grasshoppers on 22 June (before densities were manipulated), and again on 3, 15, and 27 July. Twenty sets of five sweeps (net diameter: 38 cm) were taken in each plot on each date (see Evans et al. 1983 for details of the sweeping technique). All arthropods collected were allowed to escape and return to the plot.

The numbers of individuals of short-horned (Acrididae) and long-horned (Tettigoniidae) grasshoppers were recorded; acridids were identified to species while tettigoniids were recorded as a single taxon.

The plots were sampled in similar (but destructive) fashion a final time on 11 August. On this occasion, the entire contents of the net were transferred to a plastic bag after each set of five sweeps. These samples were frozen until sorted, to record numbers of individuals per sample for individual species of Acrididae, and for Tettigoniidae collectively. In addition, the number of individuals was determined for the other major groups of phytophagous insects sampled: Phasmatidae (walkingsticks), Homoptera (especially leafhoppers and planthoppers), and phytophagous Hemiptera (primarily Lygaeidae, Pentatomidae, and Tingidae) and Coleoptera (especially Chrysomelidae and Curculionidae). The first two groups are folivores, while the latter two groups include insects that feed not only on leaves and stems, but on other plant parts as well (flowers, fruits, seeds).

In mid-August, aboveground plant biomass was clipped at ground level in 20 randomly located plots of 0.1 m² in each plot. The clipped vegetation was sorted in the laboratory into three categories: live grasses, dead grasses, and forbs (live and dead forb tissues were not distinguished). Sorted vegetation was dried for 48 h at 60°C and then weighed.

Analyses

Statistical comparisons of biomass of plant tissue and the number of insects of individual species or groups

TABLE 2. Total number of individuals of Acrididae collected in sweeping on particular dates (all six plots combined) and % of individuals belonging to particular species or species complexes.

Species*	% of individuals					All dates combined
	22 Jun	3 Jul	15 Jul	27 Jul	11 Aug	
<i>Phoetaliotes nebrascensis</i> (Thomas)	70.4	72.5	72.6	79.2	76.4	73.7
Other Acrididae						
Grass feeders:	6.0	7.7	9.7	7.8	10.6	7.9
<i>Orphulella speciosa</i> (Scudder)	4.2	5.8	8.4	6.6	7.8	6.1
<i>Arphia</i> spp.†	1.3	1.4	...	1.1	2.1	1.2
<i>Schistocerca lineata</i> Scudder	0.5	0.2	0.4	0.2
<i>Pardalophora</i> spp.§	...	0.1	0.5	...	0.7	0.2
<i>Mermiria bivittata</i> (Serville)	...	0.1	0.4	0.1	...	0.1
<i>Boopedon auriventris</i> McNeill	0.1	0.1	0.1
Forb and mixed feeders:	23.6	19.8	17.8	13.0	13.1	18.4
<i>Melanoplus bivittatus</i> (Say)	8.4	6.3	6.3	1.8	1.0	5.3
<i>M. scudderi</i> Morse	4.8	3.6	3.3	4.4	6.3	4.4
<i>M. femurrubrum</i> (DeGeer)	3.2	3.3	2.8	3.2	2.6	3.1
<i>Hypochlora alba</i> (Dodge)	4.2	3.0	2.3	2.1	1.2	2.8
<i>Melanoplus keeleri luridus</i> (Dodge)	2.5	2.7	1.8	1.2	1.5	2.1
<i>Hesperotettix</i> spp.	0.5	0.9	1.2	0.4	0.4	0.7
Total number of individuals	1316	1216	569	848	681	4630

* Species are grouped by whether they feed predominately on grasses or on forbs (mixed feeders feed to a limited degree on grasses as well as forbs; see Mulkern et al. 1969 and Campbell et al. 1974).

† *Arphia conspersa* Scudder or *A. simplex* Scudder or *A. xanthoptera* (Burmeister).

‡ Species not collected on this date.

§ *Pardalophora apiculata* (Harris) or *P. haldemanni* (Scudder).

|| *Hesperotettix speciosus* (Scudder) or *H. viridis* (Scudder) or *Campylacantha olivacea* (Scudder).

collected on a given day were made using randomized complete block (RCB) ANOVA with three blocks (pairs of plots) and two treatments (*P. nebrascensis* added or removed). For Acrididae and Tettigoniidae (sampled repeatedly), a repeated-measures RCB ANOVA was performed in a single analysis including all sampling dates. The analysis performed was a variant of the split-plot design wherein subunits (dates) occur in strips (Cochran and Cox 1957: 306 ff.). Differences between treatment means for individual sampling dates were tested for significance by LSD (least significant difference). For other insects and plants (sampled only once at the end of the experiment), simple RCB ANOVA was performed. In all analyses, mean values ($\times 100$) for the 20 samples per plot were used to compare paired plots (e.g., A- vs. A+) (see Hurlbert 1984:201). Except where indicated, the *P* values reported below are for two-tailed tests.

RESULTS

Thirteen species and species complexes (i. e., groups for which individual species could not be distinguished reliably) of acridid grasshoppers occurred on the plots during the study. Of these, seven were grass feeders and six were mixed and forb feeders (Table 2). *Phoetaliotes nebrascensis* was the most abundant species throughout the summer, constituting 70–80% of individuals collected on any given sampling date, while *Orphulella speciosa* was the second most abundant species.

The experimental manipulations produced large dif-

ferences in densities of *P. nebrascensis* between paired plots (Fig. 2). Repeated-measures (RM) ANOVA revealed a significant interaction between treatment and date (Table 3); densities of *P. nebrascensis* did not differ between paired plots before nymphs were transferred (Fig. 2; two-tailed LSD test: $P > .05$), but after the transfer, densities became and remained significantly greater in plots that had received nymphs than in paired plots from which nymphs had been removed (one-tailed LSD test: $P < .025$ for each date from 3 July on). On individual sampling dates in July and August, *P. nebrascensis* mean densities were estimated as 1.7–3.1 (A plots), 1.7–3.5 (B), and 1.6–3.8 (C) times as large on addition as on paired removal plots.

After elevation of densities in late June, populations of *P. nebrascensis* nymphs dropped sharply in number over the first half of July in plots A+ and B+ compared with paired populations in removal plots (Fig. 2). Curiously, the addition of *P. nebrascensis* nymphs to plot C+ in late June did not lead to measurably greater numbers of this species in sweep samples taken on 3 July (although numbers in plot C- were depressed). The subsequent transfer of an additional 1000 nymphs from plot C- to C+ on 8 July prevents one from determining whether unusually large numbers of *P. nebrascensis* also disappeared during the first half of July from plot C+ vs. C-.

Despite large differences in densities of the grass feeder *P. nebrascensis* between paired plots, no significant differences between treatments were detected in the biomasses of live or dead grass, or forbs, present in mid-

August (Fig. 3; simple RCB ANOVA: $P = .48, .82$, and $.72$ for live and dead grass, and forbs, respectively). No significant differences were detected between treatments throughout the experiment in the number of acridid grasshoppers present (all species combined, excluding *P. nebrascensis*) (Fig. 4; RM ANOVA as in Table 3: treatment $P > .50$, treatment \times date interaction $P > .10$). In both treatments, the number of grasshoppers present declined as the season progressed (Fig. 4; RM ANOVA: date $P < .001$). The number of grass-feeding acridids in particular (again excluding *P. nebrascensis*) also did not differ with treatment (or with date) (Fig. 4; RM ANOVA: treatment $P > .50$, date $P > .25$, treatment \times date $P > .50$). Neither did the number of forb- and mixed-feeding acridids differ with treatment (Fig. 4; RM ANOVA: treatment $P > .75$, treatment \times date $P > .25$), although numbers declined in both treatments as the season progressed (date $P < .001$). Finally, in analysis of all acridid species and species groups (excluding *P. nebrascensis*) considered

TABLE 3. Repeated-measures ANOVA for *Phoetaliotes nebrascensis* sampled on five dates in 1987, for paired plots with *P. nebrascensis* nymphs either removed or added ("treatment").

Source of variation	df	MS	F	P
Blocks	2	68 880.8		
Treatment	1	716 107.5	80.08	<.05
Error a	2	8 942.5		
Date	4	206 592.9	15.04	<.001
Error b	8	13 739.2		
Treatment \times date	4	112 984.6	6.01	<.05
Error c	8	18 788.3		
Total	29	83 113.2		

individually (vs. pooled above), there were no significant treatment effects (or significant interactions involving treatment; Table 4).

The number of tettigoniid grasshoppers also showed no overall treatment effect, although there was a significant interaction of treatment with date as the number of Tettigoniidae declined over the season (Table 5 and Fig. 4). The interaction was consistent with a weak competitive, depressant effect of *P. nebrascensis* on tettigoniid numbers, as the number of tettigoniids shifted over the season from slightly greater to slightly fewer on plots with *P. nebrascensis* added than on plots with *P. nebrascensis* removed (Fig. 4). The slight differences between treatments were not significantly different, however, on any given sampling date ($P > .20$ in two-tailed LSD tests for all individual sampling dates).

The numbers of Phasmatidae, Homoptera, and phytophagous Hemiptera and Coleoptera present in August also did not differ significantly between plots with *P. nebrascensis* added or removed (Fig. 5, $P > .42$ for Hemiptera, $P > .89$ for the other three taxa). Given that no clearcut trends emerged in treatment comparisons for any of the above plant and insect variables (with the possible exception of the Tettigoniidae; see Figs. 3–5), there is little support for the argument that the lack of statistical significance simply reflects the limited number of replicates.

DISCUSSION

There is little evidence that the most abundant acridid grasshopper at Konza Prairie, *P. nebrascensis*, competes strongly (or interacts strongly in other ways) with co-occurring grasshoppers or other phytophagous insects. Year after year, grasshoppers (including *P. nebrascensis*) cause little noticeable damage to the tall-grass prairie of the Flint Hills, and the grasshoppers have not multiplied to capitalize on the seemingly abundant available food (Knutson and Campbell 1976). No reduction in standing crop biomass of vegetation, or increase in litter (see Mitchell and Pfadt 1974) was observed in plots with elevated densities of *P. nebrascensis*. Nevertheless, it is not unreasonable to hypothesize a priori that interspecific interactions involving

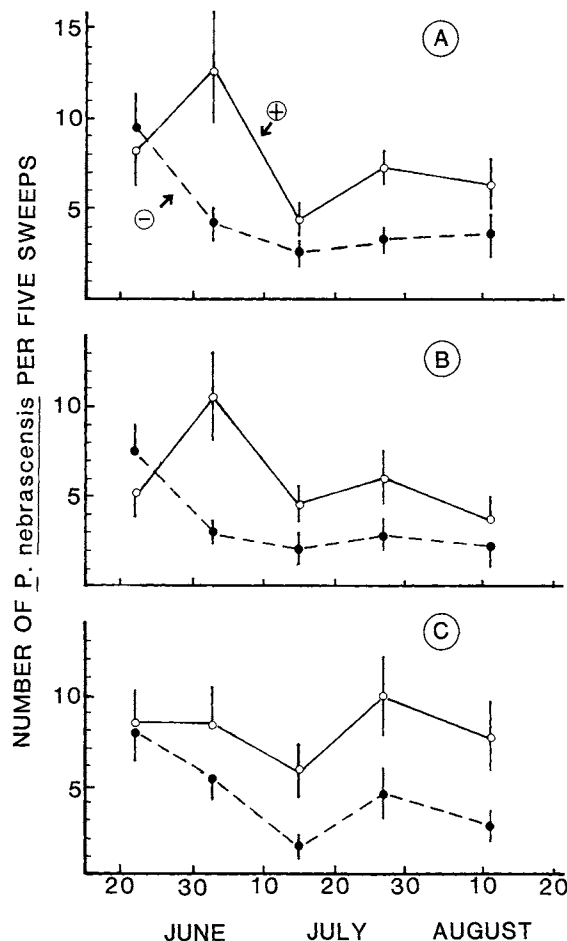


FIG. 2. Number of nymphs (mean \pm 2 SE) of *Phoetaliotes nebrascensis* per five sweeps on different dates in 1987 in paired plots (A, B, C) with nymphs removed (—, ●—●) or added (+, ○—○) in late June and early July. $N = 20$ sets of five sweeps for each plot on each date.

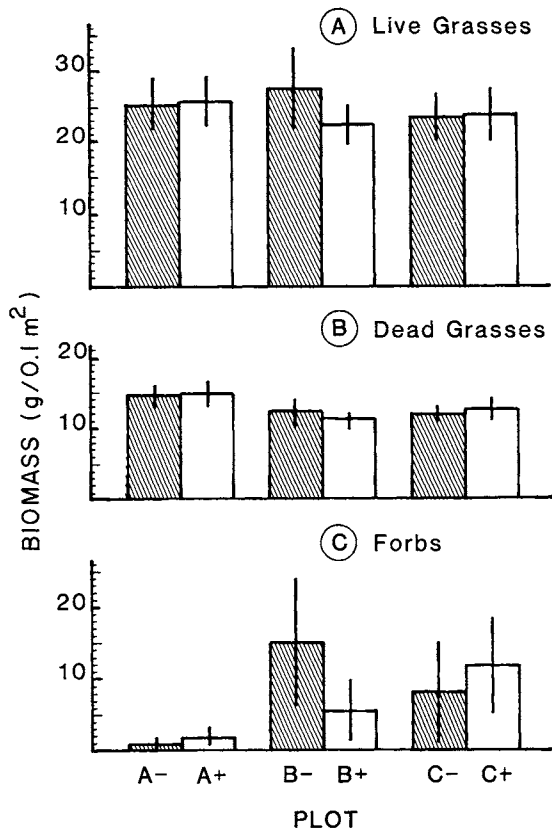


FIG. 3. Biomass (mean \pm 2 SE) of live (A) and dead (B) grass, and (live + dead) forbs (C) in mid-August 1987 in 20 random quadrats of 0.1 m² in each plot with nymphs of *Phoetaliotes nebrascensis* removed (-) or added (+).

P. nebrascensis might occur. Recent studies of plant responses to herbivory (e.g., Haukioja and Niemela 1979, Rhoades 1985) suggest that the feeding activities of an abundant folivore such as *P. nebrascensis* may lead to changes in host plant chemistry that affect other folivores also feeding on the plant (e.g., Janzen 1973, Strong et al. 1984, Faeth 1986).

Of the many species of phytophagous insects that occur with *P. nebrascensis* on the study plots, *Orphulella speciosa* is most similar in diet, and therefore might be expected to compete most intensely with *P. nebrascensis*. No changes in densities of *O. speciosa* were observed, however, as a result of manipulation of *P. nebrascensis* density. Other grass-feeding acridids also failed to change in density in response to the manipulations. Finally, there was no evidence that *P. nebrascensis* densities might be linked indirectly to densities of forb-feeding acridid grasshoppers, e.g., as mediated by grass-forb competition.

The study focused on the potential interactions of *P. nebrascensis* with other grasshoppers during only the nymphal and not the adult period. Grasshoppers may interact most intensely as adults since adults probably have greater individual impact on their host plants

than do nymphs (especially those in early instars). The study also only considered the abundance (survivorship) of other grasshoppers, and not their growth and subsequent reproduction as adults (e.g., see Wall and Begon 1987). Too few other grasshoppers were collected when the experiment was terminated in August to compare meaningfully growth and development between treatments.

Previous studies have also generally not provided strong support for interspecific competition among grasshoppers at most densities in North American grasslands, although researchers differ in their assessments. Mulkern (1980) concluded that there was little

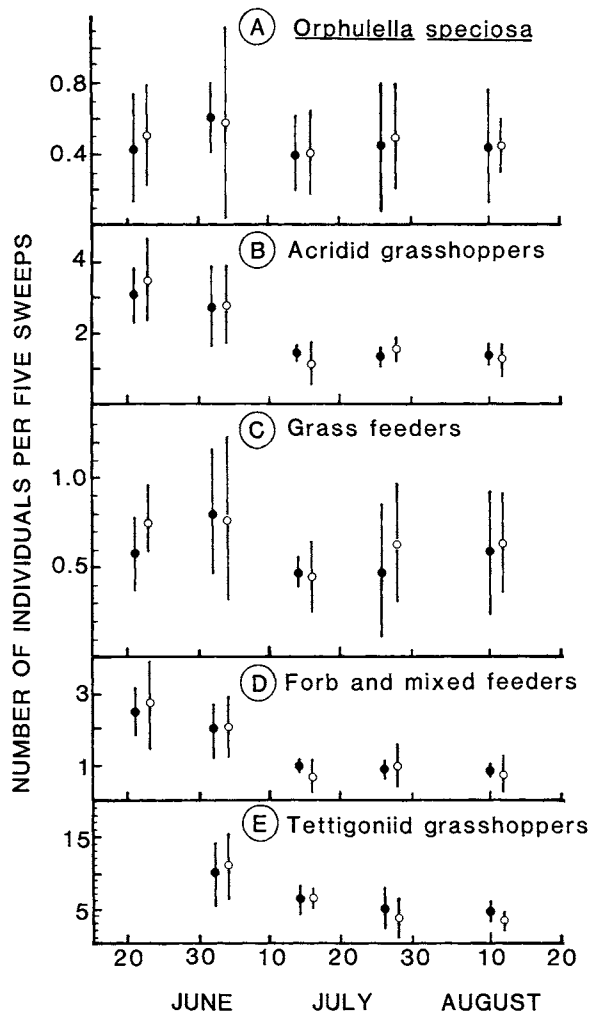


FIG. 4. Number of individuals (mean \pm 2 SE) per five sweeps on different dates in 1987 in plots with nymphs of *Phoetaliotes nebrascensis* removed (●) or added (○): for *Orphulella speciosa* (A), acridid grasshoppers excluding *P. nebrascensis* (B), grass-feeding acridids excluding *P. nebrascensis* (C), forb- and mixed-feeding acridids (D), and tettigoniid grasshoppers (E; not sampled 22 June). $N = 3$ plots for each treatment on each date (i.e., the mean shown is the mean of means for individual plots which in turn are based on sample sizes of $N = 20$ sets of five sweeps).

TABLE 4. Repeated-measures ANOVA for all species/species complexes of Acrididae excluding *Phoetaliotes nebrascensis* sampled on five dates in 1987, for paired plots with *P. nebrascensis* nymphs removed or added ("treatment").

Source of variation	df	MS	F	P
Blocks	2	1258.8		
Treatment	1	30.6	.06	>.75
Error a	2	476.9		
Species	11	8325.4	12.15	<.001
Treatment × species	11	142.6	.21	>.75
Error b	44	685.5		
Date	4	4215.4	13.62	<.005
Error c	8	309.6		
Treatment × date	4	119.7	.74	>.50
Species × date	44	740.6	4.56	<.001
Treatment × species × date	44	72.8	.45	>.75
Error d	184	162.3		
Total	359	591.3		

evidence of competition among grasshoppers in the grasslands of North Dakota. Joern (1979a, b, 1982a, b, 1986, Joern and Lawlor 1980, 1981) did not find strong evidence of interspecific competition in his extensive studies of grasshoppers in arid grasslands of west Texas and the sandhills grasslands of western Nebraska. Community patterns of food and microhabitat utilization were suggestive, however, of interactions among species; these interactions may be mediated through shared predators rather than direct interspecific competition. Ueckert and Hansen (1971) found that extensive niche differentiation minimizes present-day interspecific competition among grasshoppers in mixed-grass prairie of eastern Colorado. Belovsky (1986), in contrast, has suggested from controlled cage experiments that interspecific competition among grasshoppers may exist at high densities in the grasslands of Montana.

Manipulation of *P. nebrascensis* density produced no clearcut changes in densities of other phytophagous insects, including the other major groups of folivores (Tettigoniidae, Phasmatidae, and Homoptera). The significant interaction of date with treatment for Tettigoniidae may reflect a slight depressant effect of *P.*

TABLE 5. Repeated-measures ANOVA for Tettigoniidae sampled on four dates in 1987, for paired plots with *Phoetaliotes nebrascensis* nymphs removed or added ("treatment").

Source of variation	df	MS	F	P
Blocks	2	360 438.5		
Treatment	1	204.2	.007	>.75
Error a	2	30 982.3		
Date	3	556 816.7	17.7	<.005
Error b	6	31 371.9		
Treatment × date	3	22 070.8	9.17	<.025
Error c	6	2 407.3		
Total	23	118 364.5		

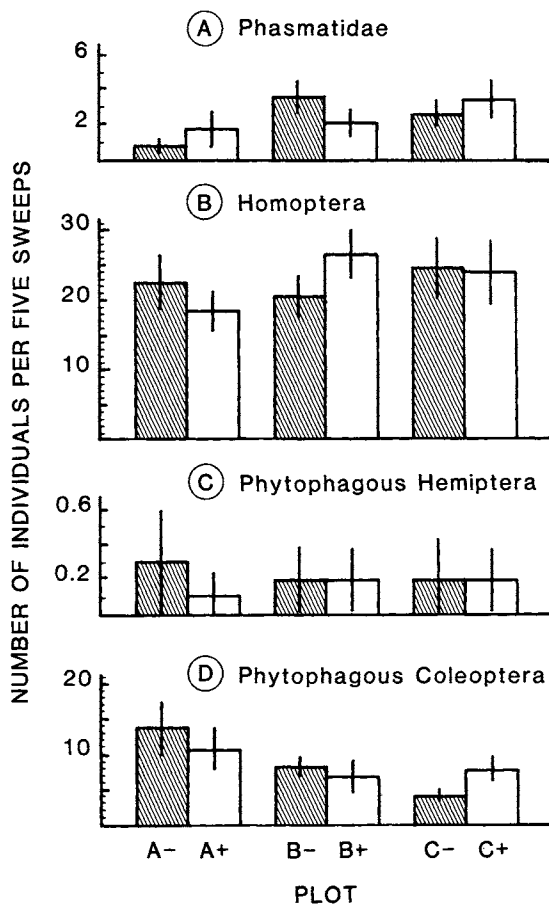


FIG. 5. Number of individuals (mean \pm 2 SE) per five sweeps in mid-August 1987 in each plot with nymphs of *Phoetaliotes nebrascensis* removed (-) or added (+): for Phasmatidae (walkingsticks) (A), Homoptera (B), phytophagous Hemiptera (C) and Coleoptera (D). $N = 20$ sets of five sweeps each.

nebrascensis on these insects, but the experimental design was not sufficient to establish clearly the existence of such a weak effect. The Tettigoniidae were almost all meadow grasshoppers (*Conocephalus* spp., Conocephalinae) with broad diets including both grasses and forbs (Gangwere 1961). These species likely fed heavily on grasses, as they are common at sites on Konza Prairie where grasses are abundant but forbs are rare (E. W. Evans, personal observation). The diets of the Phasmatidae on the plots (*Diaperomera* sp., Heteroneuriniinae) are unknown (Gangwere 1961), but probably included grasses and some forbs (Ball et al. 1942). The Homoptera were a diverse assemblage of many kinds of fluid (sucking) feeders. For example, the most common family, the leafhoppers (Cicadellidae), includes >110 species in the tallgrass prairie of the Flint Hills that vary from host specialists to generalists in feeding on grasses or forbs (DeLong 1965, Cwikla and Blocker 1981, Whitcomb et al. 1988). Because no differences occurred between treatments in the overall number of

Homoptera, a more careful breakdown of numbers into individual species was not attempted (thus leaving unpursued the possibility that negative effects of *P. nebrascensis* manipulations on some species were exactly offset by positive effects on other species).

The study must also be assessed by placing the restricted set of experimental conditions within the broader range of conditions that can occur in the tallgrass prairie. Data from other, similar uplands of Konza Prairie suggest that 1987 was a year of moderate primary productivity: the overall average of 320 g/m² of live plant biomass (grass + forbs) present in mid-August 1987 compares with 200–600 (median: 350) g/m² on burned upland sites in 1975–1984 (Abrams et al. 1986). Similarly, in early August on similar, recently burned upland sites, grasshopper populations varied in 1982–1986 from 0.2 to 5.4 grasshoppers per five sweeps for *P. nebrascensis* in particular and from 0.3 to 8.5 for Acrididae in total (E. W. Evans, *personal observation*). Thus numbers of *P. nebrascensis* (2.8 and 5.9) and Acrididae in total (4.2 and 7.1) collected per five sweeps in removal and addition plots, respectively, suggest that the two experimental treatments were intermediate to relatively high compared with natural densities of grasshoppers (the experimental densities for acridid grasshoppers as a group can be estimated for August 1987 as in the range of 1–4 acridids/m²; Evans et al. 1983). Hence the experiment succeeded in testing for competition within the range of natural conditions. Competition remains a possibility under more extreme conditions (e.g., when less plant biomass is present); i.e., interactions among these grasshoppers may conform to the density-vague model of population and community dynamics outlined by Strong (1986).

Because the density of only one species was manipulated, one cannot assess the relative strengths of intra- vs. interspecific competition (Connell 1983). Strong intraspecific interactions may weaken interspecific competition. The unusually large drop in *P. nebrascensis* density after the addition of individuals to plots A+ and B+ may reflect large rates of mortality from intraspecific competition and/or large emigration rates in response to high conspecific density (it might also reflect increased predation, although if so, this increase was apparently not experienced by other grasshopper species). Thus, intraspecific interactions may prevent local densities of *P. nebrascensis* from becoming high enough to result in detectable effects on co-occurring species. Additional experiments on the importance of intraspecific interactions in *P. nebrascensis* are clearly called for.

The present experiment was intended to test especially for exploitative (consumptive sensu Schoener 1983) and/or interference (encounter sensu Schoener 1983) competition involving *P. nebrascensis* and other phytophagous insects. But, as Connell (1983) notes, interpretation of results is complicated by the many complex indirect effects (e.g., changing impacts of pred-

ators; Holt 1977, Holt and Kotler 1987) that may accompany direct effects of density manipulation on target species. Tilman (1987) has concluded that such field experiments are of limited usefulness because they only reveal the overall effects of density manipulations and not the underlying mechanisms that produce possibly counteracting indirect and direct effects. But given the great difficulties of teasing apart direct and indirect effects, "simple" density manipulations remain important initial means of exploring how strongly the population dynamics of coexisting species are interlinked. While it is desirable to determine underlying mechanisms, it is equally desirable to establish the net effects of natural fluctuations in densities of a given species (as mimicked by density manipulations) on the densities of co-occurring species.

Tilman (1988) discusses another limitation of this and similar experiments: such "pulse experiments" (Bender et al. 1984) focus only on short-term dynamics, which may be quite different from long-term consequences (see also Murdoch 1970). It is possible, for example, that although no changes were detected in densities of other species following manipulation of *P. nebrascensis* numbers, growth patterns and eventual fecundity of individuals of these other species may have been sufficiently altered so as to affect densities in future years. The present experiment was not designed to test for such long-term effects.

In summary, fluctuations from year to year in population densities of *P. nebrascensis* are characteristic of the tallgrass prairie. The present experiment suggests that at least in years of moderate primary productivity, fluctuations of this abundant folivore have little short-term impact on the population dynamics of co-occurring species of phytophagous insects.

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LITERATURE CITED

- Abrams, M. D., A. K. Knapp, and L. C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. *American Journal of Botany* 73:1509–1515.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- Ball, E. D., E. R. Tinkham, R. Flock, and C. T. Vorhies. 1942. The grasshoppers and other Orthoptera of Arizona. Arizona Agricultural Experiment Station Technical Bulletin 93:255–373.
- Belovsky, G. 1986. Generalist foraging and its role in competitive interactions. *American Zoologist* 26:51–69.

- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* **65**:1-13.
- Campbell, J. B., W. H. Arnett, J. D. Lambley, O. K. Jantz, and H. Knutson. 1974. Grasshoppers (Acrididae) of the Flint Hills native tallgrass prairie in Kansas. Kansas Agricultural Experiment Station Research Paper 19.
- Cochran, W. G., and G. M. Cox. 1957. Experimental designs. Second edition. John Wiley and Sons, New York, New York, USA.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661-696.
- Conner, E. F., and D. Simberloff. 1986. Competition, scientific method and null methods in ecology. *American Scientist* **74**:155-162.
- Cwikla, P. S., and H. D. Blocker. 1981. An annotated list of the leafhoppers (Homoptera: Cicadellidae) from tallgrass prairie of Kansas and Oklahoma. *Transactions of the Kansas Academy of Sciences* **84**:89-97.
- DeLong, D. M. 1965. Ecological aspects of North American leafhoppers and their role in agriculture. *Bulletin of the Entomological Society of America* **11**:9-26.
- Evans, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. *Oikos* **43**:9-16.
- . 1988a. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography and vegetation. *Canadian Journal of Zoology* **66**:1495-1501.
- . 1988b. Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? *Oikos* **52**:283-292.
- Evans, E. W., R. A. Rogers, and D. J. Opfermann. 1983. Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: night trapping vs. sweeping. *Environmental Entomology* **12**:1449-1454.
- Faeth, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* **67**:479-494.
- Freeman, C. C., and L. C. Hulbert. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. *Transactions of the Kansas Academy of Sciences* **88**:84-115.
- Fritz, R. S., C. F. Sacchi, and P. W. Price. 1986. Competition versus host plant phenotype in species composition: willow sawflies. *Ecology* **67**:1608-1618.
- Gangwere, S. K. 1961. A monograph on food selection in Orthoptera. *Transactions of the American Entomological Society* **87**:67-230.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421-425.
- Haukioja, E., and P. E. Niemala. 1979. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. *Oecologia (Berlin)* **39**:151-159.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197-229.
- Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. *American Naturalist* **130**:412-430.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**:187-211.
- Janzen, D. H. 1973. Host plants as islands. II. Competition in evolutionary and contemporary time. *American Naturalist* **107**:786-790.
- Joern, A. 1979a. Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia (Berlin)* **38**:325-347.
- . 1979b. Resource utilization and community structure in assemblages of arid grassland grasshoppers (Orthoptera: Acrididae). *Transactions of the American Entomological Society* **105**:253-300.
- . 1982a. Distribution, densities, and relative abundances of grasshoppers (Orthoptera: Acrididae) in a Nebraska sandhills prairie. *Prairie Naturalist* **14**:37-45.
- . 1982b. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera, Acrididae). *Southwestern Naturalist* **27**:197-209.
- . 1986. Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. *Oikos* **46**:243-249.
- Joern, A., and L. R. Lawlor. 1980. Arid grassland grasshopper community structure: comparisons with neutral models. *Ecology* **61**:591-597.
- Joern, A., and L. R. Lawlor. 1981. Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos* **37**:93-104.
- Karban, R. 1986. Interspecific competition between folivorous insects on *Erigeron glaucus*. *Ecology* **67**:1063-1072.
- Knutson, H., and J. B. Campbell. 1976. Relationships of grasshoppers (Acrididae) to burning, grazing, and range sites of native tallgrass prairie in Kansas. *Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management* **6**:107-120.
- Lawton, J. H., and D. R. Strong, Jr. 1981. Community patterns and competition in folivorous insects. *American Naturalist* **118**:317-338.
- May, R. M., and J. Seger. 1986. Ideas in ecology. *American Scientist* **74**:256-267.
- Mitchell, J. E., and R. E. Pfadt. 1974. A role of grasshoppers in a shortgrass prairie ecosystem. *Environmental Entomology* **3**:358-360.
- Mulkern, G. B. 1980. Population fluctuations and competitive relationships of grasshopper species (Orthoptera: Acrididae). *Transactions of the American Entomological Society* **106**:1-41.
- Mulkern, G. B., K. P. Pruess, H. Knutson, A. F. Hagen, J. B. Campbell, and J. D. Lambley. 1969. Food habits and preferences of grassland grasshoppers (Acrididae) of the North Central Great Plains. *North Dakota State University Agricultural Experiment Station Bulletin Number* 481.
- Murdoch, W. W. 1970. Population regulation and population inertia. *Ecology* **51**:497-502.
- Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist* **125**:205-238.
- Schoener, T. W. 1982. The controversy over interspecific competition. *American Scientist* **70**:586-595.
- . 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.
- Seastedt, T. R., T. C. Todd, and S. W. James. 1987. Experimental manipulations of the arthropod, nematode and earthworm communities in a North American tallgrass prairie. *Pedobiologia* **30**:9-17.
- Slobodkin, L. B., F. E. Smith, and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *American Naturalist* **101**:109-124.
- Southwood, T. R. E. 1978. Ecological methods with particular reference to the study of insect populations. Second edition. Chapman and Hall, London, England.
- Strong, D. R., Jr. 1982a. Harmonious coexistence of hispine beetles on *Heliconia* in experimental and natural communities. *Ecology* **63**:1039-1049.
- . 1982b. Potential interspecific competition and host specificity: hispine beetles on *Heliconia*. *Ecological Entomology* **7**:217-220.
- . 1986. Density-vague population changes. *Trends in Ecology and Evolution* **1**:39-42.
- Strong, D. R., Jr., J. H. Lawton, and T. R. E. Southwood.

1984. Insects on plants: community patterns and mechanisms. Blackwell Scientific, Oxford, England.
- Tilman, D. 1987. The importance of the mechanisms of interspecific competition. *American Naturalist* **129**:769–774.
- . 1988. Ecological experimentation: strengths and conceptual problems. Pages 136–157 in G. E. Likens, editor. Long-term studies in ecology. Springer-Verlag, New York, New York, USA.
- Ueckert, D. N., and R. M. Hansen. 1971. Dietary overlap of grasshoppers on sandhill rangeland in northeastern Colorado. *Oecologia* (Berlin) **8**:276–295.
- Wall, R., and M. Begon. 1987. Individual variation and the effects of population density in the grasshopper *Chorthippus brunneus*. *Oikos* **49**:15–27.
- Whitcomb, R. F., A. L. Hicks, D. E. Lynn, H. D. Blocker, and J. P. Kramer. 1988. Host specificity: a major mechanism enhancing insect diversity in grasslands. Article 11.06 in A. Davis and G. Stanford, editors. The prairie: roots of our culture; foundation of our economy. Native Prairie Association of Texas, Dallas, Texas, USA.