ABSENCE OF INTERSPECIFIC COMPETITION AMONG TALLGRASS PRAIRIE GRASSHOPPERS DURING A DROUGHT[1]

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Abstract. The grasshoppers *Phoetaliotes nebrascensis* and *Orphulella speciosa* overlap extensively in both diet and habitat in native tallgrass prairie at Konza Prairie, Kansas. I tested for interspecific competition between these two species during a drought year when primary productivity in the prairie was unusually low. In late June 1989, I transferred young nymphs of *P. nebrascensis* among enclosed plots (each 550–900 m²) to produce three pairs of plots with grasshoppers removed or added. Pretransfer densities in the six plots were estimated at 6 nymphs/m². Experimental transfers resulted in densities of *P. nebrascensis* in addition plots 2–3 times as large as in paired removal plots; significant differences in density between addition and removal plots persisted throughout the summer.

Densities of *O. speciosa* in plots with *P. nebrascensis* removed or added did not differ significantly throughout the growing season of 1989, nor in early summer of 1990. Furthermore, growth and development of *O. speciosa* in these plots (as measured by rate of maturation, and adult femur length and mass in 1989) were not reduced in the presence of high densities of *P. nebrascensis,* nor was reproductive potential (measured as the ratio of young nymphs present in early summer 1990 to adults in late summer 1989). These results are similar to those of a previous experiment at the same site during 1987 when primary productivity was moderate. Even under the extreme conditions of 1989, with particularly high ratios of grasshoppers to available food resources, variation in *P. nebrascensis* density did not adversely affect populations of *O. speciosa*. These results contrast with recent results for sedentary phytophagous insects, but are consistent with the hypothesis that free-ranging insect herbivores may rarely experience interspecific competition for food resources.

Key words: Acrididae; grasshoppers; grassland; herbivory; interspecific competition; Konza Prairie; Orphulella speciosa; Phoetaliotes nebrascensis; phytophagy; tallgrass prairie.

INTRODUCTION

Rathcke (1976), Lawton and Strong (1981), and Strong et al. (1984) concluded from critical reviews of the literature that interspecific competition among phytophagous insects is generally weak or nonexistent. Their conclusions have spurred additional field experimentation, which collectively suggests that interspecific interactions may indeed often be important (e.g., Stamp 1984, Stiling and Strong 1984, Edson 1985, Faeth 1986, Fritz et al. 1986, Harrison and Karban 1986, Karban 1986, 1989, Crawley and Pattrasudhi 1988, Mopper et al. 1990, Moran and Whitham 1990; but see also McEvoy 1986, Karban 1987, Antolin and Addicott 1988, Fritz 1990, Fritz and Price 1990). An emerging generalization seems to be that such interactions typically are asymmetrical, and indirect in that they are mediated by host plant quality as affected by herbivory (Lawton and Hassell 1981, Karban 1989, Mopper et al. 1990, Moran and Whitham 1990).

These recent experimental investigations have focused on sedentary insects, in which individuals spend

much of their lives on single plants. In contrast, there has been little experimental study of competition in free-ranging insects, in which individuals move among and consume parts of many plants during their lifetimes (but see Howard and Harrison 1984). As Karban (1989) notes, such vagile insects may be able to minimize the impact of interspecific competition by avoiding host plants heavily attacked by other herbivores (but see also Kareiva 1982). In an experimental study of free-ranging grasshoppers in large, open pens in tallgrass prairie, I did not detect interspecific competition (Evans 1989). While these findings differ from those of many recent studies of sedentary insects, my results are consistent with conclusions of previous, nonexperimental studies of grasshoppers in grassland biomes (e.g., Ueckert and Hansen 1971, Gangwere et al. 1976, Joern 1979a, b, 1986, Joern and Lawlor 1980, 1981, Mulkern 1980). However, I conducted the field experiment during a year when the consumer/resource ratio (numbers of grasshoppers present per kilogram of available forage) was relatively favorable. As has been suggested for animals in general (e.g., Wiens 1977, Strong 1986), strong interspecific competition among grasshoppers may only manifest itself under more extreme conditions when the ratio of consumers to avail-

able resources is unusually high (e.g., Belovsky 1986, Pfadt et al. 1988).

To test this hypothesis for grasshoppers in tallgrass prairie, I repeated the field experiment conducted in 1987 (Evans 1989) at the same study site in 1989. In comparison to 1987, very little rain fell at the site during the spring of 1989, thus creating the potential for reduced primary productivity during the growing season and therefore more intense interactions among grasshoppers. As in 1987, I manipulated densities of the most abundant grasshopper inhabiting the prairie, *Phoetaliotes nebrascensis* (Thomas) (Orthoptera: Acrididae), early in the summer of 1989. Here I assess effects of these manipulations on density, growth, and development of *Orphulella speciosa* (Scudder) in 1989 and 1990. Both *P. nebrascensis* and *O. speciosa* are univoltine, hatching in June from overwintering eggs and maturing over the summer (Smith 1981). *Orphulella speciosa* was the second most abundant grasshopper at the study site, and overlaps extensively with *P. nebrascensis* both in diet (Mulkern et al. 1969, Campbell et al. 1974) and habitat use at Konza Prairie (Evans 1988*a*, *b*). It is therefore reasonable to hypothesize a priori that competition during extreme periods may occur between *P. nebrascensis* and *O. speciosa*.

METHODS

Study plots

The field experiment was conducted at the Konza Prairie Research Natural Area, a native tallgrass prairie preserve of The Nature Conservancy, operated by the Division of Biology at Kansas State University. I manipulated densities of *P. nebrascensis* using the same six large enclosed plots (all plots but one 900-m² plot were 550–600 m²) subjected to similar density manipulations in 1987 (the physical layout of the plots and the species composition of the plant communities in these plots are described in Evans 1989). These contiguous plots were each surrounded by 0.8 m high, sheet metal fencing. All plots were burned in April 1989 (the plots were neither burned nor otherwise disturbed during 1988). Thereafter, a 1-m strip just inside the fencing around each plot was mowed once every 2 wk to make it more difficult for grasshopper nymphs to cross over the fencing. As in 1987, adjacent plots (with similar plant species compositions) were blocked as pairs A, B, and C for analysis. Nymphs of *P. nebrascensis* were removed from one plot of each pair (A−, B−, C−) and added to the other plot of the pair (A+, B+, C+). Plots received the same treatment as in 1987, when treatments were randomly assigned between paired plots.

There were two major reasons for using a limited number of large plots vs. a greater number of smaller plots in the experimental design. First, large plots more than small plots allow for the local dispersal (trivial movement sensu Southwood 1962) characteristic of free-living grasshoppers, including nymphs (Riegert et al. 1954, Joern 1983). Secondly, in open plots between which there will inevitably be some migration of grasshoppers, large plots serve to reduce the rate of this migration, such that manipulated grasshopper densities do not quickly re-equilibrate across plots. By leaving plots open, one can allow for mediation of interspecific effects through such factors as predators in addition to food quality and quantity. The simple experimental design permits a relatively full range of natural factors to operate, but is not intended to identify which factor, if any, may be most critical to the experimental results.

Experimental manipulations and sampling

Densities of *P. nebrascensis* were manipulated on the plots 26 June–1 July 1989 by using sweep nets to collect and redistribute nymphs (mostly second instars); all other insects collected simultaneously were allowed to escape back into the plots from which they had been swept. In all, 4000 nymphs of *P. nebrascensis* were removed from plots A− (1260), B− (1091), and C− (1649), and added to plots A+ (1350), B+ (1300), and C+ (1350). The same number of sweeps was taken in addition as in removal plots to control for any effects of sweeping on experimental results; the insects collected in addition plots were simply released immediately back into the plots.

Grasshoppers were sampled in the plots by sweeping, following the general procedures used and justified by Evans (1989). On each sampling occasion, 100 sweeps were taken as 20 sets of five sweeps (net diameter: 38 cm) in each plot. Although plot C+ was somewhat larger than the other plots, the same area was swept for grasshoppers in all plots. Grasshoppers were either counted and identified to species before being allowed to escape back into the plot immediately following capture (nondestructive samples, taken by E. Evans), or were transferred from the sweep net to plastic bags to be frozen until counted and identified in the laboratory (destructive samples, taken by T. Haner). The plots were sampled nondestructively on 26 June (before hopper transfers began), 1 July, and 10–13 August in 1989 (each plot was sampled on five occasions during the August period, for a total of 500 sweeps), and on 30 June and 1 July in 1990. Destructive samples were taken from the plots on 26 July and 19 September 1989. In addition, 20–30 individuals of *O. speciosa* were collected from each plot on 13 August 1989 to assess growth and development (the grasshoppers collected represented only a very small fraction of those present in each plot). Except on 1 July 1989 (see *Analyses* below), all sweep samples were taken on calm, clear days when the wind was ≤15 km/h, and cloud cover was ≤50%.

As in 1987, aboveground plant biomass was clipped at ground level in 20 randomly located quadrats of 0.1 m² in each plot in mid-August 1989. The clipped veg-

etation was sorted as live or dead grass, or forbs (live and dead tissue not distinguished), dried for 48 h at 60°C, and weighed. Grasshoppers collected on 26 July and 13 August 1989 were also dried for 48 h at 60°C before they were weighed (because individuals often lost one or, less frequently, both hind legs upon freezing and rethawing, both hind legs were removed from all grasshoppers before weighing). Masses of adult grasshoppers reflect both nymphal and adult feeding and other activities. To assess nymphal growth alone, lengths of adult hind femurs were determined as a measure of final exoskeleton size achieved by individuals of *O. speciosa* (de Souza Santos and Begon 1987, Wall and Begon 1987*a, b*).

Analyses

Analysis of variance (ANOVA) with a repeated-measures randomized complete block (RCB) design was performed to compare numbers of individuals of *P. nebrascensis* or *O. speciosa* in addition vs. removal plots across six 1989 and 1990 sampling periods (26 June, 1 July, 26 July, 10–13 August, 19 September 1989, and 30 June–1 July 1990). The dependent variable tested was the number of individuals collected per 100 sweeps (this was computed as a mean for 10–13 August 1989 from a total of 500 sweeps per plot, and for 30 June–1 July 1990 from a total of 200 sweeps per plot). The statistical procedures were those described by Evans (1989); differences between treatment means for individual sampling dates (periods) were tested for significance by least significant difference (LSD). For other variables measured only once during the study (e.g., standing plant biomass in August), simple RCB ANOVA (with three blocks) was performed on mean values for individual plots. Measures of growth and development (mean developmental stage, mass, and femur length) were analyzed simultaneously for both sexes of *O. speciosa* by nesting sex within treatment (*P. nebrascensis* addition or removal) in split-block RCB ANOVA. Except where noted, the P values reported below are for two-tailed tests.

Statistical tests were based on only three replicates per treatment; thus, the experiment had low power to detect significant differences. I therefore calculated, for each statistical test, the minimal difference between treatments that could be detected as significant at $P = .05$. I determined these minimal differences using appropriate modifications of Fisher's LSD procedure (Cochran and Cox 1957).

To aid in interpreting the experimental results biologically, the numbers of individuals of grasshoppers per square metre on individual sampling dates were estimated from sweep samples using results of Evans et al. (1983) (note that raw numbers, rather than these estimates, were used in the statistical analyses described above). In particular, sweep samples were converted to absolute densities by multiplying the number of individuals per 100 sweeps by 0.06 (late June and

early July 1989 and 1990), 0.0265 (26 July 1989), 0.02 (10–13 August 1989), and 0.0265 (19 Sept 1989); these multipliers were derived from Table 4 of Evans et al. (1983), given their estimate that night trapping captured 75% of the grasshoppers present. Cloudy, windy weather during sampling on 1 July 1989 resulted in only 72% as many grasshoppers captured per 100 sweeps as a few days earlier on 26 June. Therefore, sweep sample results on 1 July were first multiplied by 1.38 (=1/0.72) before being converted to numbers per square metre. The resultant estimates of numbers of *P. nebrascensis* on addition and removal plots on 1 July closely approximate those predicted from the combination of estimated absolute densities on 26 June and the known number of nymphs per square metre added or removed between the two sampling dates.

RESULTS AND DISCUSSION

Phoetaliotes nebrascensis and *Orphulella speciosa* were the most and second-most abundant of 17 species identified in sweep samples from the study plots in 1989 and 1990. From June through August 1989, *P. nebrascensis* was 5–6 times as abundant as *O. speciosa* (Table 1). The experimental manipulations resulted in a 2.5-fold difference in the mean density of *P. nebrascensis* between addition and removal plots on 1 July 1989 (Fig. 1A). Repeated-measures RCB ANOVA indicated a significant interaction between treatment and date (Table 2). Densities of *P. nebrascensis* did not differ significantly between paired plots before nymphs were transferred (Fig. 1; two-tailed LSD test: $P > .05$), but after the transfer, densities remained significantly greater in addition than in removal plots through August (one-tailed LSD test: $P < .025$ on 1 and 26 July, and 10–13 August 1989; $P > .05$ on 19 September 1989 and 30 June–1 July 1990).

Much drier weather prevailed at Konza Prairie in 1989 than had occurred in 1987; from April through August, only 40% as much precipitation fell in 1989 vs. in 1987 (amount of precipitation received in April–August at the Konza Prairie Headquarters: 331 mm in 1989 vs. 531 mm in 1987). Consequently, live aboveground plant biomass (grasses + forbs) in the plots was on average only 207 g/m² in mid-August 1989 (Table 3). This low standing crop approximates the minimum reported for burned upland sites on Konza Prairie reported by Abrams et al. (1986) in their long-term study of primary production, and is only 65% of that measured at the plots in mid-August 1987 (Evans 1989: Fig. 3; RCB ANOVA for total aboveground plant biomass, two years [treatments] × six plots [blocks]: $F = 141.6$, df = 1,5, $P < .0001$). As in 1987, however, no significant differences between addition and removal plots were detected in the biomasses of live or dead grasses, or of forbs (Table 3). Densities of grass-feeding grasshoppers (including *P. nebrascensis* and *O. speciosa*) were similar on the plots in 1987 and 1989; consequently the number of these grasshoppers per ki-

TABLE 1. Total number of Acrididae collected in sweeping on particular dates (all six plots combined) and percent of individuals belonging to *P. nebrascensis, O. speciosa,* and other species (grouped by diet).

	Percent of individuals				
Species	26 Jun and 1 Jul 1989	26 Jul 1989	10–13 Aug 1989	19 Sep 1989	30 Jun and 1 Jul 1990
Phoetaliotes nebrascensis	64.4	72.3	69.4	75.6	36.6
Orphulella speciosa	14.1	11.3	15.1	6.7	27.1
Other grass-feeding species*	2.1	2.4	3.7	4.1	7.4
Mixed and forb-feeding species*	19.5	14.1	11.7	13.5	28.9
Total number of individuals	1663	1223	3394	193	1096

* Species were grouped by whether their diet is predominately of grasses or includes forbs to a significant degree (see Mulkern et al. 1969, Campbell et al. 1974).

logram of aboveground grass biomass (live + dead), as measured in mid-August, was 1.64 times as great in 1989 as in 1987 (Fig. 2; RCB ANOVA for two years × six plots: $F = 13.00$, df $= 1,5$, $P = .016$).

Despite the potential for more intense interspecific competition created by the greater consumer/resource ratio in 1989 vs. 1987, *O. speciosa* was not adversely affected by increased densities of *P. nebrascensis* in 1989. Densities of *O. speciosa* did not differ significantly on addition vs. removal plots throughout 1989, or in late June–early July 1990 (Fig. 1B; repeated-measures ANOVA as in Table 2: treatment $P > .50$, date $P < .005$, treatment × date $P > .75$; the overall difference between treatments was 2.49 individuals per 100 sweeps, whereas the minimal difference for significance at $P = .05$ for Fisher's LSD test would be 13.88). As an additional test of the hypothesis that increased densities of *P. nebrascensis* negatively affect densities of *O. speciosa,* I examined the seasonal decline in density of the univoltine *O. speciosa* in individual plots during 1989 (expressed as the ratio of the densities present in mid-August vs. in late June before transfer). RCB ANOVA of such ratios reveals no significant difference between treatments ($F = 0.80$, df $= 1,2$, $P = .47$; observed difference between treatment means $= .038$ vs. Fisher's LSD $= 0.180$ at $P = .05$). While the ratio of August to June density was substantially lower for *O. speciosa* in plot B+ than in plot B−, it was nearly identical in addition and removal plots in both blocks A and C (Fig. 3A).

TABLE 2. Repeated-measures randomized complete block ANOVA for *Phoetaliotes nebrascensis* sampled on six occasions ("date") in 1989–1990, for paired plots with *P. nebrascensis* nymphs either removed or added ("treatment").

Source of variation	df	MS	F	P
Blocks	2	2904.06		
Treatment	1	9983.34	12.89	<.10
Error a	2	774.69		
Date	5	12604.14	12.55	<.001
Error b	10	1004.61		
Treatment × date	5	1050.97	5.39	<.025
Error c	10	194.86		
Total	35	2788.89		

There was also no indication that the growth and development of *O. speciosa* was affected negatively by increasing the density of *P. nebrascensis.* By 26 July 1989, individuals of *O. speciosa* were in the fourth or fifth nymphal instar, or had molted into adults. De-
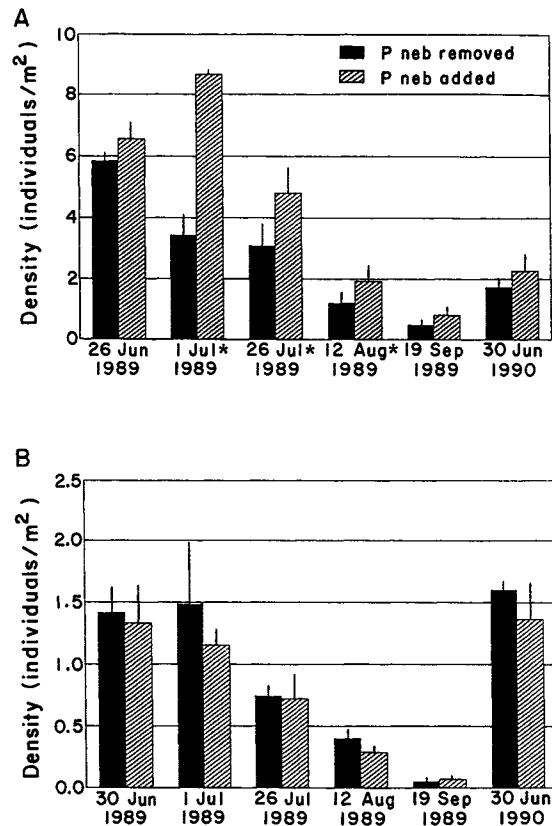
FIG. 1. Density of individuals of (A) *P. nebrascensis,* and (B) *Orphulella speciosa* on different dates in 1989 and 1990 in plots with nymphs of *Phoetaliotes nebrascensis* either removed or added (means and 1 SE). $N = 3$ for each treatment on each date (i.e., the mean shown is the mean of means for individual plots, which in turn are based on sample sizes of $N = 20–100$ sets of five sweeps; note that 12 Aug 1989 and 30 June 1990 on the X axis refer to the periods 10–13 August 1989 and 30 June–1 July 1990). Starred dates in (A) indicate significant differences ($P = .05$) between treatments (see *Results and discussion*).
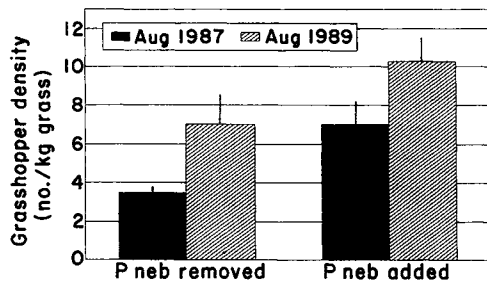
Fig. 2. The number of grass-feeding grasshoppers (including *Phoetaliotes nebrascensis* and *Orphulella speciosa*) per unit grass biomass (live + dead) for individual plots in mid-August of 1987 and 1989 (values are means and 1 se of estimates for three removal or addition plots, which were calculated from measured quantities of aboveground plant biomass per 0.1 m^2 and numbers of grasshoppers per unit area estimated from sweep samples).

velopment (as measured by mean stage of development among individuals on 26 July, derived by assigning fourth-instar nymphs a score of 4, fifth-instars 5, and adults 6), was not significantly reduced in addition vs. removal plots for either males or females (mean + 1 se for addition vs. removal plots, for females: 5.26 + 0.21 vs. 5.07 + 0.17, for males: 5.80 + 0.06 vs. 5.62 + 0.09; values for individual plots based on 5–14 females and 10–20 males; split-plot RCB ANOVA with sex nested within treatment: treatment $P > .10$, sex $P < .025$, treatment × sex $P > .75$; observed difference between treatment means = 0.181 vs. Fisher's LSD = 0.332 at $P = .05$). Sizes of *O. speciosa* adults (indicated by length of hind femur) collected on 26 July and 13 August provide another means to assess nymphal growth in the plots. Neither males nor females of *O. speciosa* differed significantly in size between addition

TABLE 3. Aboveground dry biomass of live and dead grasses and forbs in mid-August 1989 (means ± 1 se), as measured in 20 random quadrats in each plot with nymphs of *Phoetaliotes nebrascensis* removed (−) or added (+).

Plot	Aboveground dry biomass (g/0.1 m²)		
	Live grass	Dead grass	Forbs
A−	17.52 ± 0.87	7.09 ± 0.33	1.33 ± 0.43
A+	16.55 ± 1.21	6.41 ± 0.57	3.10 ± 1.02
B−	17.22 ± 1.32	6.66 ± 0.48	5.87 ± 1.25
B+	13.22 ± 0.96	4.36 ± 0.41	3.53 ∓ 1.25
C−	17.24 ± 0.87	6.31 ± 0.49	4.44 ± 1.17
C+	19.03 ± 1.16	6.54 ± 0.32	5.29 ± 1.66
P (+ vs. −)*	.59	.34	.94
LSD†	(1.06, 7.19)	(0.92, 3.18)	(0.09, 5.36)

* *P* values are for randomized complete block (RCB) ANOVA of values for addition vs. removal plots (two treatments × three blocks).

† LSD: the observed difference between means for the three addition vs. the three removal plots is shown in parentheses, followed by the minimum difference necessary for significance at $P = .05$ as determined by Fisher's LSD procedure modified for RCB ANOVA.

and removal plots (Table 4; split-plot RCB ANOVA: treatment $P > .50$, sex $P < .001$, treatment × sex $P > .25$; observed difference between treatment means = 0.150 vs. Fisher's LSD = 1.081 at $P = .05$). Continued growth and development of *O. speciosa* as adults can be assessed by examining adult masses. Adult females in particular gained considerable mass between 26 July and 13 August (Tables 4 and 5; note the significant interaction of sex with date in Table 5). However, adult mass of the two sexes did not vary significantly in addition vs. removal plots on either sampling date (nor were there significant interactions involving treatment; Table 5; overall difference between treatment means = 0.085 vs. Fisher's LSD = 0.938 at $P = .05$).

The possibility remains that reproductive success of *O. speciosa* was particularly reduced on addition plots by competition with *P. nebrascensis*. To test this hypothesis, I compared the ratio of the densities of this species in individual plots early in the summer of 1990 vs. in August 1989 (the two densities represent one year's population of young nymphs vs. the previous year's population of adults). The percentage increase in density from late summer 1989 to early summer 1990 did not differ significantly between the treatments (RCB ANOVA: $F = 0.66$, df = 1,2, $P = .50$; observed difference between treatment means = 0.74 vs. Fisher's LSD = 3.94 at $P = .05$). Again, the percentage increases were nearly identical on plots A− vs. A+ and C− vs. C+, while the percentage increase on plot B+ was considerably higher than on B− (Fig. 3B).
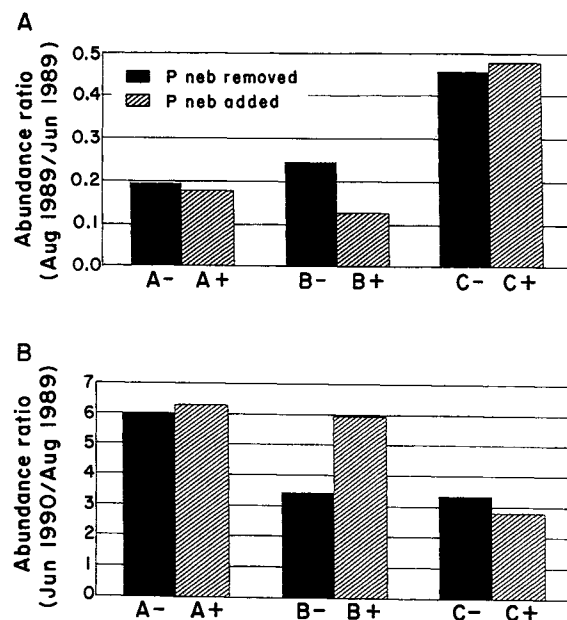

Fig. 3. Ratios of the number of individuals of *Orphulella speciosa* in (A) August vs. June 1989, and (B) June 1990 vs. August 1989. Values are provided for individual plots with nymphs of *Phoetaliotes nebrascensis* either removed or added.

TABLE 4. Hind femur length (combined samples for 26 July and 13 August 1989), and body dry mass (with hind legs removed) on 26 July and 13 August 1989, for adult males and females of *Orphulella speciosa* collected from individual plots (1 SE: one standard error of the mean; *N*: number of individuals).

	Femur length (mm)				Adult mass (mg)							
					26 July 1989				13 August 1989			
	Females		Males		Females		Males		Females		Males	
Plot	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N
A−	12.55 ± 0.09	17	10.80 ± 0.09	21	29.8 ± 3.5	6	25.7 ± 1.6	10	49.4 ± 3.5	12	31.2 ± 0.9	13
A+	12.14 ± 0.16	13	10.37 ± 0.08	33	33.2 ± 3.1	6	27.5 ± 1.4	16	45.7 ± 4.0	8	29.8 ± 1.1	19
B−	12.15 ± 0.12	14	10.66 ± 0.09	23	29.3	···	23.2 ± 1.2	11	57.0 ± 3.1	13	30.7 ± 1.3	13
B+	12.06 ± 0.12	11	10.32 ± 0.09	18	32.6 ± 3.5	4	27.5 ± 1.6	9	51.3 ± 2.2	8	30.7 ± 1.3	9
C−	11.77 ± 0.39	6	10.56 ± 0.07	27	34.5	···	25.9 ± 1.6	9	50.3 ± 3.8	8	30.7 ± 0.9	19
C+	12.09 ± 0.15	11	10.61 ± 0.15	14	28.2	···	29.4 ± 3.1	7	54.1 ± 1.9	12	28.6 ± 1.4	8

In summary, despite drought conditions and low primary productivity in 1989, I detected no negative impacts of enhanced densities of *P. nebrascensis* on densities and growth and development of *O. speciosa.* Furthermore, I detected no reductions in growth rate or in size and mass achieved by *P. nebrascensis* nymphs in addition vs. removal plots (E. W. Evans, *personal observation*), indicating little or no intraspecific competition occurred among these nymphs at the densities tested. The absence of competitive interaction between *P. nebrascensis* and *O. speciosa* even under these relatively extreme conditions supports the hypothesis that these two abundant grasshoppers of tallgrass prairie lead generally independent lives despite extensive spatial mixing and high overlap in diet. The lack of interaction between these grasshoppers is consistent with Karban's (1989) suggestion that vagile phytophagous insects are less likely than sedentary species to experience interspecific competition. It is noteworthy that even in 1989, grasshopper densities in relation to food resources at Konza Prairie were considerably lower than those that characterize more arid grasslands dur-

ing outbreak years (e.g., Pfadt et al. 1988). It remains unclear why grasshoppers in tallgrass prairie fail to achieve densities sufficiently high for interspecific competition to act as a potent force.

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TABLE 5. Repeated-measures randomized complete block ANOVA for dry masses of male and female *Orphulella speciosa* adults collected on 26 July and 13 August 1989, for paired plots with *Phoetaliotes nebrascensis* nymphs removed or added ("treatment").

Source of variation	df	MS	F	P
Blocks	2	3.932		
Treatment	1	0.034	0.12	>.75
Error a	2	0.285		
Sex	1	994.597	264.46	<.001
Treatment × sex	1	5.320	1.41	>.10
Error b	1	3.761		
Date	1	848.470	88.64	<.025
Error c	2	9.572		
Treatment × date	1	15.200	1.32	>.25
Sex × date	1	397.720	34.51	<.005
Treatment × sex × date	1	2.100	0.18	>.50
Error d	6	11.523		
Total	23	103.270		

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