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Source: Journal of Orthoptera Research, 11(2) : 215-221

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/1082-6467(2002)011[0215:GOACCA]2.0.CO;2

Journal of Orthoptera Research 2002,11(2): 215-221

Grasshopper (Orthoptera: Acrididae) community composition and temporal variation in the Pampas, Argentina

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Abstract

To evaluate temporal changes in grasshopper communities over a 5-y period (1997-2001), density and species relative abundance were estimated at 27 sites in Benito Juárez county, Southern Pampas, Argentina, established across vegetation associations with different disturbance histories. A total of 22 grasshopper species were collected, Melanoplinae being the most abundant and diverse subfamily, followed by Gomphocerinae, Acridinae, Copiocerinae and Leptysminae. Results allowed us to categorize years into nonoutbreak (1997, 1998,1999), transitional (2000) and outbreak (2001) based on the spatiotemporal characteristics of grasshopper density trends. On average, grasshopper density was over 7 times greater in 2001 than in nonoutbreak years. During nonoutbreak years, grasshopper densities showed no significant variation across disturbance categories. During the outbreak year, densities were significantly higher in pastures and halophilous steppes, with highly disturbed pastures being the most affected sites of all. Species richness changed significantly in outbreak versus nonoutbreak years: nearly twice as many species were collected during the outbreak year. Although 22 species were collected, results showed that a small number influence overall abundance from nonoutbreak to outbreak conditions. Although *Dichroplus elongatus, Covasacris albitarsis,* and *Scotussa lemniscata* were the three top-ranked species throughout the studied period, *D. elongatus* contributed most to overall shifts in grasshopper density.

Key words

Acrididae, community ecology, grasshopper outbreaks, *Dichroplus elongatus*

Introduction

Grasshoppers have been an important variable in the Pampas farm economy since agriculture and the livestock industry began in the region, approximately a century ago. Grazing and agricultural activities have intensified in recent decades, and natural pasture areas have been drastically reduced or altered (Soriano 1992, Llorens 1995). Occasionally grasshoppers cause extensive damage to grasslands and crops in the Pampas (Cigliano & Lange 1998, Cigliano *et al*. 2000).

Grasshopper communities exhibit large temporal oscillations in abundance (Gage & Mukerji 1977; Joern & Pruess 1986; Johnson & Worobec 1988; Joern & Gaines 1990; Kemp 1987, 1992a; Belovsky & Joern 1995; Cigliano *et al*. 1995). However, little effort has been directed towards an understanding of the variation in natural communities as they move from nonoutbreak to outbreak densities. Much of the literature concerned with temporal variation in grasshopper communities is based on samples of adult density data, without considering species composition information, except for a few studies conducted in the Great Plains of North America (Pfadt 1977, Joern 1982, Joern & Pruess 1986, Capinera & Thompson 1987, Kemp 1992a, Onsager 2000). Besides, as Cigliano *et al.* (1995) and Lockwood (1997) state, studies of rangeland grasshoppers frequently concentrate on changes over short periods of time at single locations. To understand the impact of grasshoppers at the ecosystem level requires that the densities and fluctuations of populations, as well as the species composition of entire assemblages, be understood (Joern 1982).

Despite the importance of grasshoppers in the Pampas, temporal surveys including density data and species composition were nonexistent for the region. In order to provide information on factors that may inhibit pest species for future management programs, we conducted a study to determine whether it was possible to identify nonoutbreak versus outbreak years in terms of grasshopper density trends as well as whether all species contributed equally to grasshopper densities each year. We were also interested in determining whether densities were equally distributed across vegetation associations with different disturbance histories.

Materials and Methods

Study area.— The study area was located in Benito Juárez county (530.772 ha), in the southeast of Buenos Aires province (lat 37°15'S - lat 38°00'S, long 60°30'W - long 59°15'W) in the Southern Pampas phytogeographic subregion (Cabrera 1968) (Fig. 1). Mean temperature is 21°C in summer and 7°C in winter. Average annual precipitation ranges from 700 mm in the west to 800 mm in the east. The dominant native vegetation in the region formerly consisted of perennial grasses (mostly species of *Stipa* and *Piptochaetium)* (Cabrera 1968). The area is flat and is principally used for crop production (winter and summer crops covering 28% of the area) and livestock production (pastures and rangelands covering 60%), with the exception of some hilly portions (10%) where pristine vegetation can still be found.

Sampling procedures.—Twenty sites were selected in 1997, expanded to 27 in 1998 and held constant through 2001. Sites were located to represent a variety of native and exotic plant associations and different degrees of disturbance. Ten sites were native communities: five of

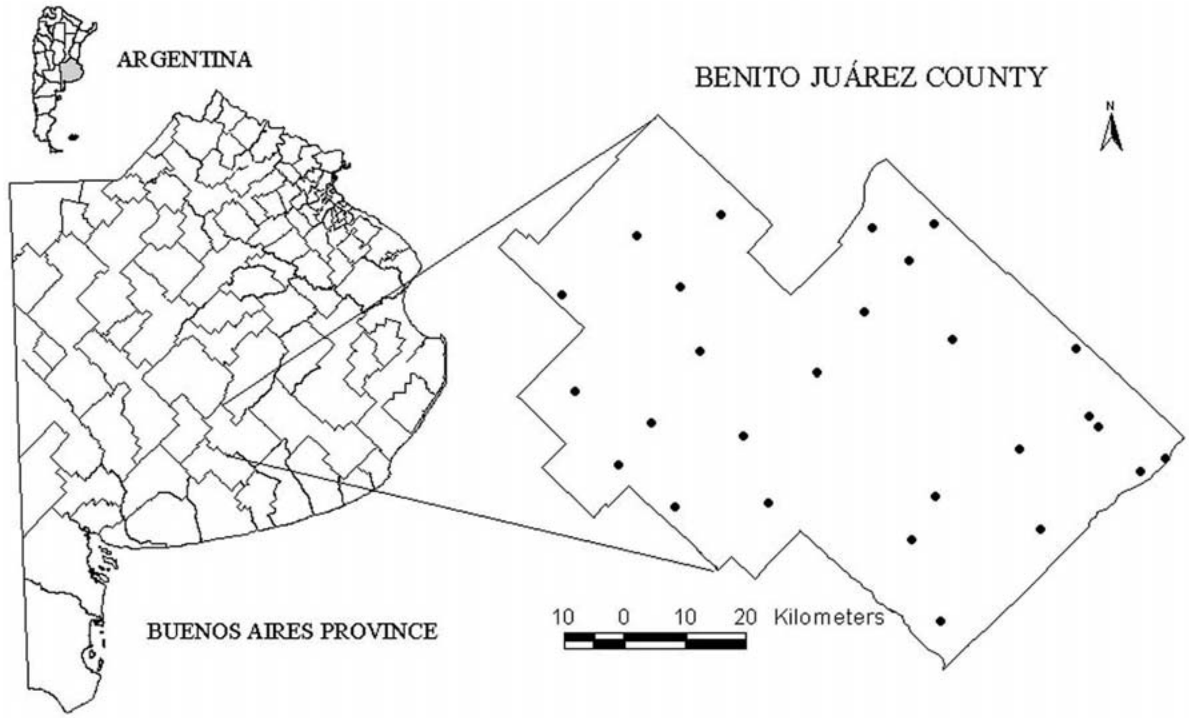

Fig. 1. Sites used for collection of grasshopper data, Benito Juárez county, Southern Pampas, Argentina, 1997-2001.

them perennial grasslands dominated by *Stipa caudata, S. neesiana, S. papposa, Piptochaetium stipoides, P. medium*, and *Paspalum quadrifarium;* five of them on halomorphic soils comprising a short grass steppe, dominated by a sparse cover of the grass *Distichlis spicata* (Soriano 1992). Six sites were pastures with seeded grasses and dicots (annual and perennial, *Avena sp, Melilotus officinalis, Medicago sativa, Lolium multiflorum, Thynopyrum ponticum*, among others). The remaining eleven sites were disturbed pastures invaded by introduced weeds (perennial and annual forbs) and grazed by livestock.

Sites were classified into five categories according to the dominant vegetation which reflected disturbance history: "native grasslands", "halophilous grasslands", "pastures", "moderately disturbed pastures" and "highly disturbed pastures". Details on site classification are given in Torrusio *et al.* (2002).

Grasshopper sampling.—Adult grasshoppers were sampled at each site three times during the summer (late December, mid-January and early February) to maximize chances of detection of species with different phenological patterns. Density was estimated by counting the number of grasshoppers flushed from a series of 30 rings ($0.1 m^2$), each placed at *ca* 5-m intervals along three transects, following the method developed by Onsager and Henry (1977). Species composition was determined from 200 net sweeps per site in each sampling period, taken between 0930 and 1700 h under sunny skies and light winds. Each sweep traversed an arc of 180° through the vegetation with a net as described by Evans (1984, 1988). Grasshoppers collected via sweep net were placed in plastic bags, put on ice, and returned to the laboratory for identification to species.

Analyses.—Density data from the three samples per site per year were averaged for analyses. In order to determine whether it was possible to distinguish between densities in years of nonoutbreak and outbreak among all sample sites, mean grasshopper densities were plotted by year and standard nonparametric statistics, Kruskall-Wallis test and Wilcoxon 2-sample test (SYSTAT 5.02, 1993), were used to test differences among years and disturbance categories in mean grasshopper density and mean grasshopper abundance.

To assess differences in species richness and to estimate if the relative abundance of grasshopper species were constant through time and among disturbance categories, sweep-net collections were used to compute yearly species richness and species relative abundance. Relative abundance of grasshopper species was calculated as the abundance of species *i*, relative to the total abundance of all species collected at each site X 100. Species richness was quantified as the total number of species present at each site. Species richness and relative abundance of grasshopper species from the three samples per site per year were averaged for analyses. Standard nonparametric statistics, Kruskal Wallis test and Wilcoxon 2-sample test (SYSTAT 5.02, 1993), were used to test for differences among years in mean species richness and in species-relative abundance.

Density of each species was calculated by multiplying the proportion of each species, as determined by sweeps, times overall grasshopper density, as determined by rings. To estimate if the density of each species was constant through time, Wilcoxon 2-sample test (SYSTAT 5.02, 1993) was used in the analysis.

Results

In total, 22 grasshopper species (12 Melanoplinae, 4 Gomphocerinae, 4 Acridinae, 1 Copiocerinae and 1 Leptysminae) were collected (Table 1). *Dichroplus elongatus* Giglio-Tos was the most widespread species, followed by *D. pratensis* Bruner.

Analysis of mean density values by year revealed that 2001 had significant higher densities than 1997, 1998 and 1999, with 2000 apparently a transitional year (Kruskal Wallis test, $P<0.0001$). On average, grasshopper density was over 7 times greater in 2001 than

Table 1. Mean relative abundance and number of sites (N) where each species was collected for 22 grasshopper species, during nonoutbreak (1997, 1998, 1999), transitional (2000) and outbreak (2001) years in Benito Juárez, Southern Pampas.

	Mean relative abundance						
	Nonoutbreak years 1997-98-99 (N = 74)		Transitional year 2000 (N = 27)		Outbreak year 2001 (N = 27)		
Subfamily/species	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	N	Sig. diff. ($\alpha = 0.05$)*
Melanoplinae							
Dichroplus pratensis Bruner	10.4	30	7.31	14	6.1	17	NS
Dichroplus elongatus Giglio-Tos	14.8	41	17.11	21	43.0	24	+
Dichroplus conspersus Bruner	5.6	4	2.72	4	1.5	3	NS
Dichroplus maculipennis (Blanch.)	1.1	1	2.56	3	2.5	3	NS
Dichroplus patruelis (Stal)					3.3	5	
Dichroplus obscurus Bruner					0.8	2	
Scotussa daguerrei Libermann	1.4	2	1.53	4	2.9	2	NS
Scotussa lemniscata (Stål)	6.6	26	14.61	11	12.5	18	+
Baeacris punctulatus Thunberg	4.5	13			0.8	2	-
Baeacris pseudopunctulatus (Ronderos)	1.7	4	3.57	9	2.7	3	NS
Leiotettix pulcher (Rehn)			1.26	2	2.6	2	
Ronderosia bergi (Stål)					0.6	1	
Gomphocerinae							
Borellia bruneri (Rehn)	10.9	28	10.65	11	5.2	10	NS
Sinipta dalmani Stål	4.7	11	2.8	7	0.6	2	-
Scyllinula variabilis (Bruner)	1.7	2	1.26	1	0.8	2	NS
Staurorhectus longicornis Giglio-Tos					0.6	1	
Acridinae							
Covasacris albitarsis Liebermann	25.9	28	25.06	12	10.7	13	-
Cocytotettix argentina (Bruner)					1.6	4	
Allotruxalis strigata (Bruner)	1.1	2	3.07	1	3.1	1	NS
Parorphula graminea Bruner	5.2	14					
Copiocerinae							
Aleuas lineatus Stål	3.6	14	3.67	15	1.7	12	-
Leptysminae							
Leptysma argentina Bruner	0.7	2	2.3	1			

*Wilcoxon 2-sample test to compare mean relative abundance during outbreak and non outbreak years: + or – indicate significant differences ($P<0.05$); NS indicates no significant differences; blank indicates no test conducted.

Table 2. Mean values of grasshopper population measures by disturbance category during nonoutbreak (1997-98-99) and outbreak (2001) years, Benito Juárez, Southern Pampas.

Grasshopper variables	Disturbance category									
	Native grasslands (n=5)		Halophilous steppes (n=5)		Pastures (n=6)		Moderately disturbed pastures (n=5)		Highly disturbed pastures (n=6)	
	Non-outbreak	Outbreak	Non-outbreak	Outbreak	Non-outbreak	Outbreak	Non-outbreak	Outbreak	Non-outbreak	Outbreak
Density (individuals/ m^2)	2.72	8.46_a	5.31	31.6_b*	4.16	34.6_b*	3.1	19.9_b*	4.1	42.3_b*
Individuals/ 200 sweeps	13.1	22.2_a	30.9	96.6_b*	16.5	165.1_b*	11.5	87.3_b*	16.6	137.2_b*

* Values significantly different between nonoutbreak and outbreak years in each disturbance category ($P < 0.05$). Categories followed by the same letter are not significantly different ($P > 0.05$). Categories followed by different letter are significantly different between them (Wilcoxon 2- sample test, $P < 0.05$)

Table 3. Grasshopper species richness during nonoutbreak, transition and outbreak years, Benito Juárez, Southern Pampas, 1997-2001.

Years	Classification	$\bar{x}$(SE) species per locality	Total species
1997_a,98_a,99_a	Nonoutbreak	2.9 (0.3)	11.6*
2000_b	Transition	4.3 (0.3)	16
2001_b	Outbreak	4.6 (0.3)	20

Years followed by the same letter are not significantly different (Wilcoxon 2-sample test, $P>0.05$) between them; years followed by different letters are (Wilcoxon 2-sample test, $P < 0.05$).
* Mean value for nonoutbreak years.

in nonoutbreak years. The trend and magnitude of the differences between the years in mean grasshopper density, allowed us to categorize years 1997, 1998 and 1999 as nonoutbreak, 2000 as a transitional year, and 2001 as an outbreak year (Fig. 2).

During nonoutbreak years grasshopper densities showed no significant variation across disturbance categories. However, during the outbreak year, grasshopper density varied significantly among sites with different ecological characteristics (Table 2). Densities showed a significant increased in all sites compared to native grasslands, and tended to be higher in highly disturbed pastures. Additionally, densities showed significant increases from nonoutbreak to outbreak over all disturbance categories, except for native grasslands (Table 2).

We were also interested to determine whether there were differences in species richness during the outbreak, transitional, and nonoutbreak years. Analyses showed that there were no differences in species richness during nonoutbreak years (Kruskal Wallis test, $P>0.05$). There were also no differences in mean species richness during years classified as transitional and outbreak (Kruskal Wallis test, $P>0.05$). However, analyses did show that species richness means were significantly different during outbreak versus nonoutbreak years (Wilcoxon 2-sample test, $P<0.05$, Table 3). On average, nearly twice as many species were collected during the transitional/outbreak years than during the nonoutbreak years (Table 3).

Ranking species based on their relative abundance, given that they occurred at more than one site, showed that the top five species during the outbreak year (in decreasing order) were *Dichroplus elongatus*, *Scotussa lemniscata*, *Covasacris albitarsis*, *D. pratensis* and *Borellia bruneri*. Comparing the same species ranks in nonoutbreak years showed that the rank order changed for all of the top-ranked species, in decreasing order, as follows: *C. albitarsis, D. elongatus, B. bruneri, D. pratensis* and *S. lemniscata* (Table 1). The five top-ranked species made up approximately 69% of the total communities during the nonoutbreak and 78% of the communities in the outbreak situation.

Because grasshopper outbreaks are mostly composed of several species, we also wanted to identify if the density of each species was constant with time. Four (*D. elongatus, S. lemniscata, C. albitarsis* and *D. pratensis*) out of the 22 collected species showed significant increase (Wilcoxon 2-sample test, $P<0.05$) in their densities from nonoutbreak to the outbreak year (Fig.3).

In order to determine if species contributed equally to overall levels of grasshopper abundance during outbreak and nonoutbreak years, we analyzed if the mean relative abundance of each grasshopper species was constant through time. Results were quite variable on this point (Table 1). Of the 22 species collected over all years, only 6 were found during the outbreak year; one (*L. argentina*) was collected during nonoutbreak and transition years, and one (*P. graminea*) was found only during nonoutbreak years. Of the remaining

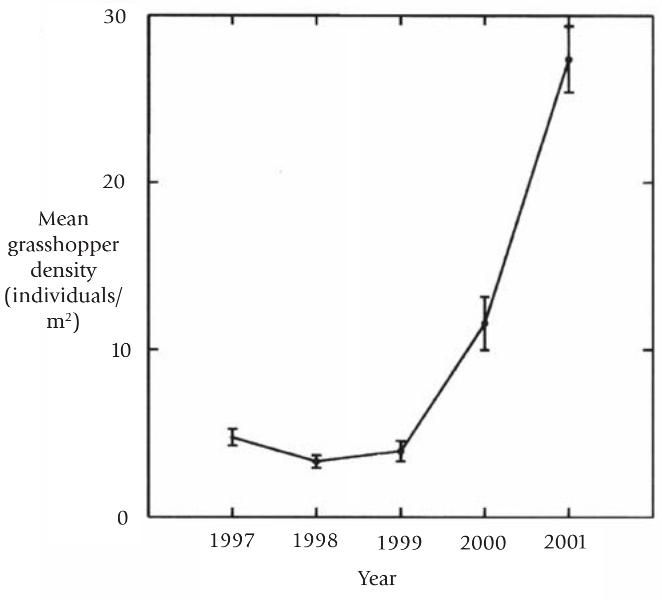

Fig. 2. Mean grasshopper density, ± 2SE, by year in Benito Juárez county, Southern Pampas, Argentina, 1997-2001.

14 species collected during both outbreak and nonoutbreak years, 8 showed decreases in the relative abundance of the community that they represented when densities increased from nonoutbreak to outbreak levels. Only 4 (*C. albitarsis, B. punctulatus, Sinipta dalmani,* and *Aleuas linneatus*) of those 8 species showed significant decreases in relative abundance when densities increased from nonoutbreak to outbreak levels. Finally, 6 species showed increases in relative abundance when densities increased between nonoutbreak and outbreak years. However, *D. elongatus* and *S. lemniscata* were the only two species that showed significant increases in relative abundance between nonoutbreak and outbreak years.

Discussion

Cigliano *et al.* (1995), in their study on spatiotemporal characteristics of rangeland grasshopper regional outbreaks in Montana, USA, suggested the need for an extension of the paradigm concerning insect outbreaks. More recently, Lockwood (1997) provided an ecological definition of outbreaks for North American rangeland grasshoppers, one suitable for both scientific and management concerns. Combining space, time, and density, Lockwood (1997) defined a rangeland grasshopper outbreak tentatively as an increase in acridid density of > 6 grasshoppers m^{-2} over the period of 1 to 2 years across one or more habitat types. The density criterion considered in the definition is based on the density at which the population exceeds the carrying capacity of the resource. At a regional level in Montana, USA, Kemp and Dennis (1993) found that grasshopper densities fluctuate according to a gamma distribution, with a mean of 6.2 grasshoppers m^{-2} and frequently range from 3.4 - 5.2 grasshoppers m^{-2}, which compares favorably with the estimates of Hewitt and Onsager (1983). Although information on grasshopper densities and the carrying capacity of grasslands in the Pampas is lacking, our results showed that on average grasshopper density was over 7 times greater in 2001 than in nonoutbreak years, with a mean density of 27.4 grasshoppers m^{-2} during the outbreak year. Densities also showed significant increase across sites with different ecological conditions (Table 2). Thus, in this study, it was possible to classify years into nonoutbreak (1997, 1998, 1999), transition or growing (2000) and outbreak (2001), based on the spatiotemporal characteristics of grasshopper density trends registered in Benito Juárez county, Southern Pampas.

As expected, densities were higher in highly disturbed pastures during the outbreak year (Table 2). Similar results were observed by Joern (1982) in a Nebraska sandhills prairie where disturbed habitats resulted in increased overall grasshopper densities. Fielding and Brusven (1993a), in a study conducted during years of gener-

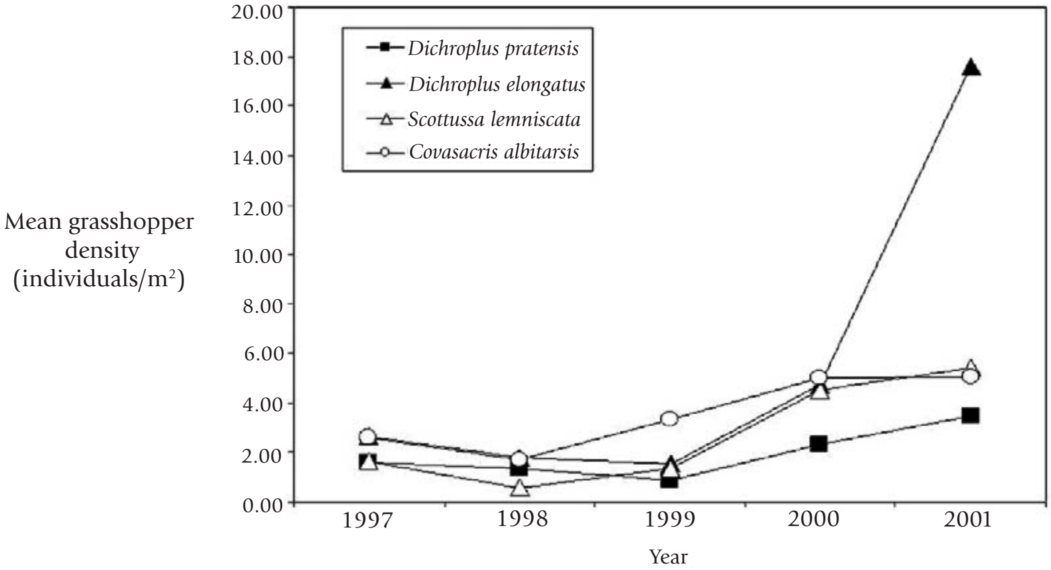

Fig. 3. Mean density of four top-ranked species by year in Benito Juárez county, Southern Pampas, Argentina, 1997 - 2001.

ally low grasshopper density on southern Idaho rangeland, found that grasshopper assemblages on sites dominated by exotic plant communities were characterized by relatively high densities. This relationship between overall density and disturbance categories holds during years of intermediate and high grasshopper densities (Fielding & Brusven 1993b).

Major differences in grasshopper assemblages were observed between our study and a long term study conducted by Cigliano *et al.* (2000) in the Western Pampas phytogeographic subregion (Cabrera 1968) under the same sampling intensities and on similar habitats. In Benito Juarez (Southern Pampas subregion), *D. elongatus, S. lemniscata, C. albitarsis, B. brunneri* and *D. pratensis* made up more than 69% of the total communities in both outbreak and nonoutbreak years (Table 1), while the five most abundant species in the 12 communities studied by Cigliano *et al.* (2000) were *D. elongatus, D. pratensis, S. longicornis, D. vittatus* and *L. pulcher.* In Benito Juárez, *S. longicornis* and *L. pulcher* were encountered only during the outbreak year and represented only a minor proportion of the communities (Table 1), while *D. vittatus* was not collected. Differences in species richness between the two studies were also observed: in Benito Juárez, mean species richness ranged from 2.9 to 4.9 species per locality, while in Western Pampas, mean species richness ranged from 4 to 12 species among the 12 studied sites (Cigliano *et al.* 2000). These contrasts suggest the possibility of a large-scale association between vegetation and grasshopper communities in the Pampas. However, there are some species like *D. elongatus* and *D. pratensis* that may be insensitive in this spatial sense.

A complex group of interrelated factors influences the dynamics and distribution of grasshopper densities (see Uvarov 1966, 1977; Dempster 1963; Capinera 1987; Joern & Gaines 1990; Belovsky & Joern 1995**;** Gangwere *et al*. 1997; and Lockwood *et al*. 2000, for reviews), many of which show a degree of spatial and temporal heterogeneity. Our results support the hypothesis that grasshopper communities in the Pampas are sensitive to resource fluctuations in time as well as in space. This is suggested by temporal shifts in mean species richness. Nearly twice as many species were documented as being present during the transition-outbreak years compared with nonoutbreak years. However this may also imply that there are some species abundances that were difficult to detect by our sampling techniques during nonoutbreak years. Additionally, variability in species sensitivity to resource fluctuations is suggested by the differences observed among the individual grasshopper species relative abundance in time. Although 22 species were collected, it appears that a small number of species influence overall abundance from nonoutbreak to outbreak conditions. Most of the species collected during nonoutbreak and outbreak years showed no significant differences in relative abundance as grasshopper densities increased from nonoutbreak to outbreak situations. Three (*C. albitarsis, D. elongatus,* and *S. lemniscata)* of the five top-ranked species encountered in this study, showed significant differences in their relative abundance in nonoutbreak versus outbreak years. *C. albitarsis*, the third-ranked species during the outbreak year was the highest ranked during nonoutbreak years and showed a significant decrease in relative abundance as general densities increased to outbreak levels. *D. elongatus* and *S. lemniscata* showed a significant increase in relative abundance from nonoutbreak to outbreak condition. Interestingly, *D. elongatus* and *S. lemniscata* were found to be associated with sown pasture plants (grasses and dicots) and introduced forbs, dominant in pastures and disturbed sites, and negatively correlated with natural communities (native vegetation and halophilous species) in a recent study on grasshopper and plant community relationships conducted in Benito Juarez (Torrusio *et al* 2002); in this study *C. albitarsis* was closely associated with native halophilous associations.

The mean density of *D. elongatus* in 2001 was 18 m^{-2} (Fig. 3) or roughly 66% of the 27 grasshoppers (all species combined) present per m^2 (Fig. 2). Certainly these results show that this species in particular is overwhelmingly responsible for the huge difference in abundance of grasshoppers in the outbreak versus nonoutbreak years. *D. elongatus* is historically regarded as one of the most harmful grasshopper species in Argentina and is widely distributed in this country, Chile, Uruguay and Southern Brazil (COPR 1982, Cigliano & Lange 1999).

Temporal changes in grasshopper communities observed in Benito Juárez are similar to those observed by Kemp (1992a) in the steppe region of Montana, USA, with more species being documented as present in outbreak situations. Any particular outbreak in the Great Plains of North America is dominated by one to five species (Onsager 1987). Kemp (1992a) stated that grasshopper communities overall are sensitive to temporal changes in resources, even though responses of individual species differed. Although results showed that there were three top-ranked species in both outbreak and nonoutbreak years, *Melanoplus sanguinipes* Fabricius was the one that contributed most to overall shifts in grasshopper intensity during the outbreak registered in the steppe region of Montana (Kemp 1992a). Furthermore, Kemp (1992b) classified *M. sanguinipes* as a patch-insensitive species in the spatial sense. Thus, considering the responses to temporal and spatial changes in resources of *M. sanguinipes* in the steppe region of Montana and of *D. elongatus* in the southern Pampas, it is hypothesized that these are ecologically equivalent species.

Results of this study suggest that there are temporal shifts related with grasshopper communities in Benito Juárez county. However, much additional work remains to be done to identify the actual processes and key mechanisms driving grasshopper outbreaks in Southern Pampas.

Acknowledgements

We thank William P. Kemp for valuable comments on earlier versions of the manuscript. This study was funded in part by a grant (PIP 4015/963/97) from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, and is the result of a cooperative program between the "Facultad de Ciencias Naturales y Museo, UNLP", the "Dirección de Aplicación de Imágenes Satelitarias, DAIS, Ministerio de Obras y Servicios Públicos de la Provincia de Buenos Aires", and the "Municipalidad de Benito Juárez, Provincia de Buenos Aires".

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