Zoological Studies **50**(6): 737-744 (2011)

Zoological Studies

Seasonal Occurrence of Life Stages of Grasshoppers (Orthoptera: Acridoidea) in the Southern Pampas, Argentina

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(Accepted June 30, 2011)

Yanina Mariottini, María L. De Wysiecki, and Carlos E. Lange (2011) Seasonal occurrence of life stages of grasshoppers (Orthoptera: Acridoidea) in the southern Pampas, Argentina. *Zoological Studies* **50**(6): 737-744. The seasonal occurrence of life stages of grasshopper species of the Southern Pampas was studied through sampling of representative habitats for 5 seasons (Nov. 2005 through Jan. 2010) in Laprida County, Buenos Aires Province. Twenty-two species were collected, 11 of which were very abundant. Ten species had 1 generation per year (univoltine), of which 9 (*Aleuas lineatus*, *Borellia bruneri*, *B. pallida*, *Covasacris pallidinota*, *Dichroplus conspersus*, *D. elongatus*, *D. maculipennis*, *D. pratensis*, and *Scotussa lemniscata*) spent the winter in the egg stage, with younger nymphs (instars I, II, and III) occurring from mid-spring (Oct.-Nov.). The period of maximum abundance of nymphs was from Nov. to mid-Dec. From Jan., most species had a higher proportion of adults, which was the dominant state by mid-autumn (Mar.-Apr.). Only 1 species (*Sinipta dalmani*) spent the winter as a nymph. *Baeacris pseudopunctulactus* was the only species with more than 1 generation per year. http://zoolstud.sinica.edu.tw/Journals/50.6/737.pdf

Key words: Acrididae, Univoltine, Multivoltine, Nymph, Adult.

Grassland ecosystems cover 30%-40% of the Earth's terrestrial surface, are key habitats for many species, and support major economic activities such as crop and livestock production (Branson et al. 2006). Temperate grasslands of the Argentine Pampas region comprise approximately 15% of the country's area (Ghersa 2005). As in other temperate grasslands of the world, grasshoppers are among the most important native herbivores throughout the Pampas. Of the 201 grasshopper species known from Argentina, about 110 species inhabit grassland systems (Carbonell et al. 2006). The economic importance of these insects has been recognized in the country since the mid- to late-nineteenth century, and outbreaks of different species are a recurring phenomenon (Lange et al. 2005). Since the early 1990s, an increase in grasshopper populations seems to be the trend in various parts of the country, and these have caused considerable damage to natural and planted pastures and a variety of crops (maize, soybean, sunflower, barley, sugarcane, sorghum, and olives) (Cigliano et al. 1995 2000 2002, Cigliano and Lange 1998 1999). However, despite the economic importance of grasshoppers in Argentina, knowledge of basic aspects of the biology and ecology of most species is still limited or fragmentary. Only 2 contributions dealing with the phenology of some species have been published (Sanchez 1980, Luiselli et al. 2002).

Therefore, the aim of this study was to determine the seasonal occurrence of life stages of the most abundant grasshopper species of the southern Pampas region through sampling for 5

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successive seasons.

MATERIALS AND METHODS

Study area

The study was conducted in Laprida County (36°2'S, 59°6'W), Buenos Aires Province, in the southern Pampas region as defined by Cabrera and Willink (1973) (Fig. 1). The mean temperature is 22°C in summer and 6°C in winter. The average annual precipitation ranges 800-900 mm. The area is a plain that reaches 210 m of elevation. Grasslands are the dominant vegetation type of the region (Batista et al. 1988, Chaneton 2005), and farming and livestock production are widespread (Perelman et al. 2001, Batista et al. 2005).

Sampling procedures

Grasshopper sampling sites were selected in Nov. 2005, and we used the same sites for the entire duration of the study (5 seasons: Nov. 2005 through Jan. 2010). Sampling sites, which reflect the history of land use (Batista et al. 1988, Fielding and Brusven 1993, Torrusio et al. 2002), represented the most common plant communities in the area. Sites were classified into 4 categories: native grasslands (dominated by native grasses such as *Festuca pampeana*, *Stipa formicarum*, *S. trichotoma*, *S. caudata*, and *Panicum bergii*), halophilous grasslands (dominated by *Distichlis spicata*), planted pastures (mostly of *Agropyron* spp.), and disturbed grasslands (grazed native grasslands with significant coverage of introduced weeds such as *Cardus pycnocephalus*, *Centaurea calcitrapa*, and *Ammi majus*). Three replicates of each category were established, giving a total of 12 sites. Sampling was conducted from mid-spring to mid-autumn, and averaged 6 samples per season. Each sample consisted of grasshoppers captured by 200 sweeps of entomological nets (40 cm in diameter, 75 cm deep, with a 180° arc of each sweep) along vegetation transects at each site as described by Evans (1988); this is an efficient method for obtaining representative samples of grasshopper communities (Larson et al. 1999). Soon after collection, grasshoppers were taken to the laboratory for identification of species, stage of development, and sex. Because several species were relatively scarce (i.e., not frequently or widely enough recorded), only those species for which more than 200 individuals were collected throughout the 5-season period were considered. Grasshoppers were categorized according to their development as younger nymphs (instars I, II, and III), older nymphs (instars IV, V, and VI) (Santoro et al. 1975), and adults. In order to detect the seasonal occurrence of life stages, data from all sites for each species were lumped together, and the percentage (mean ± SE) of individuals in each category was determined for each collecting time. Dates of collection were categorized as early (1-10), mid (11-20), and late (21-31) in the month.

RESULTS

Twenty-two grasshopper species were collected during the span of the study (Table 1). Of these, 11 were very abundant (with more than 200 individuals) and also most often recorded. There were 6 melanoplines (*Baeacris pseudopunctulatus*, *Dichroplus conspersus*, *D. elongatus*, *D. maculipennis*, *D. pratensis*, and *Scotussa lemniscata*), 3 gonfocerines (*Borellia bruneri*, *B. pallida*, and *Sinipta dalmani*), 1 acridine (*Covasacris pallidinota*), and 1 copiocerine (*Aleuas lineatus*). The remaining species were collected only sporadically and with very low numbers (Table 1).

Hatching began in early Nov. for *B. bruneri* (Fig. 2A), *B. pallida* (Fig. 2B), *C. pallidinota* (Fig. 2C), and *D. maculipennis* (Fig. 2D). As corroborated by the presence of a large percentage of younger nymphs, most of the hatching of these species occurred from Nov. to mid-Dec. In early Nov. of the last season (2009-2010), 100% of younger nymphs of the 4 species were present, and at the end of the month, the 5-yr mean percentages of nymphs were 73.2% ± 12.8% for *B. bruneri*, 83.15% ± 8.6% for *B. pallida*, 69.05% ± 15.3% for *C. pallidinota*, and 72.85% ± 15% for *D. maculipennis*. Although younger nymphs were also recorded in Dec., the percentages of individuals collected in this category were lower (20.45% ± 10% for *B. bruneri*, 22.1% ± 12.5% for *B. pallida*, 21.5% ± 10.7% for *C. pallidinota*, and 22.75% ± 8.9% for *D. maculipennis*). Older nymphs began to appear from late Nov. through Jan., and this was the most common stage of development in Dec. (56.7% ± 6.1% for *B. bruneri*, 52.8% ± 7.15% for *B. pallida*, 40.1% ± 4.2% for *C. pallidinota*, and 45.2% ± 9.6% for *D. maculipennis*). Adults were recorded from mid- to late-Dec., and in early Jan. they represented the dominant stage of development (74.05% ± 8.73% for *B. bruneri*, 64.05% ± 12.13%

for *B. pallida*, 68.53% ± 6.7% for *C. pallidinota*, and 66.36% ± 10.99% for *D. maculipennis*). At the end of Jan., almost 100% of the individuals of each of these species were adults. It should be noted that during the 1st season (2005-2006), a smaller percentage (3.92%) of *C. pallidinota* adults was observed from the end of Nov. In mid-Dec. 2008, 70.33% of *D. maculipennis* was in the adult state, a percentage much greater than that recorded in mid- (or even late) Dec. of other seasons. *Borellia bruneri* showed a similar trend, although it was less marked. In mid-Dec. 2008, the percentage of adults (44.15%) was higher than in samples taken in mid-Dec. of 2005-2006 (2.53%) and 2009-2010 (10.91%).

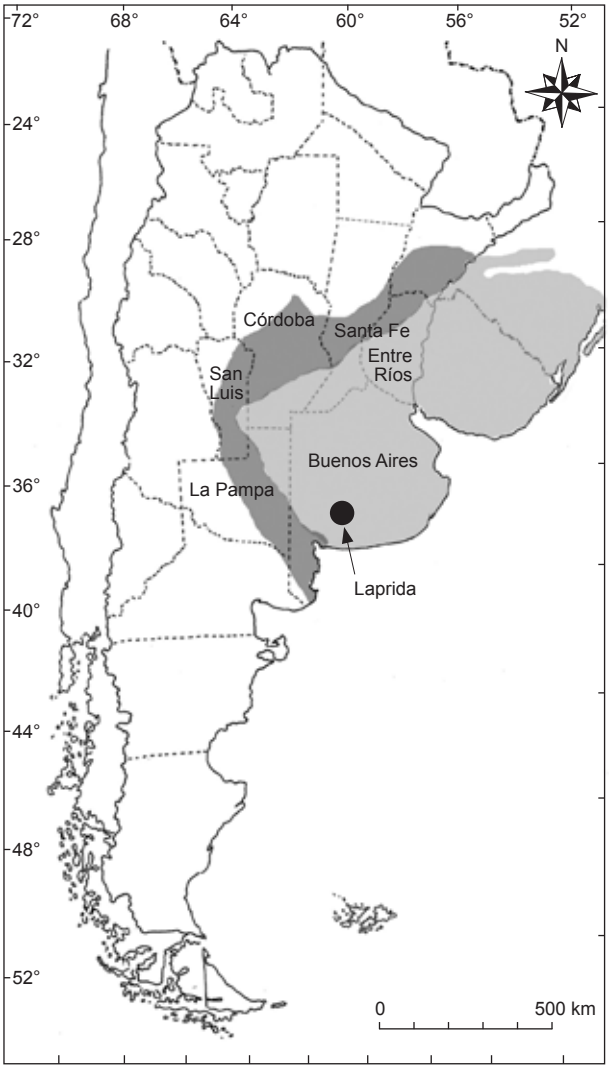

Fig. 1. Map of Argentina and neighboring countries showing the Pampas region (gray), the Espinal region (dark gray), and the study area in Laprida County (arrow).

Other species that hatched in early Nov. were *D. conspersus* and *S. lemniscata*. While *D. conspersus* (Fig. 2E) was not recorded until early Jan. and early Dec. in the 1st and 2nd seasons, respectively, younger nymphs of this species were observed from early Nov. in the last season. The mean percentage of younger nymphs collected in early and mid-Dec. was 20.97% ± 38.66%. In late Dec., it was 21.9% ± 7.11%, lower than the percentage of older nymphs (51.94% ± 17.5 and 66.74% ± 5.99%, respectively). In Jan., the most common stage of development was the adult, representing 55.9% ± 9.14% (early Jan.) and 95.5% ± 2.7 (late Jan.). Older nymphs of *S. lemniscata* (Fig. 2F) predominated in late Nov. (41.16% ± 15.4%) and mid-Dec. (65.62% ± 7.46%). Adults accounted for the 23.4% ± 8.5% by mid-Dec. and were the dominant stage in early Jan. (79.52% ± 5.51%). It should be noted that *S. lemniscata* was not recorded during the last season.

Table 1. Species of grasshoppers registered in Laprida (2005-2006 through 2009-2010), and number of individuals (*N*) collected per species

Grasshopper species	*N*
Acridinae	
Covasacris pallidinota (Bruner)	5470
Parorphula graminea (Bruner)	82
Cocytotettix argentina (Bruner)	66
Copiocerinae	
Aleuas lineatus (Stål)	773
Aleuas vitticollis (Stål)	69
Leptysminae	
Tucayaca gracilis (GiglioTos)	5
Melanopliane	
Baeacris punctulatus (Thumberg)	17
Baeacris pseudopunctulatus (Ronderos)	268
Dichroplus conspersus (Bruner)	1418
Dichroplus elongatus (GiglioTos)	3253
Dichroplus maculipennis (Blanchard)	7387
Dichroplus pratensis (Bruner)	631
Leiotettix pulcher (Rhen)	6
Scotussa lemniscata (Stål)	547
Gomphocerinae	
Borellia bruneri (Rhen)	10514
Borellia pallida (Rhen)	1866
Scyllinula variabilis (Bruner)	5
Sinipta dalmani (Stål)	373
Staurorhectus longicornis (GiglioTos)	65
Amblytropidia australis (Bruner)	3
Orphulella punctata (De Geer)	9
Romaleinae	
Diponthus argentinus (Pictet y Saussure)	2

Species hatching from late Nov. to early Jan. were *A. lineatus* (Fig. 2G), *D. elongatus* (Fig. 2H), and *D. pratensis* (Fig. 2I). Percentages of younger nymphs of these species in Dec. were 52.07% ± 13.6% for *A. lineatus*, 42.3% ± 10.1% for *D. elongatus*, and 14.52% ± 0.34% for *D. pratensis*. Older nymphs were observed from late Nov. through Feb., with the highest values recorded during Dec. and Jan. (36.5% ± 10.13% and 20.11% ± 9.85% for *A. lineatus*, 52.9% ± 8.7% and 34.2% ± 6.2% for *D. elongatus*, and 66.98% ± 14.13% and 24.7% ± 8.85% *D. pratensis*, respectively). In early Jan., adults accounted for 46.7% ± 15.14% (*A. lineatus*), 38.00% ± 9.6% (*D. elongatus*), and 50.9% ± 9.67% (*D. pratensis*).

Younger nymphs of *S. dalmani* (Fig. 2J) were observed from Feb. through Mar. and Apr. Older nymphs were observed in Mar. to May, and then Oct. to early Nov. At the end of Nov., 98.04% ± 0.41% of individuals found were adults, the stage at which individuals were collected until the first days of Jan.

Baeacris pseudopunctulatus (Fig. 2K) showed the simultaneous presence of nymphs and adults in similar percentages during different sampling times in each season. Adults were observed from Oct. to Apr., younger nymphs in Nov., Dec., and Feb. to Apr., and older nymphs from Dec. to Apr.

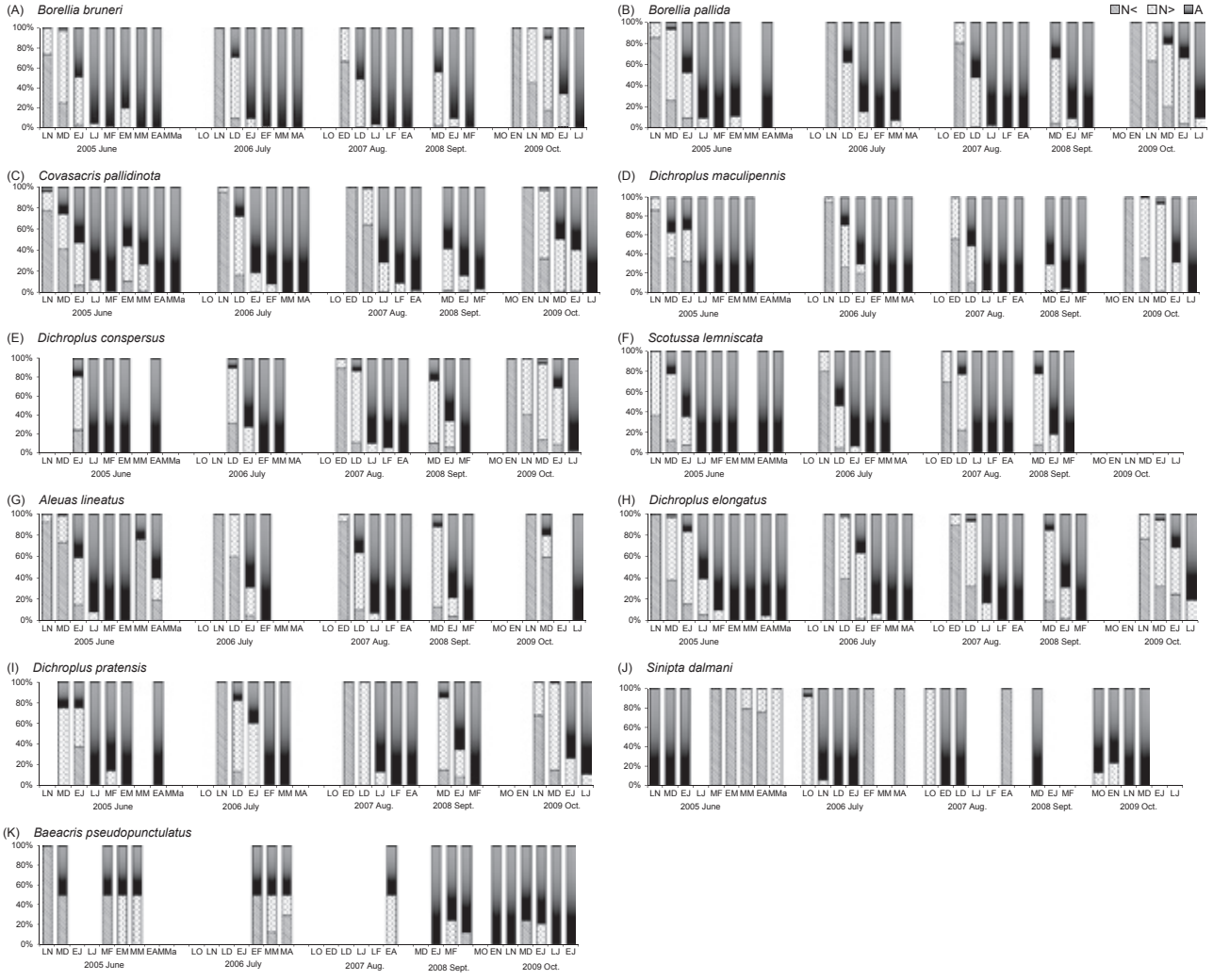

Fig. 2. Phenology of grasshopper species in the southern Pampas (Laprida County, Buenos Aires Province) (2005-2006 through 2009-2010). (A) *Borellia bruneri*; (B) *B. pallida*; (C) *Covasacris pallidinota*; (D) *Dichroplus maculipennis*; (E) *D. conspersus*; (F) *Scotussa lemniscata*; (G) *Aleuas lineatus*; (H) *D. elongatus*; (I) *D. pratensis*; (J) *Sinipta dalmani*; (K) *Baeacris pseudopunctulatus*. N<, younger nymphs; N>, older nymphs; A, adults; MO, mid-Oct.; LO, late Oct.; EN, early Nov.; LN, late Nov.; ED, early Dec.; MD, mid-Dec.; LD, late Dec.; EJ, early Jan.; LJ, late Jan.; EF, early Feb.; MF, mid-Feb.; LF, late Feb.; EM, early Mar.; MM, mid-Mar.; EA, early Apr.; MA, mid-Apr., MMa, mid-May.

DISCUSSION

Most species of grasshoppers that inhabit temperate grasslands are univoltine with long periods of embryonic diapause that usually begins a few weeks after oviposition (Uvarov 1966, Fisher et al. 1996, Squitier and Capinera 2002, Fielding 2004). Generally, the postembryonic part of the life cycle coincides with a period of vegetation growth, while the unfavorable period is spent in the egg stage (Joern and Gaines 1990). This study showed that of the 11 most abundant species of grasshopper in the southern Pampas, 9 had 1 generation per year (univoltine) and passed through a period of obligatory embryonic diapause in winter. These species were *A. lineatus*, *B. bruneri*, *B. pallida*, *C. pallidinota*, *D. conspersus*, *D. elongatus*, *D. maculipennis*, *D. prantensis*, and *S. lemniscata*. Our results showed a similar trend to the only 2 other grasshopper seasonal life history studies available in grasslands of Argentina: most species were univoltine and developed in summer. In grasslands of the northeastern Pampas, Sánchez (1980) recorded 12 species of grasshoppers during 3 sampling seasons, 11 of which had 1 generation per year. Five of the species (*A. lineatus*, *D. elongatus*, *D. pratensis*, *S. lemniscata*, and *S. dalmani*) were the same as those in our study, and all, except *S. dalmani*, had a summer development cycle. In grasslands outside of the Pampas (in west-central Santa Fe and east-central Córdoba Provinces) in the Espinal region (Cabrera and Willink 1973) (Fig. 1), Luiselli et al. (2002) monitored life cycles of the 8 most abundant species for 2 seasons; 6 of them were univoltine, while the other 2 had 2 generations per year. Two species were common to those observed in this study, *A. lineatus* and *D. elongatus*. The authors (Luiselli et al. 2002) suggested, as others have before (Campodonico 1968, Barrera and Paganini 1975), the occurrence of bivoltinism in *D. elongatus*. However, our observations indicated the presence of obligatory diapause and 1 generation annually as postulated earlier by Liebermann (1949), Turk and Barrera (1979), Sisler (1981), Lange (1986), and De Wysiecki et al. (1997). Similarly, *D. conspersus* was also mentioned as possibly being bivoltine (COPR 1982), but we found that *D. conspersus* had only 1 generation per year, proceeding through the juvenile to adult stages during the summer. Given the wide distribution of *D. conspersus* (Carbonell et al. 2006), the possible existence of intraspecific differences in voltinism cannot be ruled out. As noted for other melanopline species (Fielding 2004, Mariottini et al. 2010), depending on the region, different populations of the same species can vary in the number of generations per year.

According to the time of year when hatching occurred, *D. maculipennis*, *C. pallidinota*, *B. bruneri*, *B. pallida*, *D. conspersus*, and *S. lemniscata* could be considered relatively early-season species. On average, younger nymphs were observed from late Oct. to early Nov., older nymphs during Dec., and adults in Jan. *Aleuas lineatus*, *D. elongatus*, and *D. pratensis* could be considered relatively late-season species. Younger nymphs were observed on average from late Nov. In Dec., the percentage of younger nymphs was high, and from mid- to late-month, older nymphs prevailed. Adults were the dominant stage from mid- to late-Jan. The sequence reflects the times of grasshopper hatching adapting to different environmental conditions (Hao and Kang 2004). Soil temperature and moisture are determinant factors in egg hatching (Capinera and Sechrist 1982, Fisher et al. 1996). In addition, oviposition sites, the depth and orientation of the egg pods, embryonic development before diapause, and conditions that determine the end of diapause also influence hatching times (Kemp and Sánchez 1987). Result of the summation and interactions of these factors explain variations in the sequence of emergence of different species. During the 2008-2009 season, an unusual situation was observed in the phenology of *D. maculipennis*. By mid-Dec., up to 70% of the population was in the adult stage, which was a dramatic temporal advancement in terms of the usual seasonal development cycle of the species. Such an anomalous timing was probably related to climatic factors, particularly temperature and precipitation. In this sense, the 2008-2009 season was the driest in 47 yr, while the temperature was also well above historical records (Servicio Meteorológico Nacional 2009). To a lesser extent, *B. bruneri* showed a similar response. Drier conditions and high temperatures tend to favor the development, survival, and reproduction of many grasshopper species (Joern and Gaines 1990, Powell et al. 2007). However, as seen in our study, species, such as *D. maculipennis* and *B. bruneri*, do not react the same and may show marked differences in temporal responses to environmental factors.

The unusually dry and hot conditions of the 2008-2009 season and the concomitant almost complete lack of green vegetative coverage

might also explain the absence of *Scotussa lemniscata* from samples of the 2009-2010 season. *S. lemniscata* is typically associated with moist environments with dense and relatively tall vegetation, and contrary to most other grasshoppers, it lays its egg pods on the stems of grasses (Cigliano and Ronderos 1994). A lack of appropriate vegetation would mean the absence of needed substrate for laying egg pods. Similarly, Kemp and Cigliano (1994), in grasslands of Montana (USA), collected a significantly lower number of species in seasons following a year of extreme drought.

In contrast to the model of embryonic diapause during the winter cold, some species can overwinter as nymphs or non-reproductive adults, mature in spring, and breed in summer (Uvarov 1966). *Sinipta dalmani* is also univoltine, but unlike other species, it passes the winter in the nymph state. Younger nymphs were observed in larger quantities in autumn, with older nymphs and adults in spring to early summer. Sánchez (1980) described a similar phenology for this species in grasslands of the northeastern Pampas (Berazategui County, Buenos Aires Province). Some earlier observations suggested that *S. dalmani* spends the winter in the adult stage (Carbonell et al. 2006). Squitier and Capinera (2002) noted that in pastures of Florida (USA), contrary to expectations, few species spend the winter in the egg stage, while most species did so as adults (36%) or nymphs (27%). In our study, no species spent the winter as adults, and most species went through a period of obligatory embryonic diapause in winter.

Embryonic diapause is thus a key feature in the life cycle of these temperate-grassland insects that allows them to synchronize postembryonic development with seasonal environmental changes. Embryonic diapause may be obligatory or facultative, the latter allowing insects to develop more than 1 generation per year when conditions are favorable (Tauber et al. 1986). Adults and nymphs of *B. pseudopunctulatus* were simultaneously recorded at several samplings. This overlap in the stages of development indicates that *B. pseudopunctulatus* is not a univoltine species, which agrees with results reported by other authors (COPR 1982, Lange et al. 2005, Mariottini et al. 2008). Whether *B. pseudopunctulatus* is bivoltine or multivoltine cannot be established through data obtained in this study. Squitier and Capinera (2002) indicated that it is difficult to estimate the number of generations per year that a species may have when there is an alternation between periods of high and low abundances, as in the case of *B. pseudopunctulatus* in our study.

Knowledge of the temporal dynamics of the numerically most conspicuous grasshopper species in the southern Pampas is of value. Several species, most notably *D. maculipennis*, *S. lemniscata*, *D. pratensis*, *D. elongatus*, and *B. pseudopunctulatus*, are considered economically damaging to agriculture in Argentina (Lange et al. 2005, Carbonell et al. 2006). Knowledge of the seasonal development might assist in predicting high densities of grasshoppers and possible outbreaks and allow control efforts to be more efficient through improved timing (Luiselli et al. 2002, Przybyszewski and Capinera 1990).

Acknowledgments: This research was supported in part by Fondo para la Investigación Científica y Tecnológica (FONCYT, project PICT2006/679) and Comision de Investigaciones Cientificas (CIC) of Buenos Aires Province.

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