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Seasonal Occurrence of Different Grasshoppers Species (Orthoptera: Acridoidea) in Uruguay

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Abstract

This paper aims at knowing the seasonal occurrence of grasshoppers (Orthoptera: Acridoidea) in Uruguay. The populations of these native herbivores are generally in equilibrium, although population increases were recorded under certain conditions, causing significant economic loss. The population was monitored during five seasons on sites located in the departments of Florida and Durazno. The insects were categorized into young nymphs (I, II and III), older nymphs (IV and V), and adults. At each sampling time, data from the different sites were grouped to calculate the percentage of each category. Twenty-six species were collected, eight of which were abundant. *Borellia bruneri* (Rehn, 1906), *B. pallida* (Bruner, 1900), *Dichroplus pratensis* Bruner, 1900 and *D. elongatus* Giglio-Tos, 1894 proved to be univoltine. More than one generation of *Baeacris pseudopunctulatus* (Ronderos, 1964), *Orphulella punctata* (De Geer, 1773), *Scotussa lemniscata* (Stål, 1861) and *D. conspersus* Bruner, 1900, was recorded per year in some seasons. The first births of *B. bruneri*, *B. pallida*, *D. pratensis*, *D. conspersus*, *S. lemniscata* and *B. pseudopunctulatus* occurred in October, whereas for *D. elongatus* and *O. punctata* they happened in November. Considering the eight species, young and older nymphs predominated until early December and from late December to early January, respectively. Adulthood was predominant since the end of January. These results are the basis for establishing a monitoring plan. In order to determine the need for control and to avoid irreparable loss, samples must be intensified from early November to the beginning of December, when the young nymphs are no longer predominant.

Keywords: adult, grassland, nymph, Orthoptera: Acrididae, phenology

1. Introduction

Grasshoppers (Orthoptera: Acridoidea) are native herbivores that inhabit the grasslands of Uruguay, being a characteristic assemblage of this ecosystem (Lorier et al., 2010). Their population dynamics is highly variable; responses are non-linear, and they result from the combined effects of abiotic factors (weather) and biotic interactions (competition, predation, parasitism) (Joern, 2000). Quite often, great temporary oscillations in abundanceare recorded (Gaje & Mukerji, 1977, Joern & Pruess, 1986, Kemp & Sánchez, 1987, Johnson & Worobec, 1988, Joern & Gaines, 1990, Kemp, 1992, Cigliano et al., 1995, Cigliano et al., 2002). Populations are usually in equilibrium, but when conditions are favorable an unusual population increase can be recorded, competing with cattle for forage and causing significant economic loss (Burleson & Hewitt, 1982, Hewitt & Onsager, 1983, Cigliano et al., 1995, Fielding & Brusven, 1993, Bulacio et al., 2005, Torrusio et al., 2005). The increase in abundance, which is associated with climatic factors, soil type and use, diversity of vegetation, grazing techniques, and effectiveness of natural enemies, among other factors, has an approximate duration of a couple of years, affecting different environments (Lockwood, 1997, Lorier et al., 2010).

In Uruguay, significant problems with grasshoppers were recorded in the 1950s and recently in the spring-summer of 2008/09 (Lorier & Zerbino, 2009). The species that caused the most damage to crops and natural grassland in both events were *Borellia bruneri* (Rehn, 1906), *Borellia pallida* (Bruner, 1900), *Dichroplus pratensis* Bruner, 1900, *Dichroplus conspersus* Bruner, 1900 and *Dichroplus elongatus* Giglio-Tos, 1894. In the outbreak of 2008/2009, damage from *Scotussa lemniscata* (Stål, 1861) and *Baeacris pseudopunctulatus* (Ronderos, 1964) was also observed (Carbonell 1957, 1995; Lorier et al., 2010).

These insects complete their cycle through three stages: egg, nymph, and adult. Young nymphs (I, II, and III) have low consumption rates, while older nymphs (IV and V) and adults are very voracious. Some species have an annual generation (univoltine), while others have two or more generations per year (bivoltines or multivoltine). They reproduce and oviposit in summer or early fall. In univoltine species, once embryogenesis starts, it stops at an early stage; the eggs remain in latent form (obligatory diapause) until spring. At this moment, development restarts and the first births occur since late September or early October. In the species with more than one generation per year, the eggs develop continuously until hatching (facultative diapause), and in late summer (February-March) it is possible to record another birth moment (Turk & Barrera, 1979).

Oviposition sites, depth and orientation of the egg-pods, embryonic development before diapause (temperature dependent), and environmental conditions (temperature and soil moisture) that determine the end of diapause are all factors that have an influence on the time of hatching (Sánchez, 1980, Sisler, 1981, Kemp & Sánchez, 1987, Fisher et al., 1996). Temperature, insolation and photoperiod are involved in the nymphal development of some species of grasshoppers, regulating the speed of growth and the amount of food consumed (Amorin & Adis, 1995).

Knowing the cycle and phenology of the different grasshoppers is crucial for planning control strategies. This information helps to avoid irreparable damage (Campodonico, 1971, Sánchez & de Wysiecki, 1993, Cigliano et al., 2002). In Uruguay, the available information on aspects of the biology, life cycles, ecology and phenology of species is scarce, as a result of isolated observations, and it is sometimes controversial (Silveira Guido et al. 1958, Zolessi, 1958, COPR, 1982, Miguel, 2011, Miguel et al., 2014). This situation is similar to that of the other countries in the region. In Argentina, only three studies dealing with the phenology of some species have been published to date, despite being considered insects of economic importance (Sánchez, 1980, Luiselli et al., 2002, Mariottini et al., 2011).

Since the grasshopper outbreak recorded in 2008/09, a monitoring program of the populations in grasslands located in the southern-central region of Uruguay began. The information obtained has provided insight into the seasonal occurrence of different stages of the life cycle of the most abundant species living in this region.

2. Materials and Methods

2.1 Area Descriptions

The monitoring of grasshopper populations in natural grassland vegetation was performed during five seasons (2009-2014), in spring-summer, on eight sites located in the Departments of Florida (5) and Durazno (3), between 33º01'45" and 33º45'02" S latitude and 56º35'25" and 55º46'57" longitude W (Figure 1). In this region, the average temperatures of summer and winter are 22° and 11° C, respectively, and the annual rainfall is 1178 mm. The physiognomy of the plant cover in most of the sites where the samples were taken was characterized by a stratum of more height dominated by erect grasses and a low stratum dominated by grasses prostrated with superior vegetation cover 80%. Of the totality of the sites, two of them were dominated by the herbaceous layer of low height and another was characterized by the presence of rock cover on the soil surface.

2.2 Sampling Procedures

Samplings were conducted every 15 days since the beginning of October to late March of each season. On each sampling date, grasshoppers were collected by 200 net sweeps (ring of 42 cm in diameter and 70 cm in depth)per site, divided into three transects. The insects collected were taken to the laboratory to determine their species and stage of development (Handford, 1946, taken from Cushing 1996, Carbonell et al., 2006).

Species selection was made according to the criteria established by Mariottini et al. (2011); only those species with more than 200 specimens collected throughout the five seasons were considered. Following Mariottini et al. (2011), grasshoppers were classified according to their development as young nymphs (instars I, II, and III), older nymphs (instars IV, V, and VI), and adults. Each month’s collection dates were typified as 1 (day 1-15) and 2 (day 16-31).

2.3 Data Analysis

For the eight most abundant grasshopper species collected was calculated the average abundance (number of insect collected per sampling) for each site and each year. Data were analyzed by generalized linear model with the Poisson distribution and logarithmic function (PROC GENMOD, SAS Institute, version 9.2), as they are discrete variables and an association between means and variance was detected. The model considered years and sites as fixed effect. In all cases, results are presented as the likelihood ratio statistics of the Chi-square distribution.

In order to detect the seasonal occurrence of the different life stages, data for each species were pooled from all sites in every season and for each sampling time, calculating the percentage for each category for moments 1 and 2 of each month. From the seasons’ data, the average (mean±SE) of the different classes for the two defined moments of each month was calculated.

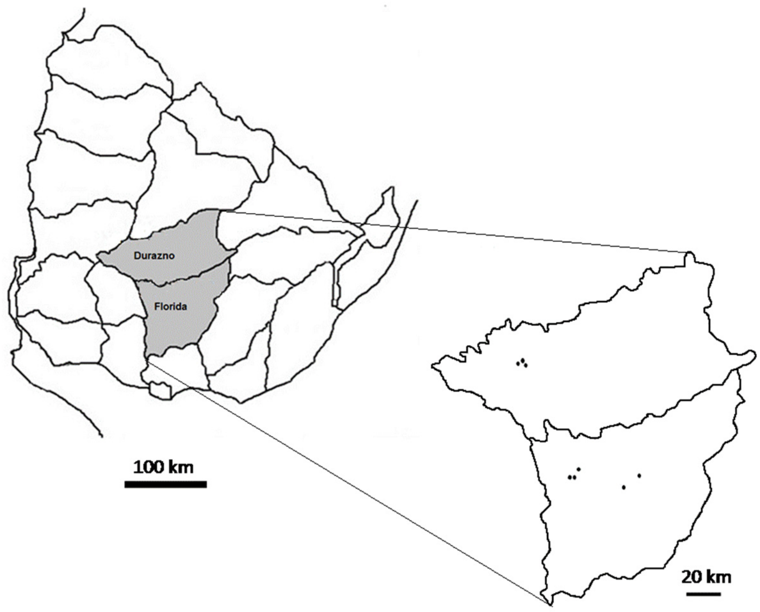

Figure 1. Location of sampling sites in the departments of Florida and Durazno (S 33°01′45″- 33°45′02″, W 56°35′25″- 55°46′57″)

3. Results

Twenty-six grasshopper species were collected during the study period (Table 1). Eight of them were abundant (with more than 200 individuals) and also the most often recorded: *D. conspersus*, *D. pratensis*, *D. elongatus*, *S. lemniscata* and *B. pseudopunctulatus*, all of them Melanoplinae, and *B. bruneri*, *B. pallida* and *Orphulella punctata* De Geer, 1773, the three of them Gomphocerinae (Table 1). The largest collection was made in 2009/10 during the outbreak. The abundance of all species decreased significantly in the remaining seasons, particularly in the case of *O. punctata*, *D. conspersus* and *D. elongatus*, of which less than 45 specimens of each species were collected throughout the four ensuing seasons (Table 2).There were some variations between seasons at the time each category was recorded (Figure 2a-h). Although the information obtained for some species was incomplete, and considering the interannual variations, the analysis of the average for the five seasons provided general patterns for the selected species (Table 3).

B. bruneri (Figure 2a), *B. pallida* (Figure 2b), and *D. pratensis* (Figure 2f) were species whose seasonal occurrence had some similarities. Young nymphs began to be recorded in October-2, and most hatchings occurred until December-1, as indicated by the high percentage of young nymphs recorded in that period (Table 3). Young nymphs of *B. pallida* and *D. pratensis* were recorded until January, and until February for *B. bruneri*, although the percentages were considerably lower (Table 3). Older nymphs of *B. bruneri* were first recorded in November-1, while those of *B. pallida*, and *D. pratensis* were collected since November-2 (Table 3, Figure 2a, b, and f). For the three species, the highest percentages of this category were recorded in December. Older nymphs of *D. pratensis* were recorded until February, while those of *B. bruneri* and *B. pallida* were recorded until March (Table 3).Adults of these three species were first recorded in December and this was the predominant development stage since January. For the three species, in the seasons following the 2009/10 outbreak there was a delay in the moment when the first specimens of the different categories were recorded (Figure 2a, b, and f).

S. leminiscata was another species that hatched early. The first young nymphs were observed in October-2 in three of the five seasons (2009/10, 2012/13, 2013/14), and the period with the highest proportion of births lasted until November (Table 3, Figure 2g). In seasons 2009/10 and 2012/13, young nymphs of this species were recorded in two moments: in spring-early summer and between mid-summer and early fall. In spring-early summer, young nymphs were only collected until December. In three seasons (2009/10, 2011/12, 2012/13), older nymphs were collected for the first time in November-2, and in the remaining two in December-1(Figure 2g). The moment in which older nymphs were predominant varied greatly between seasons (2009/10: December-2; 2010/11: February-2; 2011/12: January-1; 2012/13: November-2) (Figure 2g), which determined that this category was never predominant on average (Table 3). December-1 was the earliest moment in which the first adults of *S. lemniscata* were collected, being this the predominant development stage since December-2 (Table 3, Figure 2g).

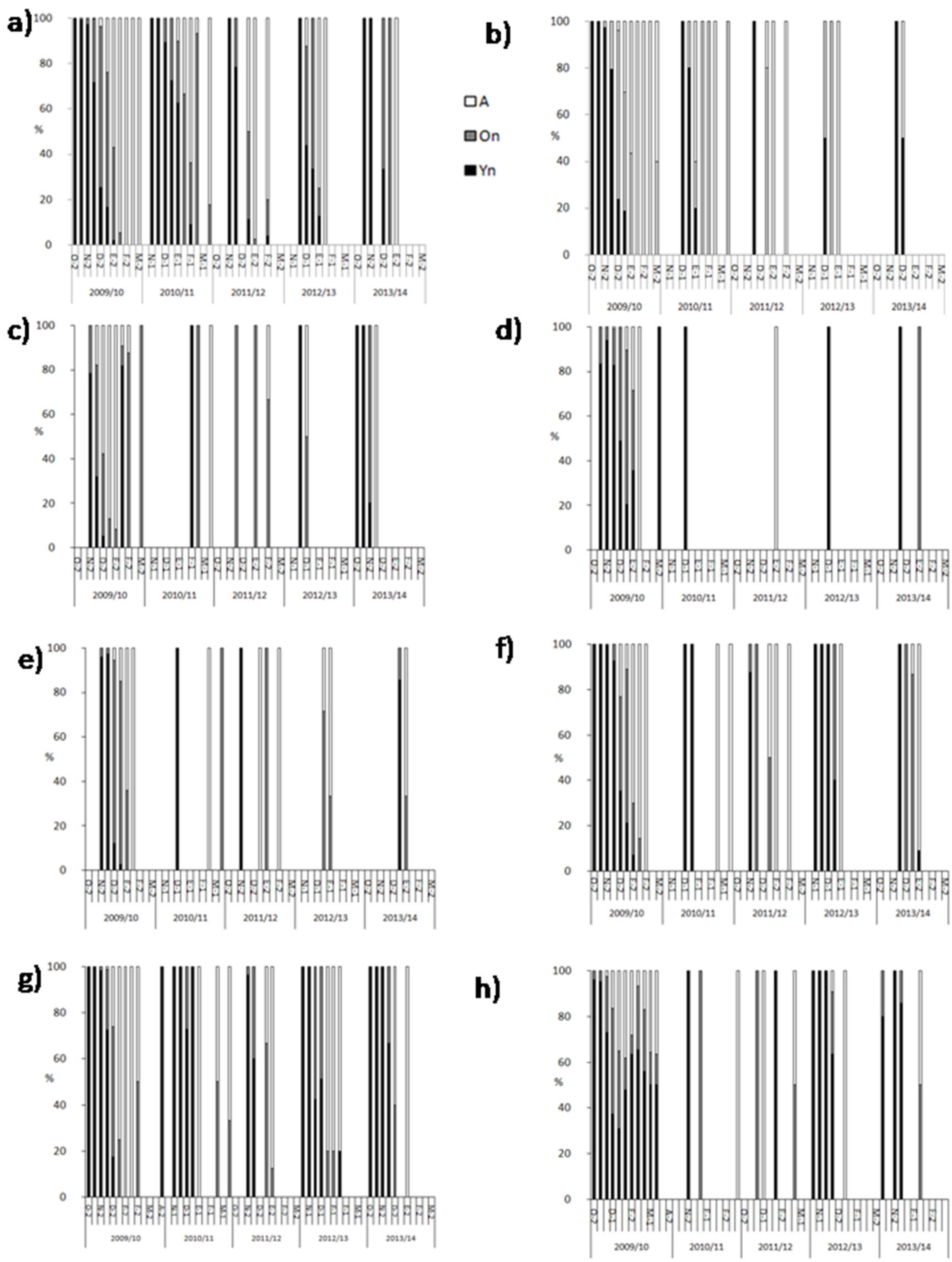

Figure 2. Phenology of grasshopper species in the south-central region (2009-2014). a) *Borellia bruneri*, b) *Borellia pallida*, c) *Orphulella punctata*, d) *Dichroplus conspersus* e) *Dichroplus elongatus*, f) *Dichroplus pratensis*, g) *Scotussa lemniscata*, h) *Baeacris pseudopunctulatus*.Yn: young nymph; On: older nymphs; A: adults.

Table 1. Species of grasshoppers collected from the south-central region of Uruguay (2009-2014), classified by subfamily and species

Family	Subfamily/Species	Total
ACRIDIDAE		
	GOMPHOCERINAE	
	Amblytropidia australis Bruner, 1904	27
	Borellia bruneri (Rhen, 1906)	6683
	Borellia pallida (Bruner, 1900)	1169
	Fenestra bohlsi Giglio-Tos, 1895	72
	Laplatacris dispar Rhen, 1939	57
	Orphulella punctata (De Geer, 1773)	334
	Sinipta dalmani (Stål, 1861)	52
	Staurorhectus longicornis Giglio-Tos, 1897	2
	MELANOPLINAE	
	Baeacris pseudopunctulatus (Ronderos, 1964)	2828
	Dichroplus conspersus Bruner,1900	1014
	Dichroplus elongatus Bruner, 1900	234
	Dichroplus pratensis Giglio-Tos, 1894	2529
	Dichroplus obscurus Bruner, 1900	10
	Leiotettix pulcher Rehn, 1913	2
	Neopedies orientalis Ronderos,1991	91
	Scotussa lemniscata (Stål, 1861)	684
	Scotussa cliens (Stål, 1861)	67
	COPIOCERINAE	
	Aleuas lineatus (Stål, 1878)	96
	ACRIDINAE	
	Allotruxalis gracilis (Giglio-Tos, 1897)	90
	Cocytottetix intermedia (Bruner,1900)	11
	Cocytottetix sp.	5
	Parorphula graminea Bruner 1900	19
ROMALEIDAE		
	Coryacris angustipennis (Bruner, 1900)	5
	Diponthus sp.	37
	Staleochlora viridicata orientalis Roberts & Carbonell, 1992	1
OMMEXECHIDAE		
	Ommexecha virens Serville, 1831	10

D. conspersus and *D. elongatus* were recorded later than the above mentioned species (Figure 2d-e). *D. conspersus* was the species that decreased more dramatically in abundance after the outbreak (Table 2). In 2009/10, the first young nymphs were collected in November-1, while at that time older nymphs were also collected, which indicates that the first births occurred earlier. Young nymphs predominated until December-1 and then their prevalence gradually decreased until January. After that, young nymphs were absent in all seasons, except in 2009/10, when there was a new recording of young nymphs in March-2 (Figure 2d). Older nymphs of *D. conspersus* were observed from November-1 to January-2 and were predominant in January-1 during 2009/10 (Figure 2d). The first adults were observed since December-1, predominating between January-2 and February-1, depending on the season (Figure 2d). The first young nymphs of *D. elongatus* occurred even later, in November-2 (Figure 2e). Same as *D. conspersus*, in 2009/10 both young and older nymphs began to be collected at the same time, which means that the first births occurred earlier. Young nymphs were the main category until December-1 in all seasons, except in 2013/14, when they represented 86% in January-1.This category was absent since January-2 (Table 3, Figure 2e). The first older nymphs were collected in November-2 and they were predominant in December-2, when adults began to be collected. Since February, 100% of the collected specimens belonged to this development stage (Table 3, Figure 2e).

For *O. punctata* and *B. pseudopunctulatus*, two moments were recorded during 2009/10 with a high percentage of young nymphs (Figure 2c, h). The first young nymphs of *O. punctata* were recorded in October-2, and they were predominant on average until November-2. This category was again predominant in February-1 (Table 3, Figure 2c). Older nymphs on spring-summer period began to be recorded in November-2, when they represented a fifth of the total collected specimens (Table 3). In the summer/autumn period, this group predominated in February-2. At several times, the mean prevalence of this category was close to 50% (Table 3). The first adults of *O. punctata* during the spring-summer period were observed in December-1; from that moment to January-2, this category represented more than 40% of the population, peaking in January-1. In March, they represented 50% of the total collected specimens (Table 3). Throughout the season, adults were only absent from October-2 to November-2. Regarding the results obtained for *B. pseudopunctulatus*, it is noteworthy that in 2009/10, from October-2 to March-2, both nymph categories coexisted (Table 3, Figure 2h). Young nymphs had two moments of predominance, one from October-2to November-2, and the other in February-1. Older nymphs were predominant in December-2 (Table 3). Adults were collected between November-2 and March-2, and two peaks were recorded, in January-1 and March-2 (Table 3). The three categories were represented in similar proportions in January-2 and February-2.

Table 2. Number of specimens of each category (young nymph, older nymph, and adult) of the eight most abundant grasshopper species collected in the 2009-2014 period in the south-central region of Uruguay

Species	Category	2009/10	2010/11	2011/12	2012/13	2013/14
Borellia	Yn[1]	3152	135	25	8	5
bruneri	On	2410	41	17	9	7
	A	754	40	69	10	1
	insects/samplig	55.4 a[2]	3.1 b	2.4 b	0.6 c	0.2 c
Borellia	Yn	573	14	1	1	2
pallida	On	394	8	4	4	1
	A	150	5	10	1	1
	insects/samplig	9.6 a	0.4 b	0.3 b	0.1 b	0.1 b
Orphulella	Yn	86	2	0	2	18
punctata	On	107	2	4	2b	4
	A	97	6	1	2	1
	insects/samplig	3.1a	0.1 b	0.1 b	0.1 b	0.4 b
Dichroplus	Yn	704	1	0	1	1
conspersus	On	287	0	0	0	1
	A	17	0	2	0	0
	insects/samplig	10.1 a	0.01 b	0.1 b	0.02 b	0.03 b
Dichroplus	Yn	70	2	1	0	6
elongatus	On	105	1	1	6	2
	A	28	1	5	4	2
	insects/samplig	1.8 a	0.1 b	0.1 b	0.2 b	0.2 b
Dichroplus	Yn	1979	7b	6	14	3
pratensis	On	406	0	5	3	14
	A	65	2	12	1	12
	insects/samplig	24.1 a	0.1 b	0.5 b	0.4 b	0.5 b
Scotussa	Yn	328	22	55	46	43
lemniscata	On	54	5	7	41	4
	A	38	5	8	20	8
	insects/samplig	3.3 a	0.4 d	1.5 bc	2.4 ab	0.8 cd
Baeacris	Yn	1529	3	1	18	19
pesudopunctulatus	On	751	1	3	3	3
	A	490	1	3	2	2
	insects/samplig	28.8 a	0.1b	0.1 b	0.5 b	0.4 b

1 Yn: young nymph (I, II, III instar), On: older nymph (IV, V instar), A: adults

2 Values followed by the same letter in each row are not significantly different ($p < 0.05$) based on the likelihood ratio

Table 3. Percentage of young nymphs, older nymphs, and adults recorded for the eight most abundant grasshopper species throughout the season (average 2009-2014)

Species	Cat.	O-2	N-1	N-2	D-1	D-2	J-1	J-2	F-1	F-2	M-1	M-2	A-1	A-2
Borellia	Yn	100[1]	99.7±0.3	99.5±0.5	70.9±9.6	41.05±10.6	20.6±10.8	0.4±0.4	4.5±4.5	1.33±1.33	0	0	0	0
bruneri	On	0	0.3±0.3	0.5±0.5	26.2±7.1	58.0±10.2	47.7±15.2	22.0±13.6	16.2±11.0	36.4±28.8	0	8.8±8.8	0	0
	A	0	0	0	3.2±3.1	0.9±0.9	31.8±13.7	77.6±13.8	79.2±15.6	62.2±28.4	100	91.2±8.8	0	0
Borellia	Yn	100	100	97.2	85.9±9.8	38.4±17.2	9.6±5.6	0	0	0	0	0	0	0
pallida	On	0	0	2.80	14.1±9.8	48.1±23.1	37.8±17.6	47.8±28.9	50.0±50.0	0	0	70.0±20.0	0	0
	A	0	0	0	0	13.5±12.2	52.6±17.9	52.2±29.0	50.0±50.0	100	100	30.0±20.0	0	0
Orphulella	Yn	100	100	66.1±23.9	7.9±7.9	5.10	0	0	90.9±9.1	0	0	0	0	0
punctata	On	0	0	33.9±23.9	50.1±20.4	37.2	13.0	54.2±45.8	4.5±4.5	84.7±9.7	0	50.0±50.0	0	0
	A	0	0	0	41.9±21.9	57.7	87.0	45.8±45.8	4.5±4.5	15.3±9.7	0	50.0±50.0	0	0
Dichroplus	Yn	0	83.30	93.9	95.7±5.8	48.9	20.4	11.9±11.9	0	0	0	100	0	0
conpersus	On	0	16.70	6.1	4.1±4.1	50.5	69.4	45.2±29.3	0	0	0	0	0	0
	A	0	0	0	0.2±0.2	0.6	10.2	42.9±29.7	100	0	0	0	0	0
Dichroplus	Yn	0	0	97.9±2.1	98.7±1.3	6.1±6.1	22.0±21.2	0	0	0	0	0	0	0
elongatus	On	0	0	2.1±2.1	1.3±1.3	76.9±5.5	32.5±18.0	56.4±21.8	0	0	0	100	0	0
	A	0	0	0	0	17.0±11.6	45.4±23.1	43.6±21.8	100	100±0	0	0	0	0
Dichroplus	Yn	100	100±0	95.7±27.8	78.5±19.7	46.2±20.6	5.3±5.3	5.4±2.7	0	0	0	0	0	0
pratensis	On	0	0	4.3±3.6	21.4±19.7	53.5±20.6	51.1±18.6	7.6±7.6	14.3±0	0	0	0	0	0
	A	0	0	0	0	7.4±7.4	43.6±20.8	87.0±8.8	85.7±0	100±0	0	100	0	0
Scotussa	Yn	100±0	100±0	87.41±11.3	64.6±4.1	29.3±23.9	0	5.0±5.0	0	0	0	0	0	100
lemniscata	On	0	0	12.6±11.3	35.1±4.2	29.1±12.3	27.9±14.0	3.1±3.1	0	50.0±0	0	33.3	0	0
	A	0	0	0	0.2±0.2	41.5±17.8	72.1±14.0	91.9±4.9	100	50.0±0	0	66.7	0	0
Baeacris	Yn	92.0±6.1	97.7±2.3	74.6±19.4	46.7±18.4	15.4±15.4	49.3±28.9	31.8±31.8	65.5	28.0±28.0	0	25.0±25.0	0	0
pseudopunctulatus	On	7.9±6.1	2.3±2.3	24.9±19.4	22.0±9.9	67.1±32.9	4.7±4.7	29.1±20.9	27.7	38.6±11.4	0	6.8±6.8	0	0
	A	0	0	0.5±0.5	31.4±23.1	17.5±17.5	46.0±29.1	39.0±11.0	6.7	33.5±16.5	0	68.2±31.8	0	0

[1]Mean±SE, values without SE, are the result of a single season; Yn: young nymph (I,II,III instar), On: older nymph (IV, V instar), A: adults.

4. Discussion

Insect phenology indirectly reflects the population responses to local environmental conditions. Grasshoppers must adjust their life cycles in order to survive and reproduce. Embryonic diapause, induced by the interaction between photoperiod and temperature, is the mechanism that allows them to face the adverse seasonal periods and make an efficient use of resources when environmental conditions are favorable (Joern & Gaines 1990). The embryonic diapause may be obligatory or facultative; the latter allows the insects to have more than one generation per year when conditions are favorable (Tauber et al., 1986). Most of the grasshopper species that inhabit temperate grasslands are univoltine and have extended periods of obligatory embryonic diapause (Joern & Gaines, 1990, Fisher et al., 1996, Fielding, 2004, Mariottini et al., 2011).

Of the eight species selected in this study as the most abundant, seven (*B. bruneri*, *B. pallida*, *B. pseudopunctulatus*, *D. conspersus*, *D. elongatus*, *D.pratensis*, and *S. lemniscata*) were included among the 11 species considered in the study performed in Laprida, Province of Buenos Aires (Argentina) (Mariottini et al., 2011). The eighth species was *O. punctata*, which was sparsely collected in the above mentioned study.

Half of the species considered in this study proved to have one generation per year (*B. bruneri*, *B. pallida*, *D. pratensis* and *D. elongatus*), while *B. pseudopuntulatus* and *O. punctata* might have more than one generation per year in some seasons, which is consistent with some previous studies (Silveira Guido et al., 1958, Barrera & Turk, 1977, Turk & Barrera, 1979, COPR, 1982, Cigliano & Otte, 2003, Lange et al., 2005, Mariottini, 2009, Mariottini et al., 2008, 2011; Miguel et al., 2014). Campodónico (1969), Barrera and Paganini (1975), Luiselli et al. (2002), and Sisler (1981) found that *D. elongatus* is a bivoltine species with facultative diapause, although the observations made by Liebermann (1949), Turk and Barrera (1979), Sánchez (1980), Lange (1986), de Wysiecki et al. (1997) and Bardi and Lange (2011) suggest that this species has obligatory diapause.

The results obtained for *D. conspersus* and *S. lemniscata* indicate that in some seasons these species recorded a second generation, contrary to what some authors have established. Mariotttini et al. (2011) stated that these two species are univoltine for the region of Laprida-Province of Buenos Aires. These variations within the same species in different latitudes may be the result of their adaptation to local climates. Several species with obligatory diapause in temperate regions lack diapause in tropical regions (Mariottini et al., 2010). In Northern provinces of Argentina such as Misiones, with subtropical climate and undefined seasonality, grasshopper cycles tend to be short and lacking an obligatory diapause, so the development of a second generation is possible. Some studies mention that *D. conspersus* is a bivoltine species. Campodónico (1969) and COPR (1982) suggest that eggs laid in early summer hatch immediately and give rise to a second generation, while those which are oviposited at the beginning of fall hibernate. Silveira Guido et al. (1958) established that although nymphs may be observed until March or April, their abundance decreases in January. Mariottini et al. (2011) consider that there may be intraspecific differences in the voltinism of *D. conspersus* as a result of its wide distribution (Carbonell et al., 2006). Concerning *S. lemniscata*, Turk (2002), in Tucumán (Argentina), found that eggs could have obligatory diapause or lack it COPR (1982), Sánchez (1983), Cigliano and Ronderos (1994), and Lange et al. (2005) considered that this species has obligatory diapause. This species also has wide geographical distribution, which explains the possible intraspecific differences in voltinism (univoltine, bivoltine or multivoltine) depending on the region considered, as it has been observed in other species of Melanoplinae (Fielding, 2004, Mariottini, 2009).

The life cycles of grasshoppers have significant variations; populations of the same species inhabiting different environments may have different number of generations, and even different numbers of instars (Joern & Gaines, 1990). The sequence of the species' hatching moment shows the adaptation of grasshoppers to various environmental conditions (Hao & Kang, 2004). Temperature and soil moisture are factors that determine hatching (Sánchez, 1980, Capinera & Sechrist, 1982, Fisher et al., 1996). Sánchez (1980) established that the interaction of these factors explain the changes in the duration of the cycle of the same species at different latitudes, because they have effects on the speed of embryonic development and mortality in spring, after the winter diapause. According to the results obtained in this work, and in contrast to all the other seasons, during the outbreak in most species births occurred before. Silveira Guido et al. (1958) determined that grasshopper cycles are more advanced in the north of Uruguay. These authors observed that when the temperature was higher the births of *B. bruneri* began in early spring. Delayed or early hatching may have significant effects on the ability to track resources (Kemp & Onsager, 1986; Kemp & Denis, 1989). When adequate food is available, phenology is driven by temperature (Joern & Gaines, 1990).

In each and every season, the first specimens of grasshopper were collected since the second half of October. *B. bruneri*, *B. pallida*, *D. pratensis*, *S. lemniscata* and *B. pseudopunctulatus* are the first species to emerge in spring, in October. In Laprida, Province of Buenos Aires (Argentina), these same species, among others, also hatch earlier, with the exception of *D. pratensis*, whose births occur later, in late November(Mariottini et al., 2011). These differences are probably due to the geographic location. Silveira Guido et al. (1958) reported that in the south of Uruguay the nymphs of *D. pratensis* were observed around mid-November. *D. conspersus* could also be included in this group, considering that at the beginning of November 2009/10 older nymphs were collected, indicating that the first births occurred in October. Pickford (1960) found that early emerging grasshoppers laid a large number of eggs because the longevity of adults and the oviposition rates are higher. All these species are considered pests of economic importance. While *B. bruneri*, *B. pallida*, *D. pratensis and D. conspersus* are considered as pest regularly of substancial importance*;* *S. lemniscata* is regarded as frecuent pest of minor importance and *B. pseudopunctulatus* is deemed as occasional pest of local importance (Carbonell et al., 2006, COPR,1982). In average, young nymphs of these species are the predominant category until the first half of December, with the exception of *B. pseudopunctulatus*, which only predominate until late November. *Orphulella punctata* and *D. elongatus* can be considered relatively late-season species; births occur in November, usually in the second half. Young nymphs of this species are predominant until the end of November and the first half of December, respectively. In Laprida, Province of Buenos Aires (Argentina), *D. elongatus* is also considered a late-season species (Mariottini et al., 2011). *Orphulella punctata* is a species of lesser significance, whereas *D. elongatus* is considered a pest of economic importance (COPR, 1982). A difference between *B. pseudopunctulatus* and *O. punctata*, the two species which record more than one generation, is that young nymphs of the former are observed all season, suggesting an overlapping of generations. In Laprida, Mariottini et al. (2011) determined that young nymphs of *B. pseudopunctulatus* are seen in two moments: November to December, and February to April.

Older nymphs of the species that emerge early in the season, start to be observed in November, first *B. bruneri* and *D. conspersus*, followed by *B. pallida*, *D. pratensis* and *S lemniscata*, with the exception of *B. pseudopunctulatus*, which appear earlier, in late October. For *B. bruneri*, *B. pallida*, *D. conspersus* and *D. pratensis*, older nymphs become predominant in the second half of December. Mariottini et al. (2011) reported that older nymphs of *B. bruneri*, *B. pallida*, *D. conspersus* and *S. lemniscata* are observed in December. Some years, older nymphs of *S. lemniscata* may prevail in November, while in others this category can prevail in the second half of December. In the spring-summer generation, older nymphs of *B. pseudopunctulatus* predominate in the second half of December.

Comparing results obtained for *B. bruneri*, *B. pallida*, and *D. pratensis* during the outbreak (2009/10), it may be inferred that the oviposition period of *B. bruneri* is longer than for *B. pallida* and *D. pratensis*, and that the duration of the nymph stage of *B. bruneri* is shorter than for the other two species.

The first older nymphs of the late-season species *D. elongatus* and *O. punctata* are recorded in the second half of November. This category prevails between December and January. These results are similar to those obtained by Mariottini et al. (2011). According to the moment when the first adults of *D. elongatus* were recorded during the outbreak, the nymph stage of this species is shorter than that of *B. bruneri*, *B. pallida* and *D. pratensis*.

B. pseudopunctulatus adults are the first to be observed (in late November), while adults of *B. pallida*, *D. pratensis* and *D. elongatus* are the last (in late December). In the remaining species, this stage of development begins to be recorded in the first half of December. Adults of *B. pseudopunctulatus*, can be observed throughout the whole season, until the end of March. In this period there are two moments in which they predominate: the first half of January and the second half of March. These results suggest that the eggs laid in early summer give rise to a new generation, part of which reaches adulthood in March, so this species probably elapses winter as adults or older nymphs. COPR (1982) mentions that adults of this species are recorded from December to April; while Mariottini et al.(2011) establish that this stage is observed from October to April. Adults of *O. punctata* and *S. lemniscata* predominate early in the season, in the first half of January, which indicates that the nymph stage is short. Conversely, adults of *D. conspersus* and *D. elongatus* predominate later, at the beginning of February.

At the moment of making management decisions to avoid irreparable damage, it is necessary to know, in addition to the density, the community composition and the development stage of grasshoppers (Campodónico, 1971, Sánchez & de Wysiecki, 1993, Berry et al., 1996). This last point is essential to avoid loss, since control treatments must be carried out when the largest proportion of the population is in the third nymph instar and not before that moment (Hewitt & Onsager, 1983). Young nymph categories (instars I, II and III) destroy little amount of forage and this generally occurs early in the season, causing negligible damage. Nymphs begin to consume larger quantities of forage during the third instar, and by the fourth instar they begin to cause irreparable loss (Hewitt, 1977). Therefore, when young nymphs cease to predominate it is very important to determine whether chemical control is justified, making sure that most of the eggs have already hatched and avoiding the implementation of advanced control measures if mortality events con still be expected among the population. However, control treatments cannot be delayed because older nymphs are less susceptible to the active ingredients (Hewitt & Onsager, 1983, Lorier et al., 2010, Miguel, 2011). It is also important to consider that the damage caused by the species is different in magnitude. Considering the economic importance of the species (COPR, 1982) and/or their abundance during the outbreak (Zerbino et al. in press), those with the greatest potential to cause losses are *B. bruneri*, *B. pallida*, *D. pratensis*, *D. conpersus* and *B. pseudopunctulatus.*

5. Conclusions

The results obtained in this study form the basis for establishing a monitoring plan. In order to determine whether the populations of grasshoppers are significant and the need for planning control measures, it is important to intensify sampling from early November to early December, which is the moment when young nymph categories prevail. Late December is not the proper time to take control decisions, given that older nymphs are, by that time, the most common category in most species and the damage has already been done.

It would be interesting for future studies to research the effects of the climate changes expected for this latitude (DINAMA, 2005) on the populations of different grasshopper species. In addition to the direct consequences this phenomenon will undoubtedly have on the life-cycle of grasshoppers, it will also have indirect effects on them through the influence of climate on host plants, the interaction of grasshoppers with other insects and natural control agents (Porter et al., 1991,Vázquez, 2011). All this will alter the population dynamics, causing changes in the size and seasonality of populations, and consequently on the pest status of these insects (COPR, 1982, Estay et al., 2009, 2012). It is possible that the cycles of the species with facultative diapause will be shorter, increasing the number of generations per year and consequently affecting the economic risk associated with them.

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