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Authors: Dias-Guerra, Wanderlei, Carla De Oliveira, Patrícia, and Barrientos-Lozano, Ludivina

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Life history and population dynamics of *Baeacris punctulatus* (Thunberg, 1824) (Orthoptera: Acrididae) in the State of Mato Grosso, Brazil

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WANDERLEI DIAS-GUERRA, PATRÍCIA CARLA DE OLIVEIRA AND LUDIVINA BARRIENTOS-LOZANO

(WD-G) Programa de Pós-graduação em Biologia Animal, Universidade de Brasília UnB, DF, Brazil. Email: wanderlei.dias@agricultura.gov.br
 (PC-O) Universidade Federal de Mato Grosso, Instituto de Biociências, Departamento de Botânica e Ecologia, UFMT, Cuiabá, MT, Brazil.
 Email: patiranjak@yahoo.com.br

(LB-L) Instituto Tecnológico de Cd. Victoria, Blvd. Emilio Portes Gil No. 1301. Cd. Victoria, Tam. México. 87010. E-mail: ludivinab@yahoo.com

Abstract

We reared *Baeacris punctulatus* (Orthoptera: Acrididae) in cages under seminatural conditions in Cuiabá, Mato Grosso, Brazil. Five nymphal instars were recorded. One generation required ~82 d (24 d egg stage + 43 d nymphal development + 15 d preoviposition period). Colony females laid ~4.4 egg pods during their ~30-d adult life. Pods contained ~13 eggs, and most eggs hatched, giving ~56 offspring per female. Survival during the nymphal stage was 38.9%, with highest mortality in 4th-5th instars. Average and maximum lifespans from hatch to adult death were 73 and 80 d, respectively. Field sampling in Campo Novo do Parecis and Parecis Plateau regions of Brazil showed that adults and older nymphs were present in all months of the year, but that oviposition and young nymphs were scarce during the dry-cool months of May to mid-August. Overall, our study suggests that in the State of Mato Grosso, there are 3.9 to 5.1 generations per year. The various instars could be differentiated by the number of antennal segments, body size, and shape and size of wing pads. Annual and regional variation in temperature and moisture may influence the life history and population dynamics of *B. punctulatus*.

Key words

Melanoplinae, agricultural pest, biology, Brazil, egg, egg pod, wing pad, antennae

Introduction

The grasshopper subfamily Melanoplinae constitutes the third largest within the Acrididae, with more than 900 species worldwide (Barrientos-Lozano *et al.* 2009); according to Amédégnato *et al.* (2003) it is the largest subfamily of Acrididae in the Americas with ~235 species for South America. Among subfamilies of South American acridofauna, Melanoplinae show perhaps the greatest diversity and geographic distribution, and includes several agricultural pests (Bentos-Pereira 1989, Ronderos & Cigliano 1991, Sánchez *et al.* 2001).

Baeacris punctulatus (Thunberg) (subfamily Melanoplinae) (Fig. 1) is an important polyphagous agricultural pest in Brazil, attacking soybean (*Glycine max*), beans (*Phaseolus vulgaris*) and various pasture crops (COPR 1982, Duranton *et al.* 1987). It has the broadest range distribution of all *Baeacris spp.*, and is found in virtually all agricultural regions of Brazil (Carbonell & Ronderos 1973, Turk & Barrera 1979, COPR 1982, Duranton *et al.* 1987). In the State of Mato Grosso, *B. punctulatus* causes major damage to soybean in the summer, especially in the Parecis Plateau region, where extensive areas are dedicated to agriculture. During winter this species is associated with several crops, including Crotalaria (*Crotalaria juncea*) and millet (*Pennisetum glaucum*), planted at this time of the year as a land cover.

Michel and Terán (2006) studied this species in captivity and the

field, and examined the anatomy and histology of the reproductive organs to document the life cycle and reproductive biology. They confirmed that *B. punctulatus* has a "facultative embryonic diapause" (as pointed out by Turk & Barrera 1979), whereby low temperature reduces egg viability, slows embryonic development, and lengthens the egg stage. They reported five nymphal stages, total nymphal development ranging from 27 to 31 d (at 30°C), and three generations per year. In contrast, work by Duranton *et al.* (1987) suggests that this species has three generations per year without embryonic dormancy. Unfortunately no studies have examined its abundance and population dynamics throughout the year in the field.

The present work aimed to study the life history and population dynamics of *B. punctulatus* in the State of Mato Grosso, Brazil, by combining rearing studies with field sampling. Because it is difficult to differentiate among the five nymphal instars, we also characterized nymphal morphology.

Materials and methods

We reared *B. punctulatus* (Fig. 1) at Cuiabá, Mato Grosso, Brazil (lat 15° 35' S, long 56° 06' W) from April to September, 2009. Eggs and nymphs were obtained from five mating pairs collected on a millet field (*Pennisetum glaucum*) at Campo Novo do Parecis municipality, Mato Grosso on April 7-8, 2009 (Fig. 2). Adults (a) and first generation nymphs (n) were reared using locust mass-production methodology (Hunter-Jones 1961, Henry 1985, Hoste *et al.* 2002), but under seminatural conditions. On April 9, the field-collected adults were placed in transparent, cylindrical, plastic cages, 17 cm high × 16 cm diameter, with a screen lid. These rearing cages were kept outdoors, but under a roof. One hour in the morning and one hour in the afternoon, cages were moved out of the shade, to expose the insects to direct sunlight. Photoperiod, which consisted of both natural and electric lights, averaged 14:10 h. A 5-cm deep layer of soil placed on each cage floor allowed females to lay eggs (Fig. 3). Soil was collected at the same place where adults were captured, and consisted of 86% sand, 4% silt and 10% clay. This soil is classified as "Neossolo Quartzarênico" (EMBRAPA 2009). Soil was kept slightly moist, and never allowed to dry. No antibiotics or chemicals to inhibit diseases were used. Cages were cleaned twice a week, removing feces. Data on mating, laying and egg hatching were recorded for each pair.

Resulting nymphs were reared in transparent, cylindrical, plastic cages, 15 cm high × 13.5 cm diameter, with screen lids, available from local packing stores. Adults and nymphs were fed potted seedlings of soybean and millet, placed into the cages daily. Cages were examined every day at 8:00 and 18:00 h and cleaned with alcohol, and exuviae removed. When Generation 1 (G1) nymphs reached adulthood, 20 mating pairs were transferred into the larger



Fig. 1. Adult male *B. punctulatus* on soybean from Mato Grosso State, Brazil. For color version, see Plate IX.

and adults collected in 2008 at the same locality were used. Field samples consisted of 200 sweeps with a standard insect sweep net (45-cm diameter opening). This is equivalent to sampling $\sim 100 \text{ m}^2$. Data were gathered monthly on days 10, 20 and 30, and analyzed as number of individual grasshoppers captured/200 sweeps at each site/number of sites visited that day. Abundance (n) was transformed using $\log_{10}(n+1)$ (Magurran 2004).

Morphological traits of different stages were studied in order to find useful characteristics to differentiate nymphs in the field. Traits examined include: number of antennal segments, body size from vertex to apex of abdomen, and shape and size of wing pads (Lecoq & Pierozzi 1994). All measurements were made on live insects placed in a thin

containers for a second generation of egg laying. A Dostmann TFA/Werthiem thermo-hygrometer recorded temperature and relative humidity both at the rearing site and in the field; additional weather data were provided by INMET (2009). We measured the timing of each instar, the adult molt, mating, oviposition, hatching, and adult lifespan.

We also made periodic trips to Campo Novo do Parecis and the Parecis Plateau region (Fig. 2) to sample nymphs (N) and adults (A) in the field, and to compare their development with that from our culture. Additional data on abundance of *B. punctulatus* nymphs

transparent plastic bag and laid against a ruler (Fig. 4). The plastic bag reduced the insect's movement and allowed direct linear measurements. A binocular lens Dimex MZS-250 was used for counting the antennal segments.

Results

Daily minimum and maximum air temperatures averaged over the 6 mo at the *B. punctulatus* rearing site at Cuiabá City were 19.8 ± 1.6 and $32.4 \pm 1.8^\circ\text{C}$, respectively (Fig. 5); average minimum relative humidity was $39.9\% \pm 15.4$ and maximum $78.4\% \pm 9.3$. In the field in the Parecis Plateau region, average minimum temperature during 2007-2009 was $23.4 \pm 1.7^\circ\text{C}$, maximum $31.6 \pm 2.0^\circ\text{C}$ (Fig. 5); average minimum relative humidity was $44.3\% \pm 10.3$ with $68.8\% \pm 9.2$ as maximum. Precipitation at Campo Novo do Parecis municipality varied throughout the year, with a strong dry season from May to mid-August (Fig. 6).

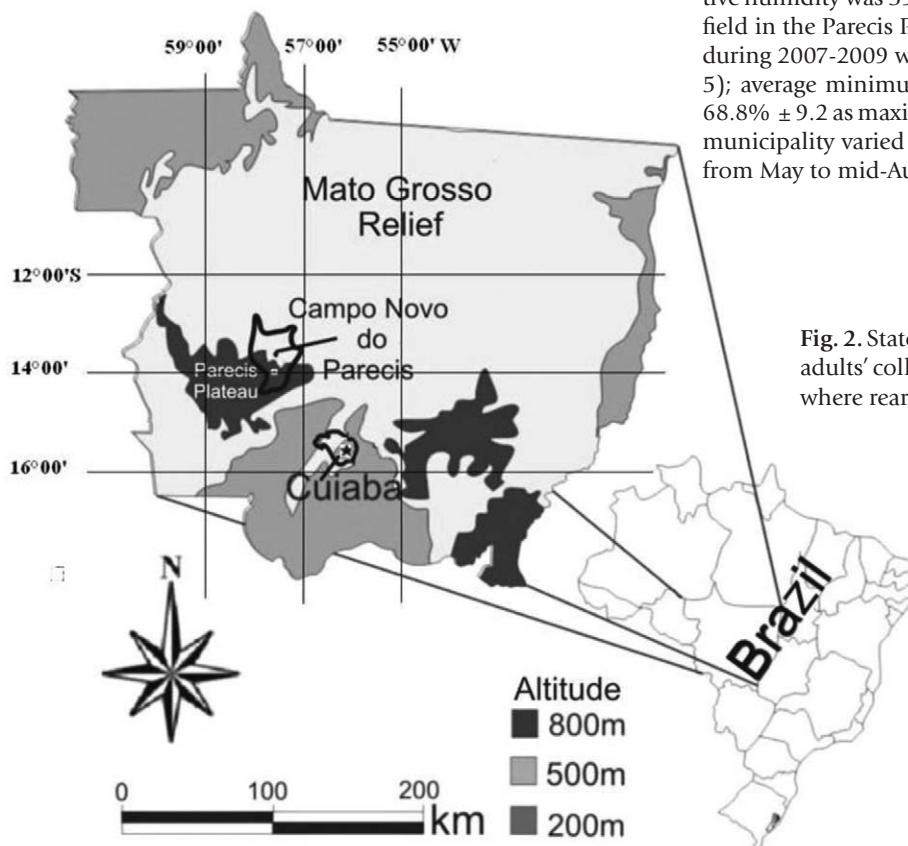


Fig. 2. State of Mato Grosso, Brazil, showing *B. punctulatus* adults' collection site at Campo Novo do Parecis, and site where rearing was established (Cuiabá).



Fig. 3. Ovipositing *B. punctulatus*. For color version, see Plate IX.

Captive breeding generation 1.—Most of the five mating pairs captured in the field began mating (Fig. 7) immediately after being placed in cages on April 9, 2009. Copulation occurred mainly in the afternoon and often continued uninterrupted for up to 14 h.

First egg laying (Fig. 3) began 6 to 15 d later, and hatching occurred from May 6 to June 27, giving 21 d as the shortest egg stage. Females laid 13.2 ± 2.1 (range = 8-17) eggs per pod; the average number of hatchlings per egg pod was 12.7 ± 2.2 (4% egg mortality). Eggs in a single pod hatched synchronously within an hour or so, and newly hatched insects immediately climbed the side of the cage or onto the plants. Egg pods were deposited underground, mostly against the sides of the container. When soil was unavailable, females laid against the sides of the cage, but these eggs quickly dried and shriveled.

We obtained 291 eggs (G1) in captivity, from 22 egg pods laid by these five females (mean = 4.4 ± 2.5 egg pods/female), and this produced 279 nymphs. Two females laid eight egg pods each, resulting in a G1 of 93 and 97 nymphs respectively; the latter being the largest number of offspring recorded by a single female. One female laid only two egg pods containing 25 eggs in total. Some females may have already laid eggs in the field before they were collected. Egg pods averaged 14.7 ± 1.5 mm in length (Fig. 8). They were deposited vertically in the soil and topped by a foam plug, which extended to within 2-3 mm of the soil surface. Eggs were 3 to 3.5×1 mm (Fig. 9).

In captivity, nymphal development (from hatch to adult molt) averaged 43.4 ± 3.9 d (Table 1). The 5th instar exhibited the longest duration, ~ 11.3 d, before molting to adult. However, within each replicate (containers), some individuals developed faster. Taking the fastest-developing individual from each container gives an average minimum hatch-to-adult development time of 40.6 d. One individual completed nymphal development in 32 d. Percentage survival from hatch to adult was 38.9% (Table 1), the highest mortality occurred in 4th and 5th instars. In captivity nymphs and adults occasionally cannibalized their dead siblings, and consumed exuviae.

Captive breeding generation 2.—Total hatch-to-death was 80 d maximum. First mating occurred 5 to 10 d after the adult molt, and continued intermittently for 45 d. However, one older male mated with a two-day old adult female. Mating occurred practically throughout adulthood. First attempts to lay eggs were observed 6 to 9 d after mating (~ 11 to 19 d after the adult molt). Time from



Fig. 4. *B. punctulatus* nymphs in plastic bag laid against ruler to measure size. Note different lengths of wing pads in different instars. For color version, see Plate IX.

Table 1. *B. punctulatus* nymphs. Development period and cumulative percentage survival from nymph to adulthood under captive breeding. The top row (n) gives the number of individuals alive at the start and the end of that stage, respectively. Minimum (Min) length of instar was derived by taking the fastest-developing individual from each rearing container and averaging those values.

Instar	1 st -2 nd		2 nd -3 rd		3 rd -4 th		4 th -5 th		5 th -imago	
n	208 - 193		193 - 177		177 - 158		158 - 117		117-81	
Cumulative % survival	92.8		85.1		76.0		56.3		38.9	
Instars length (days)	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
\bar{x}	8.4	10.1	6.1	7.6	7.7	8.6	7.3	8.3	11.1	11.6
SD	0.9	1.3	1.1	1.7	1.4	1.7	1.0	1.2	0.9	0.5

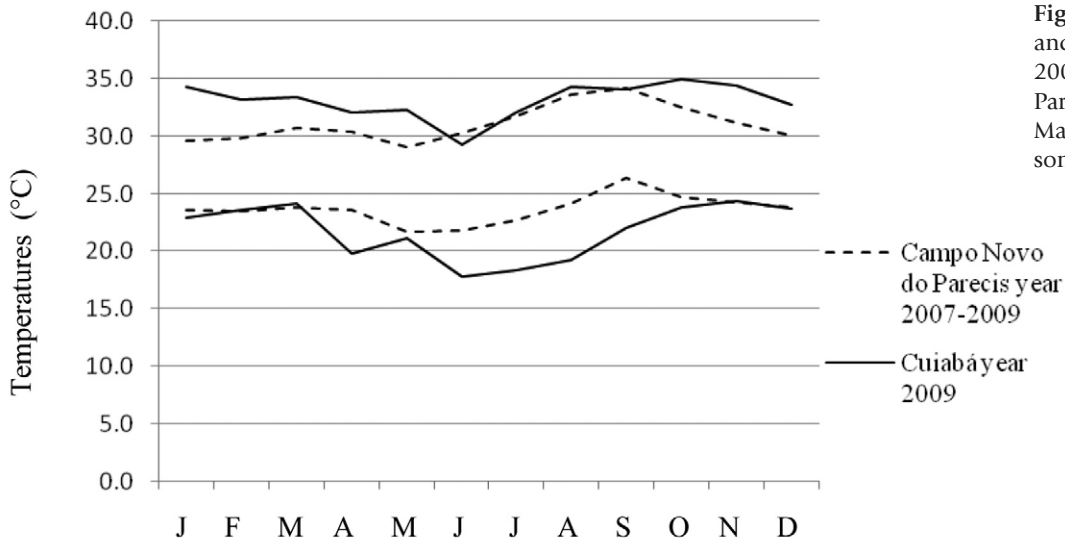


Fig. 5. Average daily minimum and maximum temperatures from 2007-2009 at the Campo Novo do Parecis municipality, and at Cuiabá, Mato Grosso, Brazil in 2009 (personal data; INMET, 2009).

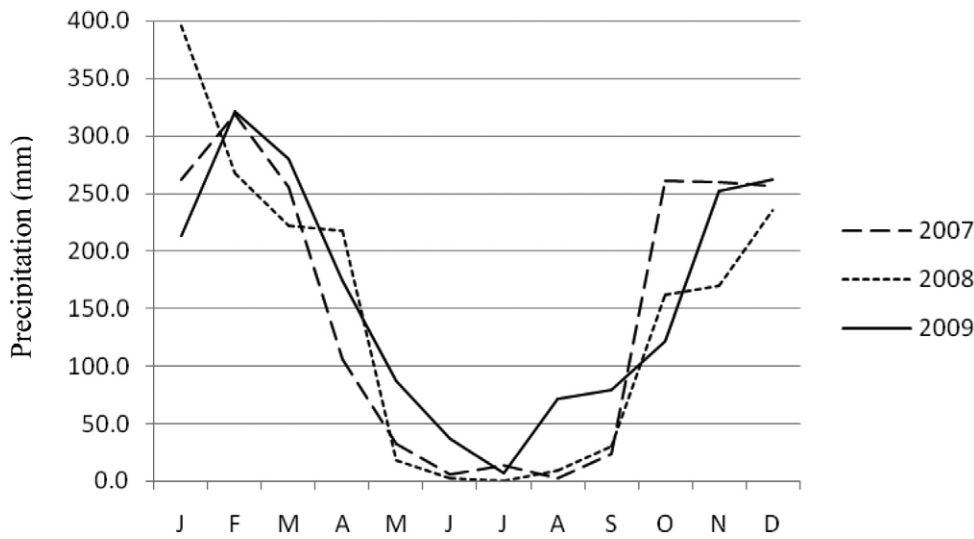


Fig. 6. Precipitation at Campo Novo do Parecis, 2007-2009.



Fig. 7. *B. punctulatus* mating pair. For color version, see Plate IX.



Fig. 8. *B. punctulatus* egg pods removed from the soil. For color version, see Plate IX.



Fig. 9. *B. punctulatus* eggs. For color version, see Plate IX.

laying to hatching ranged from 20 to 28 d. The 2nd generation (G2) of captive nymphs hatched between late July and early August, 2009, ~ 82 d after the 1st generation hatched (Table 2). Hence, under our rearing conditions, *B. punctulatus* displayed an 82-d generation time, suggesting 4.4 generations/yr. However, if we consider the minimum periods possible for each life stage (41 d as nymphs, 11 d until the first egg pod, and 20 d for eggs to hatch), a 72-d generation is possible. Conversely, using maximum values for the duration of each stage gives a 94-d generation time. Considering the above data, we estimate that *B. punctulatus* has between 3.9 and 5.1 generations/yr in the State of Mato Grosso, Brazil.

Field sampling recorded a total of 1,081 adults and 376 nymphs at 71 sampled sites (instars: 20 first, 92 second, 87 third, 73 fourth, 104 fifth). Adults and older nymphs were present throughout the year, even during the dry-cool season (Fig. 10). In contrast, egg laying

and young instars were rarely observed during the dry-cool season, suggesting that the adults and/or eggs enter dormancy at that time (Fig. 10, Table 2). A burst of hatching and young nymphs occurs at the beginning of the wet season (Fig. 10).

The five instars could be differentiated by body size (Table 3), shape and size of wing pads (Fig. 11), and number of antennal segments (Table 4), even though body length varied within the same instar as a function of extending the abdomen during feeding or growth. The number of antennal segments increased gradually from 9 or 10 in 1st instars to 19 to 20 in adults (Table 4).

Wingpads were nearly imperceptible in the 1st instar, represented by very small projections and pigmentation on the second and third thoracic segments (Figs 11a, b). This projection increases slightly in 2nd instar nymphs and may help to differentiate them. At the 3rd instar, the pads were more evident and possessed veins, and the tips pointed down (Fig. 11c). At the 4th instar, the wing pads grew to 2 mm long and changed their orientation to point upwards and backward (Fig. 11d). The last nymphal instar (5th), possessed 4-mm long wing pads that extended to about the proximal third of the hind femora (Fig. 11e). Adult wings were 13 to 15 mm long.

Discussion

Under our breeding program, the average generation time for *B. punctulatus* was ~ 82 d (24-d egg stage + 43-d nymphal development + 15-d preoviposition period). Colony females laid ~ 4.4 egg pods during their ~ 30-d adult life. Pods contained ~ 13 eggs, and most eggs hatched, giving ~ 56 offspring per female. Our captive breeding methods produced 39% hatch-to-adult survival, which is normal for grasshopper laboratory colonies (Singh & Moore 1985). These life-history characteristics match closely those reported by Michel & Terán (2006) who reared *B. punctulatus* in the laboratory at 30 ± 1°C and 50-70% RH.

Our rearing data suggest that the fastest- and slowest-developing individuals could conceivably complete a generation in 72 and

Table 2. Population dynamics of *B. punctulatus* based on both captive breeding and field sampling at the Parecis Plateau, State of Mato Grosso, Brazil.

January			February			March			April			May			June			July			August			September			October			November			December								
10	20	31	10	20	28	10	20	31	10	20	30	10	20	31	10	20	30	10	20	31	10	20	31	10	20	30	10	20	31	10	20	30	10	20	31						
N	N	N	N	N	N																																				
A	A	A	A	A	A	A	A	A																																	
	C	C	C	C	C	C	C	C	C																																
		L	L	L	L	L	L	L	L	L																															
			N	N	N	N	N	N	N	N		adults and/or eggs dormancy?																													
						A	A	A	A	A	A	a	a	a																											
						C	c	c	C	c	c	c	c	c																											
						l	l	l	l	l	l	l	l	l																											
									n	n	n	n	n	n	n	n	n																								
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A	A																																								
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G1, G2, G3, G4 & G5 generations;
 Experimental observations: (n) nymphs, (a) adults, (c) copulation, (l) lay.
 Field observations: (N) nymphs, (A) adults, (C) copulation. (see Fig. 10 for N and A).
 Expected presence (N) nymphs, (A) adults, (C) copulation, (L) lay.

Table 3. *B. punctulatus* body length (mm), 1st instar through adult. Measurements from vertex of head to apex of abdomen.

Instar	1	2	3	4	5	adult
Females (n)	23	15	23	12	21	39
\bar{x}	4.2	5.7	8.9	11.5	13.8	19.7
SD	0.6	1.1	0.9	1.2	1.2	1.8
Males (n)	17	26	32	21	22	39
\bar{x}	4.1	5.6	7.3	9.4	11.7	15.6
SD	0.4	0.6	0.6	1.0	0.7	1.1

94 d respectively, giving 3.9 to 5.1 generations a year. Of course, conditions in the field are different from those in our breeding program, and field conditions could alter grasshopper development and life history. Growth, development, reproductive rate, and even disease resistance in grasshoppers are strongly related to temperature (Chappell & Whitman 1990, Scanlan *et al.* 2001), moisture (Chapman *et al.* 1979, Joern & Gaines 1990), and food quality (Stauffer & Whitman 1990, Belovsky & Slade 1995).

The Mato Grosso region of Brazil has a seasonal climate. High temperatures (Fig. 5) and rainfall (Fig. 6) in the Brazilian spring and summer (September-March) would provide heat, moisture, and plant growth for maximum grasshopper development and uninter-

Table 4. *B. punctulatus* number of antennal segments, 1st instar through adult.

instar	1	2	3	4	5	adult
Number of antennal segments (min-max)	9-10	11-13	14-16	16-17	17-19	19-20
N examined	21	32	37	24	33	64

rupted breeding. In contrast, lack of rain in Mato Grosso from May to August dries both soil and plants, stressing nymphs and adults, and perhaps inducing egg dormancy. As such, our calculation of 43 d for *B. punctulatus* nymphal development may be high compared to the field, because we raised grasshoppers during the Brazilian winter, outside and in the shade. These cool temperatures may have slowed down development in our captive colony.

In addition, it is well known that on cool days, grasshoppers routinely bask in sunlight throughout the day to raise their body temperature (Chappell & Whitman 1990). Such thermoregulation allows some species to maintain higher temperatures, and thus substantially speed development (Whitman 1988). Our captive breeding program gave the insects little time for solar-basking. For these reasons we supplemented our captive-breeding data with field sampling to derive a better understanding of the life history of this pest.

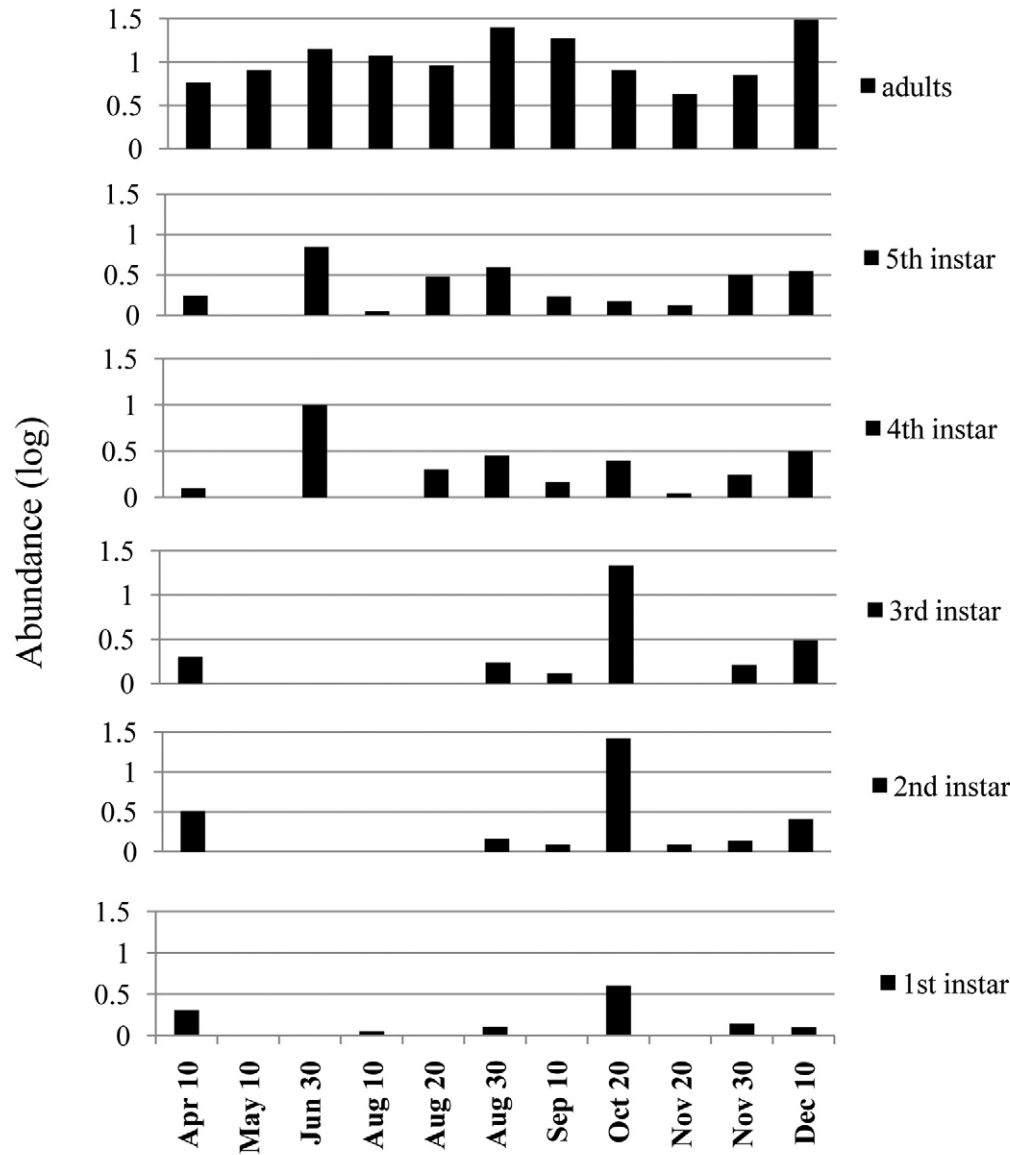


Fig. 10. Field abundance of *B. punctulatus* nymphs and adults at the Parecis Plateau, State of Mato Grosso, Brazil.



Fig. 11. Plate showing *B. punctulatus* wing pads: a) 1st instar; b) 2nd instar; c) 3rd instar; d) 4th instar; e) 5th instar. For color version, see Plate X.

Our field sampling shows that adults and older nymphs are abundant throughout the year (Fig. 10). This might suggest that *B. punctulatus* breeds year round in Mato Grosso. However, our field data for hatchlings, young nymphs, and oviposition, indicates the opposite. Hatchlings and young nymphs are scarce during the dry-cool season (May to mid-August) (Figs 5, 6, 10), suggesting that *B. punctulatus* eggs become dormant during this period, as has been noted by Turk & Barrera (1979) and Michel & Terán (2006). We did not observe oviposition in the field during this time (Table 2), suggesting that the adults might enter an adult reproductive dormancy during the dry season, as is common in other grasshopper species (Franc & Luong-Skovmand 2009). Grasshoppers often display either egg dormancy or adult reproductive dormancy dur-

ing dry or cold seasons (Tauber *et al.* 1986, Danks 1987, Schmidt 1987, Maiga *et al.* 2009). Such dormancy may be why Duranton *et al.* (1987) suggested three generations per year for this insect in the northern region of its distribution area, which includes the state of Mato Grosso.

Taking into account data from both the rearing program and our field sampling allowed us to estimate the number of generations and annual life-history patterns for *B. punctulatus* in Mato Grosso (Table 2). We estimate five generations annually, synchronized each year by the dry-cool season, which might induce either egg or adult reproductive dormancy (Table 2), followed by massive hatching at the beginning of the warm-rainy season in October (Figs 5, 6, 10). The short egg, nymphal, and adult preoviposition periods characteristic of this species, allow a rapid generation time (~82 d), and the generally warm and moist climate allows multiple annual generations. This, combined with its wide diet breadth, gives *B. punctulatus* a high potential for population outbreaks and accompanying high crop damage.

Regional and annual climatic variability add to the complexity of this pest system. For example, low, north-facing drainage areas may maintain higher local moisture and temperature during the dry season, and this could speed egg and hopper development. Likewise, occasional rainfall during the dry season, such as occurred in August 2009 (Fig. 6), might elicit abnormal hatching and plant growth. Finally, irrigation could conceivably increase local *B. punctulatus* densities. Any of these atypical conditions could increase *B. punctulatus* populations at the end of the dry season, and thus seed rapid population and pest outbreak in September and October, at the beginning of the crop-planting season.

In summary, information obtained on the life history and population dynamics of *B. punctulatus* is fundamental to understanding this crop pest. Information on instars' morphological characteristics (Figs 4, 11a-e; Tables 3, 4) provides a quick and easy method to identify nymphal development under field conditions. It is also an input for decision making if control actions are needed. Knowledge of nymphal development and population density is useful to predict the occurrence of adults and undertake preventive control measures, which minimize costs and potential losses. However, as we have shown, this system is complex, and further investigations are necessary to sort out the numerous factors that influence *B. punctulatus* population dynamics, as well as to fully characterize both the apparent egg and/or adult reproductive dormancy in this species.

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