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How climate influences the biology and behaviour of *Phyllophaga capillata* (Coleoptera: Melolonthidae) in the Brazilian Cerrado

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Abstract *Phyllophaga capillata* (Blanchard) is the most important soil pest in soybean crops in Central Brazil (Federal District and Goiás state). The objective of this work was to study the bio-ecology of *P. capillata* in the field in the Cerrado of Central Brazil, relating its biology and behaviour to the climatic characteristics of this biome. The study was conducted over three years in a soybean [*Glycine max* (L.) Merr.] production area (≈6000 ha) in the Federal District. Field samplings were taken to observe the biological stages of *P. capillata*, preferred oviposition sites and the adult swarming period. *Phyllophaga capillata* presented an univoltine cycle that lasted about 10 months of egg to inactive adults, and 12 months until the appearance of active adults. Eggs were found in the field in October and November. The larval stage occurred between November and June. Pre-pupae were observed in June and the pupae between July and August. Inactive adults were observed in August and September, and the swarming period was between September and December. Females preferred to oviposit in sites with taller plants. This species synchronises its active phases (larvae and active adults) with soybean cultivation and the rainy season (October/March) in the Brazilian Cerrado. Alternatives for pest management based on their bio-ecological characteristics are presented.

Key words bio-ecology, Central Brazil, climatic variables, soil pest, white grub.

INTRODUCTION

Climate is one of the main factors responsible for regulating insect populations, directly influencing the biology and behaviour of species (Wellington 1957; Messenger 1959, 1976; Cammell & Knight 1992; Peacock *et al.* 2006; Battisti & Larsson 2015; Sable & Rana 2016). In temperate regions, low temperatures, which occur in winter (often below zero), represent one of the main obstacles within the biological cycle of insects, requiring the use of survival strategies such as diapause (Addo-Bediako *et al.* 2002; Bale 2002; Sinclair 2015). In subtropical and mainly tropical regions, the absence of climatic extremes, such as the freezing caused by winter, and the relatively high temperatures during almost the whole year could allow, with some degree of seasonality, the continuous development of species during the year (Wolda 1978, 1988; Young 1982; Grøtan *et al.* 2012). However, even in the tropics some factors such as the irregular distribution of rainfall can decisively influence the development and regulate the biology of many insect species (Wolda 1988; Silva *et al.* 2011; Oliveira & Frizzas 2013).

Brazil presents three climatic zones and 12 types of climate, with a predominance of the tropical zone that represents 81.4% of the national territory (Alvares *et al.* 2013). The Cerrado, one of the six Brazilian biomes, is a savanna formed by a mosaic of vegetation with unique characteristics on the planet, completely covering Central Brazil (Ribeiro & Walter 2008). In its nuclear portion (250 km radius from the Federal District), including the Federal District and parts of the states of Goiás and Minas Gerais, it presents, predominantly, tropical climate with dry winter (Aw), altitudes between 600 and 1200 m, average annual temperatures between 20 and 24°C and precipitation ranging from 1300 to 1900 mm (Alvares *et al.* 2013). Its main climatic characteristic is the bimodal distribution of rainfall, with a dry period (April/September) and a rainy season (October/March), and this has been pointed out as one of the main responsible variables in the seasonality of insect populations in this biome (Oliveira & Frizzas 2008, 2013, 2015; Silva *et al.* 2011).

The genus *Phyllophaga* Harris (*sensu lato*) currently includes 865 species in the new world (Evans & Smith 2009). This genus has high abundance, biomass and wide geographic distribution (Morón 2010b) and its species exhibit great plasticity, adapting to the environmental conditions, and can develop in almost all biomes, from sea level up to 3500 m altitude (Morón 1986, 1997, 2010b). The biological cycle of *Phyllophaga* species is strongly influenced by climatic factors, mainly temperature and humidity, and can vary from six months to three years (Hayes 1925; Ritcher 1940, 1966; Reinhard 1941). Biological cycles comparatively longer are found in temperate regions or in areas with dry and hot seasons where larvae enter aestivation until the beginning of the rainy season (Moutia 1940; Ritcher 1958).

In Brazil, 31 species of *Phyllophaga* are registered (Morón & Rojas 2001). *Phyllophaga capillata* (Blanchard) has been identified as one of the main soil pests in soybean crops [*Glycine max* (L.) Merr.] in Central Brazil. Its occurrence, to date, is restricted to the state of Goiás and the Federal District. Their damage occurs in the rainy season and is caused by intense feeding of the larvae in the soybean root system, leading to reductions in plant

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productivity and death (Oliveira *et al*. 2007). For other species of *Phyllophaga* in Brazil, such as for *Phyllophaga cuyabana* (Moser), a synchronisation of the insect's biological cycle with the soybean-growing season has been demonstrated (Oliveira *et al*. 1997). Our hypothesis is that the climatic conditions of the Cerrado, mainly the rainfall distribution, directly influence the biological cycle and the behaviour of *P. capillata* determining the periods of activity and inactivity of its biological phases.

The objective of this work was to study the biological (life cycle) and behavioural aspects (oviposition behaviour and swarming period) of *P. capillata* in the field in the Brazilian Cerrado and relate these biological variables to the climatic characteristics of this biome as the basis for implementation of strategies to manage this pest.

MATERIALS AND METHODS

Study area

The studies were conducted in a soybean production area with approximately 6000 ha in Planaltina/DF, Brazil (15° 38′ 53.50″ S, 47° 25′ 27.20″ W, 972 m). In this area soybean (in rotation with maize) was cultivated annually in the rainy season (October/March) and during the dry season the wheat was cultivated under irrigation (central pivot). Laboratory studies were performed in Embrapa Cerrados (Planaltina/DF, Brazil) in growth chambers under controlled conditions (25 ± 2°C, 70% ± 23% RH and 12 h photophase). Climatic variables (average monthly temperature, average monthly relative humidity and monthly cumulative rainfall) were recorded throughout the study period by the Embrapa Cerrados weather station, located approximately 20 km from the experimental area, and by a pluviometer installed in the experimental area.

Biological cycle

To study the occurrence and duration of biological stages of *Phyllophaga capillata*, samplings were conducted every two weeks between November 2004 and Outubro 2007 (72 sampling events in total) in a field of approximately 270 ha, where soybean were sown annually in October (spring). On each sampling occasion, 40 trenches (50 × 50 cm in area and 30 cm deep) were dug at random locations within the experimental area using a mattock [using trenches is a common method for locating the biological stages of Melolonthidae that develop in soil (Oliveira *et al*. 1996; Oliveira *et al*. 1997)]. The developmental stages of *P. capillata* were recorded on site.

A subsample of the specimens found during each sampling event was transported to the laboratory, placed in plastic trays (40 cm long, 25 cm wide and 8 cm high) containing moist, sterile soil from the experimental area, and maintained under controlled conditions. Trays containing soybean plants were used as food source for larval rearing. For the egg, pre-pupae and pupa phases, the trays contained only soil. The adult specimens obtained from these samples were used for specific taxonomic identification (see below).

Determination of the number of instars

During sampling, a subsample of the *Phyllophaga capillata* larvae found was transported to the laboratory and boiled for approximately 2 min in an alcohol and water (1:1) solution (Almeida *et al*. 1998) to fixate the tissues. Next, the larvae were stored in bottles containing 70% alcohol. Later, the head capsule was measured using a micrometre attached to a stereomicroscope (Stemi SV6, Zeiss, Jena, Germany). Measurements were performed on the dorsal region of the head of the larvae between the bases of the antennae. These measurements were placed in a frequency distribution graphic to visualise the number of larval instars. The limits of each instar were defined as cephalic capsule readings less frequently (Alvan-Aguilar & Hamada 2003). To verify the pattern of growth during the larval stage, the mean measurement of the head capsule in each instar defined (response variable) was plotted against the number of larval instars (predictor variable), and a linear regression model, using R version 3.2.3 package (R Core Team 2016), was established to verify the geometric pattern of growth. According to Dyar's rule (1890), any deviation from this line would indicate that some instar was absent (Cunha *et al*. 1998; Parra & Haddad 1989). The growth rate (K) was determined by dividing the mean measurement of the head capsule in the next instar by the mean measurement of the head capsule in the previous instar. The accuracy of the larval stadium clustering process was verified using the Crosby growth rule (Craig 1975) which states that there is a possibility that an instar is absent when the difference between consecutive K growth rates is greater than 10%.

Behavioural aspects

Swarming period

To evaluate the flight periods of adults, a light trap, similar to the INTRAL model, was installed at the centre of the experimental area. The samplings were carried out weekly between January 2006 and December 2007. The trap consisted of a black light (F15T12 Black Light 350) (Havells Sylvania Brazil Ltda, São Paulo/SP, Brazil), powered by a 12 V–60 Ah automotive battery (Cral Batteries Ltd., Bauru/SP, Brazil), and was coupled to a collection vessel containing alcohol and water (1:1). The trap was fixed to a metal pole with a height of approximately 2 m, and the light remained on for 14 h (18:00–08:00). Light traps provide reliable information on changes in the real size of populations of many species of night-flying insects (Wolda 1978) when their activity patterns are measured over time. In laboratory the *Phyllophaga capillata* specimens were separated from the other insects under a stereomicroscope. During the swarming period, between 18:00 and 00:00, visual observations were made on the sexual and alimentary behaviour of adults.

The number of adults of *P. capillata* collected at each collection date was correlated with the data of temperature, relative humidity and precipitation recorded between the collection dates (current and previous) using the programme R version 3.2.3 (R Core Team 2016). The correlation was established for the period between the months in which the first adults were recorded in the

soil and the last date in which the presence of adults in the light trap was recorded.

Preferred oviposition sites

Previous studies have shown that some members of the Melolonthidae select vegetated areas, with taller plants, as aggregation sites at which to mate and place eggs nearby (Garcia *et al.* 2003; Oliveira & Frizzas 2013; Oliveira & Garcia 2003). In October and November 2006 and 2007, studies were undertaken to assess the oviposition sites of *Phyllophaga capillata* with respect to the presence of taller plants (>0.80 m in height) such as *Brachiaria decumbens* Stapf cv Basilisk, *Brachiaria plantaginea* (Link) Hitch, *Amaranthus viridis* L. and *Emilia sonchifolia* (L.) DC and with respect to surrounding vegetation with presence of smaller plants (<0.15 m in height) that had sparse distribution within the experimental area, such as *Tridax procumbens* L., *Bidens pilosa* L., *Sida santaremnensis* Monteiro, *Commelina benghalensis* L. and *Rhynchelytrum repens* (Willd.) CE Hubb. Samples were collected weekly from 40 random points within the experimental area: 20 points were located in areas with taller plants, and 20 points were located in areas with smaller plants. Trenches (50 cm× 50 cm in area and 30 cm deep) were excavated at each sampling point, and the number of eggs was recorded on site. A subsample of the eggs obtained was taken to the laboratory and maintained in Petri dishes (9 cm in diameter and 1.5 cm high) containing moist, sterilised soil covered with a perforated plastic film. After hatching, the larvae were reared until adult emergence to confirm their identification. The data on the number of eggs collected in the two areas were compared through *t*-test analysis using the R version 3.2.3 package (R Core Team 2016).

Taxonomic identification

For specific taxonomic identification, immature specimens collected during the study were reared in the laboratory until adult emergence and, together with the adults collected in the field, were compared with specimens deposited in the Embrapa Cerrados entomological collection that were previously identified by Dr. Miguel Angel Morón (Depto. de Biodiversidad y Sistemática, Instituto de Ecologia, A.C., Apartado Postal 63, 91000, Xalapa, Veracruz, Mexico) (see Oliveira *et al.* 2007). Identification was based on an examination of the external morphological characteristics and the genitalia. *Voucher* specimens of the studied material were deposited in the Embrapa Cerrados entomological collections, 'Luiz de Queiroz' College of Agriculture (ESALQ) (Piracicaba/SP, Brazil) and Instituto de Ecologia, A.C. (IEXA) (Xalapa, Veracruz, Mexico).

RESULTS

Biological cycle

Phyllophaga capillata presented an univoltine cycle completing its development, from egg to the appearance of the first sexually immature adults, in about 10 months; and approximately 12 months until the appearance of active adults (Fig. 1).

Eggs

Eggs were found in the field in October and November of each year with the highest number in November (67.2%) (Fig. 1; Table 1). They were placed inside a small chamber built by the female, in isolation, but very close to each other (Fig. 2a).

Larval phase

This stage was the longest, and larvae could be collected between November and June (Fig. 1; Table 1). First instar larvae were found in the field between November and December, with 75.8% observed in November. Second instar larvae were recorded from November to January with a population peak in December (88.3%). Third instar larvae (Fig. 2b) were observed for six months, between January and June, with prevalence in January (35.9%) (Fig. 1; Table 1). From March on, it was common to find third instar larvae building small elliptical-shaped clay chambers (pupal chamber), with internal dimensions of approximately 1.5 × 3.0 cm. From April to late May, all larvae were inside the pupal chambers.

The cephalic capsule measures confirm the existence of three instars, with a mean of 1.50 ± 0.003 mm for the first instar, 2.46 ± 0.004 mm for the second and 3.72 ± 0.005 mm for the third one (Table 2). The growth rate (K) was 1.6 between the first and second instars and of 1.5 between the second and third instars, following the Dyar rule (1890) (Table 2). Cephalic capsule measurements also followed the Crosby rule, where the difference between consecutive growth rates (K) was less than 10% (Table 2). There was no overlap of the confidence intervals for cephalic capsule values. In the regression analysis, the following equation was obtained: $y = 1.11x + 0.34$ ($R^2 = 0.9939$), indicating geometric growth for the three instars, according to the Dyar rule. In addition, the frequency distribution graph also indicates the presence of three instars (Fig. 3).

Pre-pupa and pupa

These two developmental stages occur within the pupal chambers (Fig. 1). Pre-pupae were observed only in the month of June (Table 1). At this stage, the specimens were smaller than the third instar larvae, exhibiting a wrinkled body with an opaque white colour, and dorso-ventral flattening in the terminal region of the body. The pre-pupae measured about 2.1 cm while the third instar larvae reached about 3.7 cm. Pupae (Fig. 2c,d) were found in the field in July and August, with the highest number in July (79.7%) (Table 1).

Adults

During soil samplings, adults of *Phyllophaga capillata* (Fig. 2e,f) were collected between August and October. Inactive adults were observed inside the pupal chambers, mainly in August, and active adults, outside the pupal chambers, from mid-September (Fig. 1; Table 1).

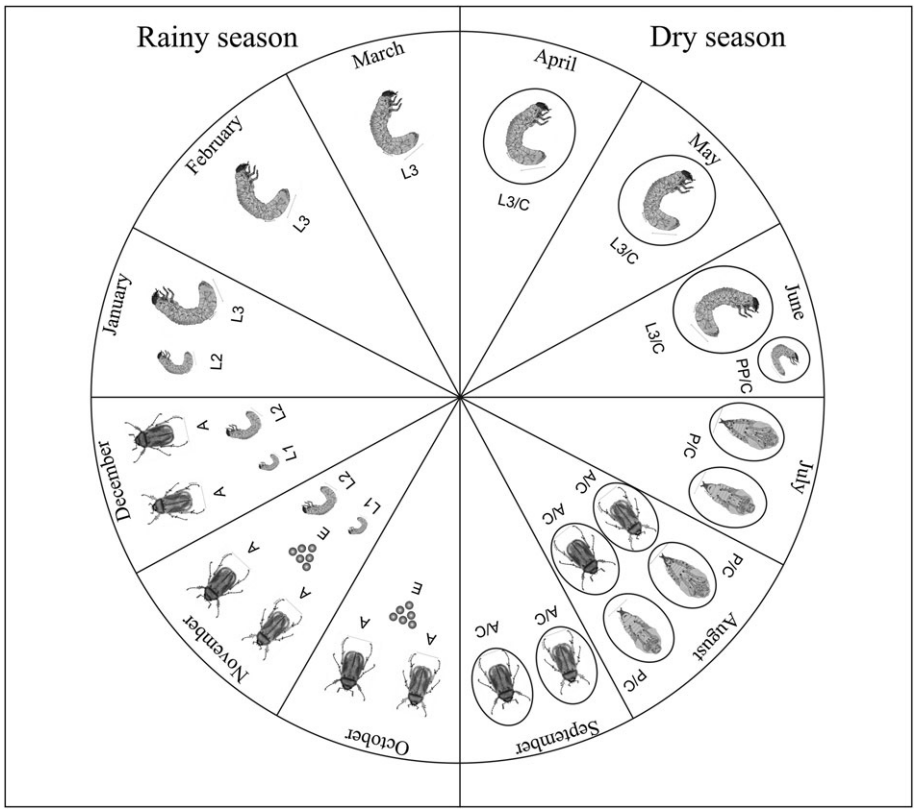

Fig. 1. Biological cycle of *Phyllophaga capillata* and temporal distribution of its developmental stages based on soil samples collected between November 2004 and October 2007 at Planaltina/DF, Brazil. A, adult; E, egg, L1, first-instar larva; L2, second-instar larva; L3, third-instar larva; L3/C, third-instar larva in diapause within the pupal chamber; PP/C, pre-pupa within the pupal chamber; P/C, pupa within the pupal chamber; A/C, adult within the pupal chamber.

Table 1 Relative percentage of developmental stage/instar occurrence of *Phyllophaga capillata* in relation to the month of the year and total number of specimens collected each month via soil samples (50 × 50 × 30 cm) in 2004, 2005, 2006 and 2007 at Planaltina/DF, Brazil

Month	Percentage (n)†						
	Eggs	1st instar	2nd instar	3rd instar	Pre-Pupa	Pupa	Adult
January	0.0 (0)	0.0 (0)	10.3 (57)	35.9 (354)	0.0 (0)	0.0 (0)	0.0 (0)
February	0.0 (0)	0.0 (0)	0.0 (0)	21.1 (208)	0.0 (0)	0.0 (0)	0.0 (0)
March	0.0 (0)	0.0 (0)	0.0 (0)	12.6 (124)	0.0 (0)	0.0 (0)	0.0 (0)
April	0.0 (0)	0.0 (0)	0.0 (0)	15.8 (156)	0.0 (0)	0.0 (0)	0.0 (0)
May	0.0 (0)	0.0 (0)	0.0 (0)	8.1 (80)	0.0 (0)	0.0 (0)	0.0 (0)
June	0.0 (0)	0.0 (0)	0.0 (0)	6.6 (65)	100.0 (15)	0.0 (0)	0.0 (0)
July	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	79.7 (55)	0.0 (0)
August	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	20.3 (14)	9.7 (48)
September	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	11.1 (55)
October	32.8 (57)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	79.2 (393)
November	67.2 (117)	75.8 (1400)	1.4 (8)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
December	0.0 (0)	24.2 (446)	88.3 (491)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Total	100.0 (174)	100.0 (1846)	100.0 (556)	100.0 (987)	100.0 (15)	100.0 (69)	100.0 (496)

†Numbers in parentheses represent the sum of specimens collected during each month of the year in 2004, 2005, 2006 and 2007.

Behavioural aspects

Swarming period

During swarming period a total of 22 378 specimens of *Phyllophaga capillata* were collected with a light trap. In 2006 (September–November) were collected 12 617 adults with a population peak in October, and in 2007 (October–December) were collected 9761, with a peak in November. Probably, the mating and egg laying occur soon after the beginning of the swarming period, since the egg stage was also observed in the field in October and November (Table 1). On average, the sexual ratio was 0.5. However, it was observed that in both years at the beginning of swarming period the proportion of males is

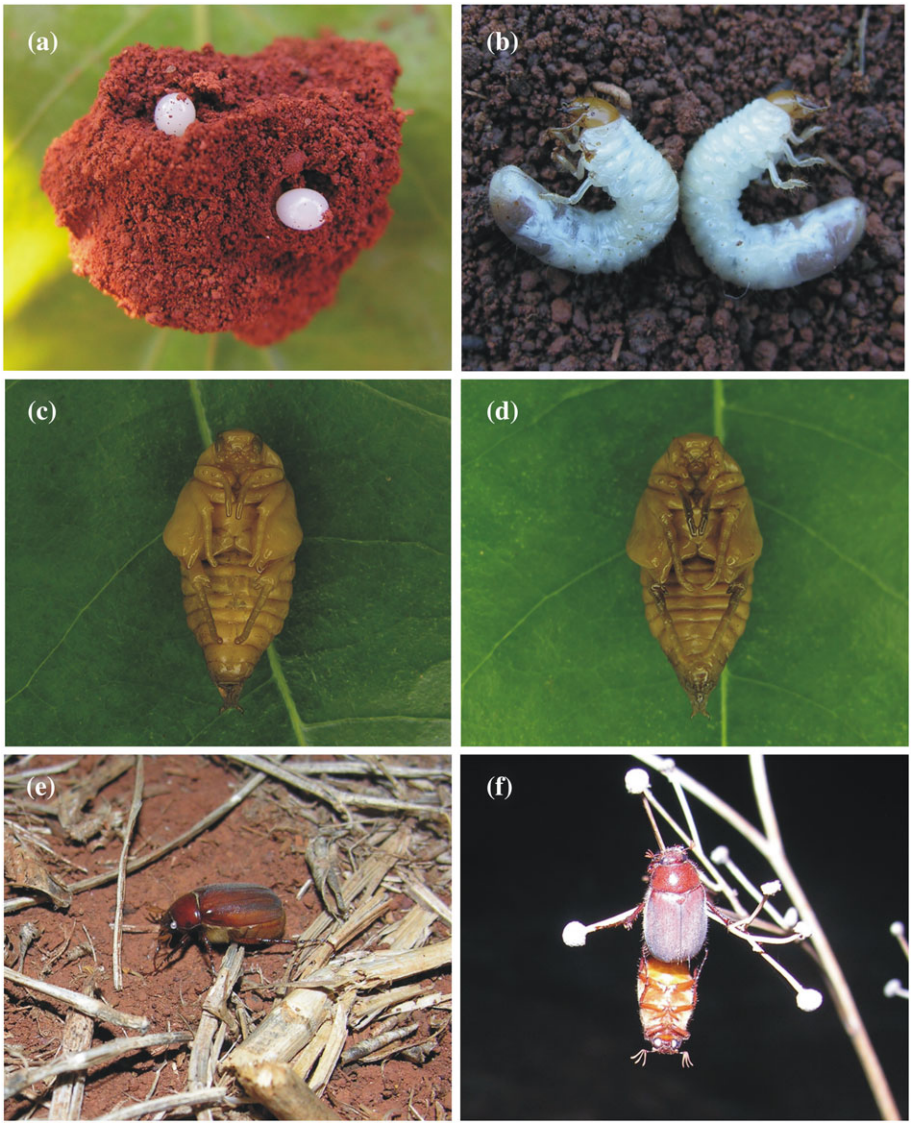

Fig. 2. Biological stages of *Phyllophaga capillata*. (a) Eggs; (b) third-instar larvae; (c) pupa (female – short antennal lamellae); (d) Pupa (male – long antennal lamellae and genital ampulla at the terminal part of the abdomen); (e) Adult (male) and (f) Adults in copula (female above and male below). [Color figure can be viewed at wileyonlinelibrary.com]

Table 2 Average head capsule width (±SEM)†, head capsule amplitude variation, confidence interval (CI) and growth rate (K) for *Phyllophaga capillata* larvae collected in the field in 2004, 2005, 2006 and 2007 at Planaltina/DF

Instar (*n*)‡	Average (mm)	Amplitude (mm)	CI ($P < 0{,}005$) (mm)§	Crosby ratio (%)	*K*¶
First (650)	1.50 ± 0.003	1.3–1.7	1.49–1.51	—	—
Second (550)	2.46 ± 0.004	2.2–2.7	2.45–2.47	—	1.6
Third (580)	3.72 ± 0.005	3.5–4.4	3.71–3.73	7.93	1.5
R^2††	0.99	—	—	—	—

†Standard error of the mean.
‡Number of specimens analysed.
§Confidence interval according to that proposed by Pimentel-Gomes (2000).
¶Growth rate (Dyar 1890).
††Determination coefficient from regression analysis.

greater than that of females, after there is a balance between number of specimens of each sex and thereafter the number of females overcome the number of males (Table 3).

Light-trap collections have shown that both sexes can fly. Sexual dimorphism was recorded by the length of the antennal lamellae which is relatively larger in males. Adult feeding on

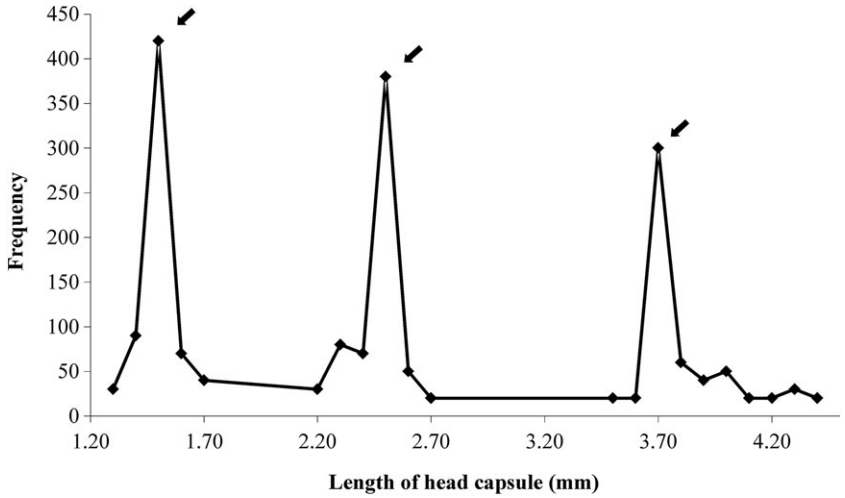

Fig. 3. Frequency distribution of head capsules of *Phyllophaga capillata* larvae collected in the field in 2004, 2005, 2006 and 2007 at Planaltina/DF, Brazil. The arrows indicate the three instars characterised by head capsule widths with higher frequencies.

Table 3 Number of adults (male and female) and relative percentage of each sex (number in parentheses) of *Phyllophaga capillata* collected with light trap during swarming period in 2006 and 2007 at Planaltina/DF, Brazil

Date	2006		Date	2007	
	Male	Female		Male	Female
25/Sep	11 (100.0)	0 (0.0)	23/Oct	180 (98.4)	3 (1.6)
29/Sep	232 (99.1)	2 (0.9)	29/Oct	1766 (50.2)	1751 (49.8)
2/Oct	677 (96.7)	23 (3.3)	5/Nov	393 (10.7)	3285 (89.3)
9/Oct	1843 (94.4)	117 (6.0)	11/Nov	581 (26.7)	1592 (73.3)
12/Oct	3064 (93.3)	221 (6.7)	14//Nov	43 (22.4)	149(77.6)
16/Oct	1307 (49.2)	1347 (50.8)	20/Nov	0 (0.0)	0 (0.0)
19/Oct	1151 (44.8)	1418 (55.2)	25/Nov	0 (0.0)	17 (100.0)
25/Oct	121 (11.2)	957 (88.8)	03/Dec	0 (0.0)	0 (0.0)
3/Nov	0 (0.0)	4 (100.0)	11/Dec	1 (100.0)	0 (0.0)
10/Nov	0 (0.0)	2 (100.0)	—	—	—
15/Nov	0 (0.0)	0 (0.0)	—	—	—
23/Nov	8 (6.7)	112 (93.3)	—	—	—
Total	8414	4203	—	2964	6797

leaves of soybean plants, *Euphorbia heterophylla* L. and *Sonchus oleraceus* L. were observed. Regarding the behaviour, it was observed that soon after the twilight, the adults leave the soil and the females seek some type of support (weeds or crop residues), preferably in the taller ones. They fixed through the anterior and middle legs leaving the hind legs free, and it seems that they begin to release the sexual pheromone. The males locate the female, attach themselves to the back one and introduce the sexual organ. After the copula begins, they release all the legs being suspended in the air and attached to the females only by the genital organ (Fig. 2f). After mating females return to the soil. On average, adult activity started at 18:40 and lasted until about 10:00.

Preferred oviposition sites

Females of *Phyllophaga capillata* showed a clear oviposition preference for areas with the presence of taller plants. We registered an average of 25.5 ± 5.87 (mean ± SEM) (n = 1019) eggs at sampling points with taller plants and 1.1 ± 0.36 (n = 44) eggs on smaller plants in 2006 and 54.6 ± 9.42 (n = 2184) e 1.4 ± 0.45 (n = 55) eggs at sampling points with taller and smaller plants, respectively, in 2007 (Table 4). Statistically significant differences were found between the oviposition sites studied (2006: $t = -4.14$, df = 78, $P < 0.001$; 2007: $t = -5.64$, df = 78, $P < 0.001$), as the number of eggs in areas with taller plants was 23–39 times higher than that of areas with smaller plants in 2006 and 2007, respectively.

Climatic variables

No significant correlations were observed for the number of adults captured and the climatic variables recorded (temperature, relative humidity and precipitation). It was observed that during the whole sample period (November 2004 to October 2007), the average temperature was 21.7 ± 1.4, the average relative humidity was 69.9 ± 14.2, and the average rainfall was 86.0 mm ± 97.3. During the dry season (April/September) these values were 21.1 ± 1.5; 61.0% ± 11.5 and 18.4 mm ± 27.0

Table 4 Average number (±SEM)† of *Phyllophaga capillata* eggs per soil sample (50 × 50 × 30 cm) collected in October and November of 2006 and 2007 at Planaltina/DF from points located in areas with taller or smaller plants (weeds)

Date	2006 Plants (weeds)		Date	2007 Plants (weeds)	
	Taller	Smaller		Taller	Smaller
24/Oct	5.5 ± 0.30	0.0 ± 0.00	23/Oct	12.8 ± 0.67	0.4 ± 0.11
31/Oct	16.4 ± 0.90	0.2 ± 0.07	31/Oct	76.0 ± 6.62	0.1 ± 0.05
7/Nov	77.2 ± 6.81	4.1 ± 0.46	7/Nov	122.7 ± 9.28	5.0 ± 0.61
14/Nov	2.8 ± 0.23	0.1 ± 0.05	13/Nov	6.9 ± 0.84	0.0 ± 0.00
Average	25.5 ± 5.87A‡	1.1 ± 0.36B	Average	54.6 ± 9.42A	1.4 ± 0.45B

†Standard error of the mean.

‡Values followed by the same letter in the row within each year are not significantly different at $p = 0.01$ as determined by t test.

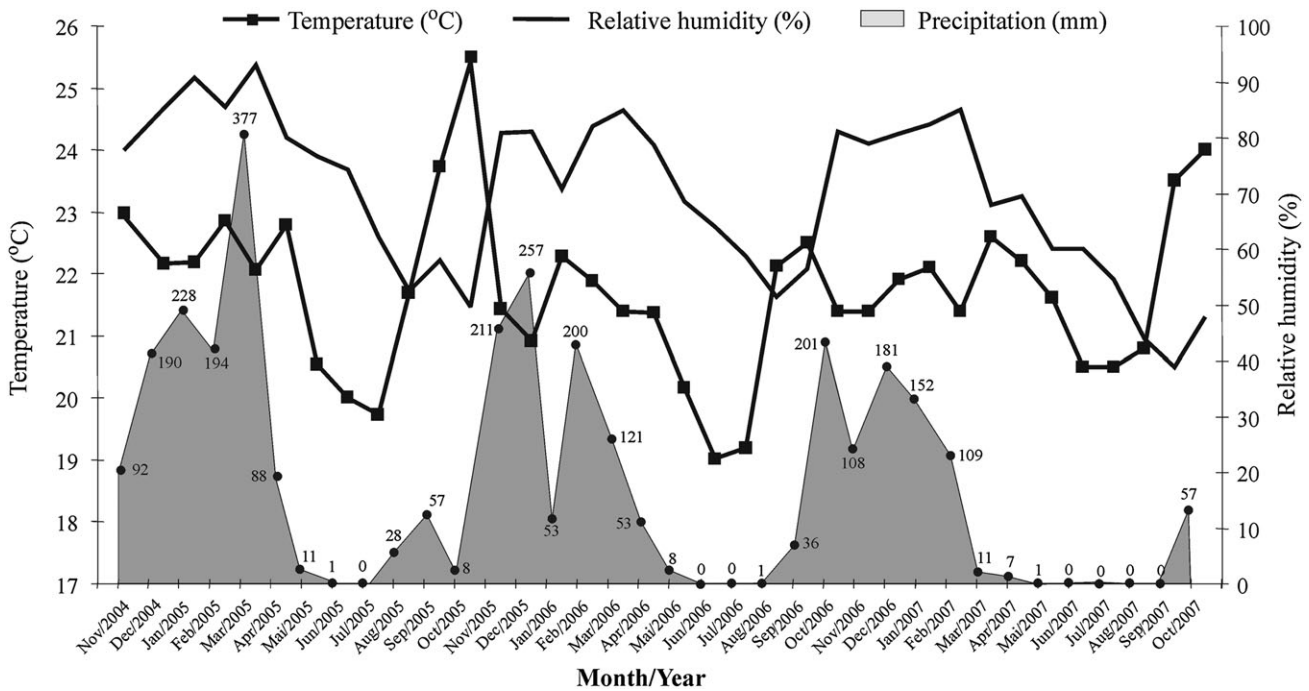

Fig. 4. Average monthly temperature (°C), monthly precipitation (mm) and relative humidity for each month (%) from November 2004 to October 2007 at Planaltina/DF, Brazil.

Table 5 Average, standard deviation, sample variance, minimum and maximum values for the climatic variables [average monthly temperature, average monthly relative humidity (RH) and monthly cumulative rainfall] recorded between November 2004 and October 2007 in Planaltina/DF, Brazil

Season		Average	Standard deviation	Variance	Minimum	Maximum
Dry (April/September)	Temperature (°C)	21.3	1.5	2.4	19.0	24.2
	RH (%)	61.0	11.5	131.8	39.0	80.1
	Rainfall (mm)	18.4	27.0	727.6	0.0	88.2
Rainy (October/March)	Temperature (°C)	22.1	1.0	1.0	20.9	25.4
	RH (%)	79.8	9.9	97.5	49.7	93.0
	Rainfall (mm)	161.5	91.8	8426.2	8.4	376.5
General average	Temperature (°C)	21.7	1.4	1.8	19.0	25.4
	RH (%)	69.9	14.2	202.9	39.0	93.0
	Rainfall (mm)	86.0	97.3	9470.4	0.0	376.5

and in the rainy season 22.1 ± 1.0; 79.8% ± 9.9 and 161.5 mm ± 91.8, respectively, for temperature, relative humidity and precipitation (Fig. 4; Table 5). The highest variances and amplitude of variation were observed for precipitation, followed by relative humidity, and the lowest values recorded for temperature (Table 5).

DISCUSSION

Our results demonstrated that the bio-ecological characteristics observed for *Phyllophaga capillata* with regard to cycle length, mating and oviposition behaviour and occurrence of larval diapause were similar to other Melolonthidae of several subfamilies that occur in the Brazilian Cerrado, such as *Aegopsis bolboceridus* (Thomson), *Geniates borelli* Camerano, *Leucothyreus alvarengai* Frey and *Le. aff. semipruinosus* Ohaus, *Liogenys suturalis* Blanchard and *Li. fuscus* Blanchard (Rodrigues *et al*. 2008, 2012; Santos & Ávila 2009; Oliveira & Frizzas 2013; Pereira *et al*. 2013). The biological cycle of *P. capillata* was also similar to other American species of *Phyllophaga* of wide geographic distribution, such as *Phyllophaga menetriesi* (Blanchard), whose cycle is annual and the developmental phases present distribution throughout the year similar to that observed in *P. capillata* (Pardo-Locarno & Montoya-Lerma 2007). The oviposition behaviour of *P. capillata* in small chambers building using a sticky secretion produced from the colleterial glands (Hayes 1929) has also been recorded for species such as *Phyllophaga cuyabana* and even in species belonging to other subfamilies of Melolonthidae (King 1984; Kuniata & Young 1992; Santos 1992; Rodrigues *et al*. 2008; Souza *et al*. 2015).

The larval phase of *P. capillata*, with approximately 8 months (240 days), was very similar to that recorded for *P. cuyabana*, which lasted about 255 days, in laboratory studies in Paraná state, Brazil (Oliveira *et al*. 1996) and for *P. menetriesi*, which lasted 203–259 days, in studies in Colombia (Pardo-Locarno & Montoya-Lerma 2007). The larvae of *P. capillata* do not build permanent tunnels and move freely in the soil. The presence of three larval instars and the pupal chamber construction by the third instar larva have also been observed in *P. cuyabana* (Santos 1992; Oliveira *et al*. 1996) and are characteristics relatively common for most of the neotropical Melolonthidae (Hayes 1929; Ritcher 1958; Morón 2004, 2010a).

The beginning of the swarming period of *P. capillata* was recorded in the months of September and October, coinciding with the beginning of the rainy season in Central Brazil. Between the observation of the first inactive adults in the soil and the collection of the first adults in light trap was recorded a cumulative rainfall of 37 mm in 2006 and 26 mm in 2007. These data suggest that was necessary an accumulation of more than 25 mm of rainfall so that the soil moisture reaches the pupal chambers containing the inactive adults and stimulate their exit. Although no significant correlation was observed for the adult collection of *P. capillata* and the climatic variables, precipitation seems to be the variable that stimulates the resumption of activity of adults that swarm with the first rains. The swarm to mating and dispersal after the onset of the rainy season is a characteristic behaviour for most of the Melolonthidae in the Cerrado (Rodrigues *et al*. 2008, 2012; Oliveira & Frizzas 2013; Pereira *et al*. 2013). Recent studies have demonstrated that rainfall is the 'trigger' for the resumption of activity of the insect species that inhabit the Brazilian Cerrado after a prolonged period of drought and food shortage (Oliveira & Frizzas 2008, 2013; Silva *et al*. 2011).

The mating behaviour in *Phyllophaga* species is very variable; however, the characteristics presented by *P. capillata* is similar to species like *P. menetriesi* (Blanchard) that performing copulation on trees or shrubs (King 1984; Morón 1986). The sex ratio during swarming period, with the observation of more males at the beginning and progressively the presence of more females, probably occurs, because, males emerge first to increase the chance of finding a mate and to perform a larger number of copulas. After females are fertilised the proportion of males decreases and females go out at night, probably more for dispersal of eggs than for mating. Other *Phyllophaga* species show similar behaviour (Morón 1986, 2010a).

The preference for areas with taller plants by Melolonthidae females for aggregation and mating, including *P. capillata*, has been suggested as a strategy that allows not only the dispersion of pheromones to locate sexual partners but also, an attempt to increase of larval survival, since that the presence of the plants implies in the presence of roots that are the food resource of the larvae of the rhizophagous species (Oliveira & Frizzas 2013). This behaviour may partially explain the characteristic attack pattern exhibited by larvae of this species in the field, which always occurs in patches. The concentration of eggs at certain sites in an area leads to a population of larvae that will consume the roots of their host plants within the site, usually in a radial design with irregular contours, forming such patches. In Brazil, *P. cuyabana* is an important soybean pest, and this species also shows a clear oviposition preference for areas with vegetation characterised by taller plants, which have been found to act as adult aggregation sites (Garcia *et al*. 2003).

The abiotic factors, mainly temperature, precipitation and relative humidity, have a great influence on the biological cycle of the insects (Wellington 1957; Messenger 1959, 1976; Cammell & Knight 1992; Peacock *et al*. 2006; Battisti & Larsson 2015; Sable & Rana 2016). For most Melolonthidae, longer biological cycles, which can last from two to five years, are recorded in species inhabiting temperate regions where temperature seems to be the factor that determine the life cycle duration (Ritcher 1958; Forschler & Gardner 1990). Shorter cycles, usually annual, are observed in tropical species with non-seasonal climate (Gressitt 1953; Morón 1986, 2004, 2010a). However, in tropical regions with prolonged periods of drought, relatively longer cycles may occur (Moutia 1940; Ritcher 1958; Beinot 2010). The record of climatic variables during the present study made it possible to observe that in this region of the Cerrado the precipitation is the factor of greater variance and more extreme amplitude; on the other hand, it was observed that the variations in temperature are very small, even between of the dry and rainy seasons. These results suggest that precipitation is probably the key factor in regulating the biological cycle of *P. capillata*.

Few species belonging to the genus *Phyllophaga* in Brazil present a known biological cycle. Only those considered as agricultural pests such as *P. cuyabana* and *Phyllophaga triticophaga* have a good level of knowledge of their bio-ecological aspects (Santos 1992; Oliveira *et al*. 1996; Salvadori & Silva 2004). *Phyllophaga capillata* presented an univoltine cycle (annual), similar to that observed for *P. cuyabana* in the state of Paraná, but different from *P. triticophaga*, which in Rio Grande do Sul

presents a biannual cycle (Oliveira *et al*. 1996, 2004). For *P. triticophaga*, a longer (biannual) cycle in southern Brazil may be a function of more extreme temperature variations, with a more rigorous winter, than in the central part of the country. For *P. capillata* the seasonality of the climate, with rainy summer and very dry winter, a longer cycle (biannual) would be expected as proposed by Moutia (1940) and Morón (1986, 2004, 2010a) for species living in these environments. However, this species presented an annual cycle, which demonstrates the great plasticity of *Phyllophaga* species in adapting to the most diverse environmental conditions (Morón 1986).

Our results support the hypothesis that *P. capillata* presents bio-ecological characteristics highly adapted to the climatic conditions of the Cerrado of Central Brazil, especially with regard to the distribution of rainfall and availability of food resources. The soybean, preferential host plant of *P. capillata* (Oliveira *et al*. 2007) is sown at the beginning of the rainy season (September/October). Thus, *P. capillata* seems to synchronise its life cycle with soybean planting and with more favourable environmental conditions, such as increased soil moisture. In this way, its active phase, represented by the larval stage, presents intense feeding activity during the rainy season (spring/summer), aiming at the accumulation of reserves. Subsequently, the larvae remain inside the pupal chambers, with pupa stages and inactive adults occurring during the dry season of the year (autumn/winter), when food is not available and soil moisture decreases to very low levels. Similar behaviour has also been observed for other Melolonthidae pest, such as *A. bolboceridus* that occurs in Central Brazil (Oliveira & Frizzas 2013).

The results presented here suggest that the months of October–November, when the rains begin, are the key period for the adoption of control measures for *P. capillata*. Management measures based on the use of insecticides to control larvae should be used during this period, when the majority of the pest population consists of first-instar larvae, which are more sensitive to insecticides. Cultural methods with the use of light traps for mass collection of adults should be implemented soon after the first rains in September/October, when most adults leave the soil for mating and dispersal. The elimination of taller plants (weeds) before the beginning of the swarming period can force *P. capillata* adults into searching for oviposition sites in other areas. This practice can also force the females to distribute more evenly in the area avoiding egg concentration and causing a 'dilution effect', reducing the damages cause to soybean crop. Measures such as ploughing soil aiming to destroy immature stages and expose the diapause larvae, which can die of dehydration or by predation, can be adopted before the beginning of the dry period (March/April), in areas that do not adopt the no-tillage system. During this period, there is still moisture in the soil, allowing access to tractors and agricultural implements.

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