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Biology, natural history and temporal fluctuation of the geometrid *Oospila pallidaria* associated with host plant phenology

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**ABSTRACT**

We investigated the temporal fluctuation of the geometrid moth *Oospila pallidaria* and related it to the leaf flush season of its host plant, *Mimosa setosa*, and to environmental factors. Aspects of the natural history of adults are also described. *Mimosa setosa* produced leaves all year round, but abundance of *O. pallidaria* larvae in the field was seasonal. The abundance of immatures showed a tendency to decrease with rainfall and temperature. Our study is pioneering in that it provides insights into factors related to the occurrence of *O. pallidaria* in natural areas. In addition, the biology of immatures is provided.

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**KEYWORDS**

Brazilian savanna; Fabaceae; herbivory; *Mimosa setosa*; swamp

**Introduction**

Among the range of folivorous insects, the lepidopterans are the most diverse and abundant (Bernays & Chapman 1994) and their intimate relationship with plants allows the investigation of the main factors that influence the caterpillars’ abundance and distribution (Price 1992). Food availability changes temporally and spatially and host plant phenology is an important temporal factor influencing the occurrence of herbivores (Wolda 1988; van Asch & Visser 2007). In fact, the timing of plant phenophases indicates the availability of floral resources, young or mature leaves for herbivores and thus creates favorable conditions for local maintenance of insect populations (Wolda 1988; Vilela et al. 2014). For caterpillars with a specialized diet, host plant phenology is considered to be crucial given that lepidopteran populations are synchronized with the phenological events (e.g. flowering, leaf flush) of the host plant (Thompson & Gilbert 2014). This synchrony may be noticed even in polyphagous caterpillars like *Operophtera brumata* (Linnaeus, 1758), a geometrid species that showed synchrony between the egg hatching and budburst of the host plant (Tikkanen et al. 2006). However, this close relationship is far from being a pattern, especially for lepidopteran herbivores. For instance, Bächtold et al. (2014) showed that the occurrence of larvae of the specialist folivorous skipper *Udranomia spitzi* (Hayward 1942) was not closely synchronized with the leafing of its hosts (species of *Ouratea*, Ochnaceae), but rather delayed for some time following the leaf flush. Therefore, generalizations on the relationship between tropical lepidopterans and the phenology of their host plants must be treated with caution, and more studies are necessary to unravel the close interactions between butterflies and their host plants (Muniz et al. 2012).

Besides plant resources, environmental factors such as rainfall and temperature can also influence the occurrence and abundance of herbivores (Lawton 1983; Cornelissen 2011; Del-Claro et al. 2013) because climate modifies the quality, abundance and geographical distribution of host plants (Schweiger et al. 2008; Bauerfeind & Fischer 2013). Moreover, not only climate, but the presence of natural enemies may represent a risk to the offspring of butterflies (Schmitz et al. 2004; Sendoya et al. 2009), thus restraining the occurrence of immatures to particular plant structures or even plants where the risk of predation is lower (Sendoya et al. 2009). Ants, wasps and birds are major threats to caterpillars (Scoble 1995; Salazar & Whitman 2001), but many species have developed defense mechanisms to avoid contact with their predators (e.g. by building shelters with leaves, by camouflage, body hairs), or escape from attacks (by beat reflex display, regurgitation on predators) (reviewed by Greeney et al. 2012). Camouflaging on the plant is also an escape strategy to avoid visually guided predators like birds and some wasps (Stamp & Wilkens 1993), and this strategy is
widespread and well developed in geometrid caterpillars (McFarland 1988).

Geometrid moths (c.21,250 species worldwide) are very diverse in the Neotropics (Heppner 1991), but information about the immature stages, host plants and distribution is still emerging (Passoa 1983; Vargas 2007, 2014; Marconato et al. 2008; Bodner et al. 2010; Robinson et al. 2015). Such knowledge, especially on the natural history, is the first step in investigating and understanding multitudes interactions in the field (Bächtold et al. 2012) and gives support to further ecological studies (Del-Claro et al. 2013). Furthermore, for insects with a specialized diet, knowledge of their relationships with the host plant is paramount as changes, both natural and anthropic, in the habitat such as fire, fragmentation and deforestation may put at risk the persistence of specialist herbivores (Araújo et al. 2015).

The aim of our study was to describe the biology of immature stages of the Neotropical specialist geometrid moth Oospila pallidaria (Schaus 1897) (Figure 1(a,b)). This moth was recorded from Argentina, Bolivia, Paraguay and Brazil but records of host plants are lacking (Cook & Scoble 1995). In current surveys in the Brazilian savanna, we observed larvae of O. pallidaria feeding on leaves of Mimosa setosa var. paludosa (Benth.) Barneby (Fabaceae, Mimosoideae). To investigate this insect–plant association we conducted observations of this moth species both in the field and in the laboratory to describe its host plant use, natural history and behavior, as well as its interactions with natural enemies. We also analyzed the annual fluctuation of

![Figure 1. Adults of Oospila pallidaria. (a) Male; (b) female (left: dorsal view; right: ventral view).]
abundance of *O. pallidaria* larvae with regard to the host plant phenology and climate conditions.

**Material and methods**

**Study area**

Fieldwork was conducted from May 2013 to April 2014 in a Brazilian savanna area (cerrado biome) in Uberlândia city, southeastern Brazil (18°59′S, 48°17′W). Local vegetation is dominated by herbaceous plants with some trees ranging between 2 and 4 m in height. We used a preexistent trail to locate plants of *Mimosa setosa*. The climate in the region is markedly seasonal, characterized by a rainy summer (October to April) which may account for up to 75% of the annual rainfall, and a dry winter (May to September) (Laboratory of Climatology, Federal University of Uberlandia).

**Host plant**

*Mimosa setosa* is a swampy-shrub species (Simon et al. 2011; Dutra & Garcia 2014) which rarely exceeds 2.0 m in height. Leaves are pinnately compound with a rachis; aculeate and glandular trichomes occur all over the rachis, the stems and inflorescences; leaves have trichomes only on the abaxial side (Barneby 1991). All *M. setosa* used in this study (*n* = 40) were located on a trail inside the cerrado reserve, near a natural pond (18°58′59″ S, 48°17′44″ W) at the end of a vereda, a swampy area located in the headwater of a stream. The trail is 3 m wide and c.1.5 km long (for more details on the area see Guillermo-Ferreira & Del-Claro 2011).

**Assessing the biology of Oospila pallidaria**

Description of the immature stages of *O. pallidaria* was based on 17 eggs collected from *M. setosa* leaves and inflorescences from May to November 2014. These eggs were taken to the laboratory where they were reared until the adult stage. Larvae were kept individually in transparent plastic pots (500 ml) which were cleaned daily, and food (leaves) was offered *ad libitum*. During the egg stage, measures of length, width and thickness were taken (according to Salkeld 1983). Head capsule width was recorded for each instar. All these measurements were made with a stereomicroscope equipped with a micrometric scale (µm).

The duration of each instar and of pupal development were recorded in days. General aspects of immature morphology, including coloration, were recorded *in vivo* with a Nikon Coolpix L810 digital camera. The terminology used in the descriptions is in accordance with Peterson (1962), McGuffin (1963), Salkeld (1983) and Stehr (1987). Larval behavior was recorded for all instars by observations *ad libitum* (sensu Altmann 1974) on plants along the trail at the study area. Two pairs of adults, which were reared from the immatures in the laboratory, were observed during mating.

**Assessing the phenology of Mimosa setosa**

Phenological observations were carried out fortnightly from May 2013 to April 2014 on 40 tagged individuals of *M. setosa*. The intensity (%) of the presence of mature leaves was recorded for each plant. The method used to evaluate these phenophases was the Fournier’s per cent index of intensity adapted by Ribeiro and Castro (1986), which ranges from zero to four, where 0 = absence of a given phenophase, and 1, 2, 3 and 4 indicate that a given phenophase was recorded in 1–25%, 26–50%, 51–75% and 76–100% of plants, respectively (adapted from Morellato et al. 2000).

**Annual variation of Oospila pallidaria abundance**

In order to assess whether the temporal variation of the larval population of *O. pallidaria* was influenced by abiotic factors, we evaluated the occurrence of larvae fortnightly from May 2013 to April 2014 on the same 40 *M. setosa* individuals used for the phenological investigation. Leaves, flower buds and flowers were carefully examined. As soon as an immature of *O. pallidaria* was found, it was collected with a fine brush and placed individually in a transparent plastic pot, which was then labeled. Immatures were taken to the laboratory and reared until the adult stage (following Bächtold et al. 2012). In order to contribute to the database of lepidopterans and their host plants, other caterpillar species found on *M. setosa* were also collected and reared in the laboratory. Climate data, such as temperature (monthly means) and rainfall (monthly values), were provided by the Laboratory of Climatology (Federal University of Uberlandia), and used as possible factors influencing *O. pallidaria* occurrence.

**Statistical analysis**

Quantitative data are displayed as mean ± standard deviation. In order to examine whether the occurrence of *O. pallidaria* larvae was related to leaf flush, we first examined the seasonality of larval abundance and leaves, as it might indicate possible
overlapping between them. Circular statistical analysis of directional data was performed by using the monthly abundance of moths as well as the percentage of plants with mature and young leaves (following Bächtold et al. 2014). Months were converted into angles (30° intervals) and were combined with the respective value of plant phenology and moth abundance. Circular statistics provide (i) the mean angle μ, which is the period when a given variable (e.g. leaves, moths) occurred most often; (ii) the vector r, which is a direct measure of seasonality (the closer to “1” the more seasonal); and (iii) the Rayleigh test (z), which indicates whether seasonality is significant. The interaction of both season (dry and wet) and mature leaf phenology in the occurrence of O. pallidaria was analyzed with a two-way Anova test. The influence of the abiotic factors (temperature and rainfall) on the temporal variation of the O. pallidaria was analyzed with Pearson correlation tests.

Results

Description of immature stages of Oospila pallidaria

Egg
Average length 0.69 mm (SD ± 0.07; n = 6), average width 0.35 mm (SD ± 0.07; n = 6) and average thickness 0.21 mm (SD ± 0.03; n = 6). Greenish in the beginning of the development and yellow near hatching (Figure 2(a)). Oval shape in top view, compressed laterally with narrow sides and flattened perpendicular to the longitudinal axis. Smooth with rounded edges and anterior pole slightly deeper than posterior. Duration: 6–7 days (n = 17).

First instar
Maximum body length 4.5 mm. Head capsule width 0.20–0.24 mm (n = 7). Orange head and light yellow body to the second day of development (Figure 2(b)). Thereafter there is a brown dorsal median line on the body. Both legs and anal plate are light yellow. Prolegs bearing eight crochets arranged in a meso-series. Duration: 5–6 days (n = 11).

Second instar
Maximum body length 6.5 mm. Head capsule width 0.30–0.34 mm (n = 7). Orange head, light yellow body with smooth cuticle (Figure 2(c)). Presence of brown dorsal median line and orange ventral median line. Head and prothorax with a pair of projections (indicated by the arrow in Figure 2(c)) which are present to the fifth (last) instar. Approximate duration: 4–5 days (n = 11).

Third instar
Maximum body length 10 mm. Head capsule width 0.44–0.49 mm (n = 6). Similar to the second instar except for body size and for more elongated projections in head and prothorax. Duration: 5–6 days (n = 11).

Fourth instar
Maximum body length 16 mm. Head capsule width 0.67–0.70 mm (n = 7). Light green head, green body with smooth cuticle, yellow ventral median line (thinner than in third instar) and brown dorsal median line maintained to the last instar (Figure 2(d)). Duration: 6–7 days (n = 11).

Fifth (last) instar
Maximum body length 28 mm. Head capsule width 0.92–1.04 mm (n = 7). Similar to the fourth instar, except for size and brown-colored anal plate (Figure 2(e)). The dorsal median line becomes thinner in the prepupa. Duration: 8–9 days (n = 11).

Pupa
Maximum body length 10 mm. Mostly green with dark red dorsal side (Figure 2(f)). Dorsal median line is a narrow dotted line. After five days the pupa becomes beige and near to hatching, wing shape and venation become visible (Figure 2(g)). Duration 8–9 days (n = 10).

Natural history of Oospila pallidaria

Oospila pallidaria eggs were found singly on different parts of M. setosa, such as the abaxial surface of leaves, flower buds and trichomes. All eggs were attached horizontally by the widest side. Larvae fed mainly on mature leaves, flower buds and rarely on young developing fruits. Adults (Figure 2(h)) were not found in the field. Mature larvae (fourth and fifth instars) resemble compound leaves (when folded) by their similar coloration (Figure 2(i)). We observed the ability for self-cleaning in O. pallidaria caterpillars. After expelling the frass pellets, the larva bent the body backwards and grabbed each pellet with the thoracic legs, and tossed it from the plant.

Six (4%) O. pallidaria larvae were parasitized by the microhymenopteran Cotesia sp. (Braconidae, Microgastrinae) in January 2014. Parasitized caterpillars had swollen bodies in the posterior half (Figure 2(j)). The solitary parasitoid larvae left the caterpillars near the fifth abdominal segment, wove a yellowish cocoon and adults hatched five days later (Figure 2(k)).
Larvae reared in the lab built shelters with silk-tied leaves just before pupation. However, this behavior was not observed in the field. Mating behavior was performed in end-to-end position and lasted about two hours. Subsequently (10–15 min later) the two females laid 70 and 60 eggs, respectively.

**Phenology of Mimosa setosa**

*Mimosa setosa* produced young leaves all year round, but leafing was concentrated in the wet season, from October to February, when up to 75% of *M. setosa* individuals were recorded with new leaves. In comparison, roughly 25% of individuals produced new leaves in the other months. Mature leaves had two peaks of occurrence, from March to April and from August to September (Figure 3). In the other periods, individuals still had mature leaves, as *M. setosa* does not shed all leaves. Because of the presence of both young and mature leaves all year round, the seasonal differences in *M. setosa* phenology were not statistically significant (Table 1).
Annual variation of abundance of *Oospila pallidaria*

The record of *O. pallidaria* larvae, on the other hand, was seasonal (Table 1) and the mean angle $\mu$ coincided with the mean angle of mature leaves (Table 1, Figure 3). We found 149 larvae throughout the year and predominantly in the dry season, which occurs from May to September (56.4%, $n = 84$ immatures); their abundance peaked in June (21%, $n = 31$ immatures) and was minimal in October (1.3%, $n = 2$ immatures) (Figure 4(a)). The interaction effect of both seasons (dry and wet) and mature leaf phenology were not significantly related to the occurrence of *O. pallidaria* larvae ($F = 3.0856$, $p = 0.0922$). During the study period, June was the driest month and December had the greatest amount of rainfall (Figure 4(b)). The abundance of larvae was negatively related to temperature and rainfall, but the test was significant only in the former case ($r = -0.5889$, $p < 0.05$ and $r = -0.4252$, $p > 0.05$).

Besides *O. pallidaria*, caterpillars of Erebidae (*Hypercompe* sp.; $n = 1$), Lycaenidae (*Hemiargus hanno* (Stoll 1790); $n = 12$), Pieridae (*Pyrisitia* sp.; $n = 2$) and another geometrid (*Macaria* sp.; $n = 18$ individuals) were also found on *M. setosa*.

**Discussion**

In general, the morphology of the immature stages of *O. pallidaria* is very similar to that of other geometrids. Eggs are flattened and pillbox-shaped, as found in other species of the Geometrinae (Salkeld 1983) and caterpillars present the well-developed prothorax with one pair of protuberant projections. This trait is also reported in other geometrid species, e.g. *Nemoria glaucomarginaria* (Porter 1986) and *Iridopsis parrai* (Vargas & Parra 2013). The presence of dorsal projections on the head in *Oospila* species seems to be common (see Janzen & Hallwachs 2009). *Oospila pallidaria* have such small dorsal projections on the head, like *O.*

### Table 1. Circular statistical analyses of the seasonality of *Oospila pallidaria* abundance together with young and mature leaves of its host plant, *Mimosa setosa*. The mean angle of larvae and mature leaves is very similar, indicating that abundance of larvae is correlated to mature leaves.

<table>
<thead>
<tr>
<th>Plant phenology – circular statistics</th>
<th>Mean angle $\mu$</th>
<th>Mean month</th>
<th>Vector $r$</th>
<th>Rayleigh Z test</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larvae</td>
<td>144.35°</td>
<td>May</td>
<td>0.322</td>
<td>15.455***</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>Mature leaves</td>
<td>142.91°</td>
<td>May</td>
<td>0.147</td>
<td>0.54 $^*$</td>
<td>$&gt; 0.05$</td>
</tr>
<tr>
<td>Young leaves</td>
<td>330.0°</td>
<td>November</td>
<td>0.331</td>
<td>2.417 $^*$</td>
<td>$&gt; 0.05$</td>
</tr>
</tbody>
</table>

$^*$p < 0.0001; ns = not significant ($p > 0.05$).
venezuelata, while other species present well pronounced dorsal projections (e.g. *O. dicraspeda* and *O. permagna*; see Janzen & Hallwachs 2009).

Geometrid caterpillars are known for the absence of three pairs of prolegs, which is why their locomotion is characterized by a looping process (Wagner 2005). It is likely that this movement type reduces the surface area of the caterpillar’s body that comes in contact with the substrate. For *O. pallidaria*, looping locomotion permits the larvae to move easily among branches covered with glandular trichomes, which are common in *M. setosa*. The presence of trichomes may also deter other potential herbivores, predators and competitors of *O. pallidaria* on *M. setosa*. In fact, only a few other insects were found on this plant, the most abundant being another geometrid moth (*Macaria* sp.).

Morphological and behavioral aspects of mature larvae of *O. pallidaria* revealed the ability to camouflage on their host plant. These larvae bear a coloration that is similar to the green leaves and their mimetic posture resembles a folded leaf. This is the strategy of cryptic coloration, a common trait in several geometrids (Montgomery 1983; Janzen 1988; Pitkin et al. 2007; Canfield et al. 2008), and represents an important defense behavior against visually guided predators like birds and wasps (see also Castellanos 2010).

Larvae of *O. pallidaria* occurred all year round on *M. setosa*, especially during the months of the dry season. This result is in accordance with the pattern of occurrence of caterpillars in seasonal environments like the Brazilian savanna (Morais et al. 1999; Scherrer et al. 2010; Diniz et al. 2012). According to Morais et al. (1999) the dry season is a period with a relatively low number of predators and parasitoids, and therefore a high abundance of caterpillars can be expected in this “enemy-free” period of the year (Diniz et al. 2012). In our study, all parasitism events occurred in January (wet season) corroborating the pattern described in the aforementioned studies.

The abundance of *O. pallidaria* larvae was seasonal and correlated to the availability of *M. setosa* with mature leaves, as the mean angle of both larvae and mature leaves overlapped. This result is opposed to the pattern reported by Morais et al. (1995, 1999) who found that caterpillar abundance in the cerrado was not correlated with host plant phenology. Nonetheless, these authors did not discriminate between specialist and generalist caterpillars. Interestingly, Pessoa-Queiroz et al. (2008) showed that the abundance of caterpillars of *Gonioterma exquisita* Duckworth, 1964, a specialist species from the cerrado, is associated to leaf phenology. Therefore, the knowledge of diet breadth, particularly for specialists like *O. pallidaria*, permits the understanding of how the host plant’s phenology may be responsible for the occurrence of herbivores (Bernays & Chapman 1994; Thompson & Gilbert 2014).

In our study, there seemed to be a delayed response in the maximum abundance of *O. pallidaria* larvae (June) following the maximum availability of mature leaves (March to April). This can be explained by the time lapse from egg to adult, which lasts about 49 days. Larvae from eggs laid in March and April turned into adults which mated and laid eggs in June, in accordance with the observed data. Bächtold et al. (2014) also noted a delayed response in the occurrence of skipper caterpillars and the availability of new leaves on their host plants. Surprisingly, the other peak of mature leaves in *M. setosa* (August to September) was not related to subsequent *O. pallidaria* occurrence. Presumably, the coming of the rainy season negatively influenced the oviposition patterns or even deterred the mating behavior of adults, thus reflecting the low abundance of geometrids in the following months.

For herbivores with restricted diets, like *O. pallidaria*, the availability of their host plants is the most important factor accounting for their occurrence in natural areas. Hence, changes in tropical habitats
caused mainly by fragmentation and deforestation may directly affect herbivore populations, especially lepidopteran larvae (Arnold & Asquith 2002). The same may be true for O. pallidaria, whose population depends exclusively on M. setosa. Despite the diversity of Oospila, which is a Neotropical genus with 74 species (Cook & Scoble 1995), host plant information is provided for only nine species (Janzen & Hallwachs 2009), three of which feed on Fabaceae, like O. pallidaria. Ecological information on geometrids remains insufficiently known, but the evidence so far indicates that Fabaceae are important hosts for these caterpillars. The present study provides insights into the natural history of O. pallidaria and provides the first record of a host plant for this geometrid species. Further investigations of the behavior and multitrophic interactions of this moth with the host plant and natural enemies shall be the focus of future studies.

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Disclosure statement

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