

Natural history of an ant–plant–butterfly interaction in a Neotropical savanna

Alexandra Bächtold^a, Kleber Del-Claro^{b*}, Lucas A. Kaminski^c, André V.L. Freitas^c and Paulo S. Oliveira^c

^aPrograma de Pós Graduação em Entomologia, FFCLRP, Universidade de São Paulo, 14040-901, Ribeirão Preto São Paulo, Brazil; ^bInstituto de Biologia, Universidade Federal de Uberlândia, C.P. 593, 38400-902, Uberlândia Minas Gerais, Brazil; ^cDepartamento de Biologia Animal, Universidade Estadual de Campinas, C.P. 6109, 13083-970, Campinas São Paulo, Brazil

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Non-mymecophilous lepidopteran larvae using plants bearing ant attractants such as extrafloral nectaries are good models for studying morphological and behavioural mechanisms against ant predation. *Udranomia spitzi* (Hesperiidae) is a butterfly whose larvae feed on leaves of *Ouratea spectabilis* (Ochnaceae), a plant with extrafloral nectaries. We described the early stages of *U. spitzi*, and used field observations and experiments to investigate the defensive strategies of caterpillars against predatory ants. Larvae pass through five instars and pupation occurs inside larval leaf shelters. Ant-exclusion experiments revealed that the presence of ants did not affect significantly caterpillar survival. Predation experiments showed that vulnerability to ant predation decreased with increase in larval size. The present study showed that predatory ants are not as relevant as demonstrated for other systems, and also illustrates how observational data and field experiments can contribute to a better understanding of the biology and ecology of a species of interest.

Keywords: *Camponotus*; defence behaviour; Hesperiidae; predation; *Udranomia spitzi*

Introduction

Ants are among the most important terrestrial animals with respect to diversity of species, abundance and biomass, and such dominance probably results from their eusocial behaviour associated with complex communication systems (Hölldobler and Wilson 1990). The richness of renewable food sources on foliage may explain why ants are so common on tropical vegetation (Davidson et al. 2003). Extrafloral nectar is a major food reward offered to ants by plants, which in turn may gain a range of benefits from ant visitation (i.e. herbivory reduction; see examples in Rico-Gray and Oliveira 2007). As generalist predators, ants may exert strong selective pressure on herbivore populations, affecting both their pattern of host utilization as well as their strategies against natural enemies (Stamp 2001; Singer and Stireman 2003). Ant presence on plant foliage may have a negative impact on herbivores (Janzen 1966; Bentley 1977), especially on tropical vegetation where ants are remarkably abundant in species and individuals (Hölldobler and Wilson 1990; Davidson et al. 2003).

*Corresponding author. Email: delclaro@ufu.br

The Brazilian cerrado is a particularly ant-rich savanna and is an excellent habitat in which to investigate ant-based multitrophic interactions (Oliveira et al. 2002; Oliveira and Freitas 2004; Del-Claro and Torezan-Silingardi 2009). In the past two decades, several studies investigated direct and indirect outcomes of these relationships in cerrado (Oliveira et al. 1987; Del-Claro et al. 1996; Oliveira 1997; Kaminski et al. 2010; Nascimento and Del-Claro 2010), usually revealing a conditionality in costs and benefits related with time and/or participant species (e.g. Del-Claro and Oliveira 2000; Sendoya et al. 2009). In general, ant-exclusion experiments on plants have shown that lepidopteran larvae present higher mortality rates on ant-visited plants (Sato and Higashi 1987; Freitas and Oliveira 1996; Dutra et al. 2006). Hence, to cope with their natural enemies, such as ants, lepidopteran larvae have evolved a wide array of defensive strategies that include morphological, chemical and behavioural traits (Dyer 1995; Salazar and Whitman 2001; Mody and Linsenmair 2004; Kaminski 2008).

Larval shelters occur in at least 18 families of Lepidoptera and are usually associated as a defensive strategy against natural enemies (Scoble 1995; Weiss 2006). The larva uses host plant leaves to build the shelter by folding, rolling or cutting pieces or the entire leaf, sometimes also joining adjacent leaves with silk (Scoble 1995). In the HesperIIDae, building leaf shelters is a widespread larval behaviour occurring in virtually all known species (Greeney 2009). However, the adaptive basis of this behaviour in lepidoptera remains poorly known (but see Weiss 2003; Weiss et al. 2004).

Udranomia spitzi (Hayward) (Lepidoptera: HesperIIDae) is a cerrado butterfly whose larvae feed on *Ouratea spectabilis* Aubl. (Ochnaceae), a plant with extrafloral nectaries, which is visited by several ant species (Byk 2006). In the present study we describe the early stages of *U. spitzi* and investigate larval behaviour. In addition, we experimentally evaluated the behavioural interaction between larvae and visiting ants, and tested the effect of ant presence on larval survival in the field.

Materials and methods

Study area

Fieldwork was carried out from October 2008 to May 2009 at the Reserva Ecológica do Clube de Caça e Pesca Itororó de Uberlândia – CCPIU (18°59' S, 48°18' W), Uberlândia, Minas Gerais State, Brazil. We used a 400-ha cerrado site consisting of a dense scrub of shrubs and trees, known as cerrado *sensu stricto* (Oliveira-Filho and Ratter 2002). The climate is markedly seasonal with a dry winter from April to September and a rainy summer from October to March (additional details in Réu and Del-Claro 2005).

Immature rearing

To investigate larval biology and behaviour, early stages were reared in the laboratory from eggs collected in the field. All immatures were placed individually in plastic pots under controlled laboratory conditions (70% humidity, c. 23°C; 12 h light: 12 h dark). Young leaves of *O. spectabilis* were offered *ad libitum* and larvae were checked daily for food replacement and cleaning when necessary. Head capsules were collected and kept for measurements. The duration of instars and pupal development were recorded. The behaviour of both immature and adult *U. spitzi* was observed in the field following Altmann (1974).

Morphological analysis

Morphological analyses of developmental stages of *U. spitzi* were conducted with the immature reared in laboratory as well as those collected in the field. These individuals were conditioned in alcohol (70%) and the generic morphological measurements were examined under stereomicroscope. We registered the duration of larval and pupal stages and also the days on which the head capsule was changed. Head capsules were measured with a stereomicroscope equipped with a micrometric scale. The terminology used hereafter in the descriptions of *U. spitzi* is in accordance with Hinton (1981) for eggs, Stehr (1987) for general morphology of larvae and Mosher (1916) for pupae.

Ant censuses on *Ouratea spectabilis*

To investigate the ant fauna visiting the extrafloral nectaries of *O. spectabilis* we performed six censuses. All plant individuals ($n = 20$) were scanned on sunny days (08.00–12.00 h) and the number and identity of ant species per plant were registered. The same plants were used in the ant-exclusion experiments (see below).

Ant–caterpillar interaction

Behavioural responses of *U. spitzi* larvae in the presence of ants were evaluated through provoked encounters in which a larva was removed from its shelter on a given plant and placed on young leaves of a plant visited by *Camponotus* ants (*Camponotus crassus* or *Camponotus blandus*). Experimental plants presented no signs of herbivory. These ants were chosen for their wide distribution in cerrado vegetation and their aggressiveness against aliens (Del-Claro and Oliveira 2000; Korndorfer and Del-Claro 2006; Sendoya et al. 2009). Interaction experiments were performed with second instar larvae (small early larvae; $n = 20$) and fourth instar larvae (large late larvae; $n = 20$). Trials were carried out on sunny days from 08.00 to 13.00 h. Plant individuals were used only once and a given larva was used in only one trial. After the ants had encountered the caterpillar, the behavioural interactions between them were registered in observation sessions lasting 10 min.

Ant-exclusion experiments

The effect of ant presence on the survival of *U. spitzi* larvae was evaluated through ant-exclusion experiments in the field. We selected 20 plants of the same size and phenological state; each plant had at least two similar branches producing new leaves. One stem was designated (by the flip of a coin) as control or treatment. Ants were manually removed from treatment branches and a strip of adhesive paper (3 cm long) covered with resin (Tanglefoot[®]; Tanglefoot Co., Grand Rapids, MI, USA) was applied to prevent further ant access. Control branches had resin applied on only one side so that ants could still reach the foliage. On both branches we placed one early larva protected by a net bag, and allowed 24 hours for establishment and construction of a leaf shelter. After this period we removed the bag and monitored larval survival every 2 days for 10 days. Missing larvae were considered dead, although we continued to check the experimental branches until the end of the experiment.

Results

Description of immature stages of Udranomia spitzi

Egg

Hemispheric, light yellow in colour, with 10–13 longitudinal ribs ($n = 15$); 1 day before hatching the exochorion becomes translucent and the larval head capsule can be seen (Figure 1A). Height 0.45–0.50 mm, diameter 0.75–0.80 mm ($n = 8$).

First instar

Entirely yellowish after hatching; after feeding, the body becomes light green and head capsule becomes pale yellow (Figure 1B). Head and body tegument smooth, without scoli or projections. Head capsule width 0.46–0.50 mm ($n = 11$), maximum body length 4.6 mm. Mean development time 2.79 ± 1.23 days ($n = 28$).

Second instar

Yellowish body, beige head. Intestinal contents dark green in colour and visible (Figure 1C). Head capsule width 0.72–0.85 mm ($n = 11$), maximum body length 7.4 mm. Mean development time 2.29 ± 0.71 days, ($n = 28$).

Third instar

Similar to second instar (Figure 1D). Head capsule width 1.10–1.46 mm ($n = 11$), maximum body length 14.5 mm. Mean development time 2.57 ± 1.13 days, ($n = 28$).

Fourth instar

Greenish body with light brightness; head light brown with several dark tiny spots. Head capsule width 1.94–2.28 mm ($n = 11$), maximum body length 18.0 mm. Mean development time 3.82 ± 1.51 days ($n = 28$).

Fifth (last) instar

Very similar to previous instar but with dark brown head (Figure 1E,F). Head capsule width 3.63–4.42 mm ($n = 11$), maximum body length 26.4 mm. Mean development time 8.82 ± 2.32 days, of which 2.32 ± 0.94 days corresponded to the pre-pupal period (Figure 1G) ($n = 28$).

Pupa

General profile elongated, without spines or appendages. General colour beige with black scattered spots (Figure 1H). Length 14.40–17.20 mm ($n = 12$). Mean development time 13.11 ± 0.78 days ($n = 28$).

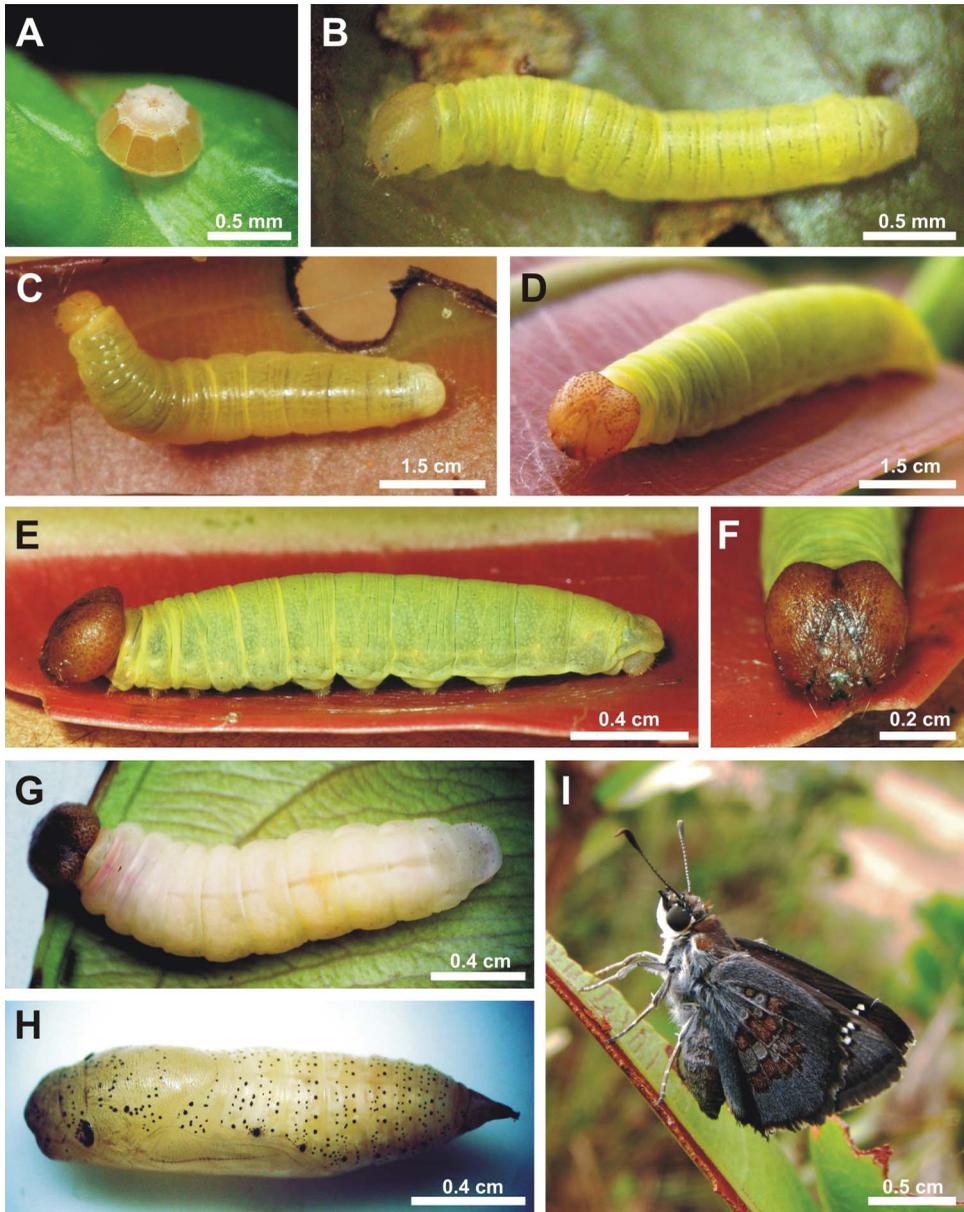


Figure 1. Life stages of *Udranomia spitzi* on *Ouratea spectabilis*. (A) egg; (B) first instar; (C) second instar; (D) third instar; (E) fifth (last) instar; (F) head capsule of fifth instar in frontal view; (G) prepupa; (H) pupa; (I) freshly emerged adult on the host plant.

Natural history of Udranomia spitzi

Ouratea spectabilis was the host plant most commonly used by *U. spitzi* in the study area, although some larvae were also occasionally observed on *Ouratea hexasperma* (St. Hil.) Baill. Adults of *U. spitzi* (Figure 1I) exhibited erratic flight near the ground.

Oviposition on young leaves of *O. spectabilis* was observed during the hottest period of the day (12.00 to 13.00 h). Eggs were found on different parts of plants such as stem and stipules, but mainly on new red leaves (Figure 2A,B). The duration from egg hatching to adult was on average 34 days. After hatching, the larva eats the exochorion and begins to build its shelter. Larvae undergo five instars until pupation, which takes place inside the leaf shelter. Larvae build leaf shelters in the first four instars (Figure 2C,D), and each shelter is occupied by a single larva. Fifth instars do not build shelters, but use previously built shelters. Larvae were observed feeding on the edge of newly built leaf shelters, remaining partially exposed. After consumption of the shelter edge, larvae start feeding on nearby young leaves. Larvae are able to eject their faeces at distance. In addition, some larvae (especially second instar) were able to build more than one shelter per instar. Two different types of shelters are built by

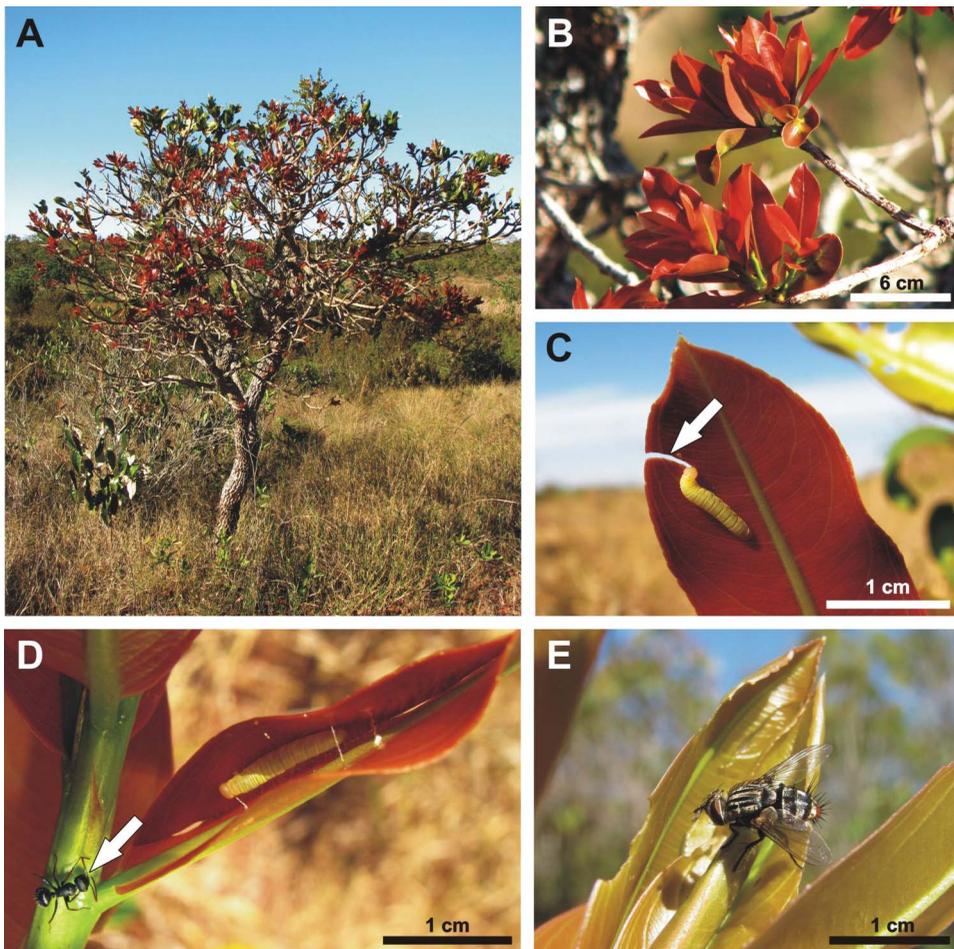


Figure 2. Natural history of *Udranomia spitzi* on *Ouratea spectabilis* in a cerrado area of Uberlândia, Brazil. (A) general aspect of the host plant; (B) detail of new red leaves; (C) early larva building a shelter; (D) an early larva inside the shelter, note the *Camponotus* worker foraging on the extrafloral nectary (arrow); (E) a parasitic Tachinidae fly on the host plant.

larvae through their development (shelter type *sensu* Greeney 2009). In general, larvae make two cuts on the leaves towards the midrib, and then the two parts of the leaf were folded and glued with silk (type 5). First instars, however, are capable of building type 1 shelter as well (no-cut shelter). Two parasitoids were registered, a fly (Tachinidae) (Figure 2E) and a wasp (Ichneumonidae).

Ants visiting Ouratea spectabilis and interactions with caterpillars

All plants were visited by ants, and a total of 17 species in six genera were recorded; *Camponotus crassus* (Mayr) and *Camponotus blandus* (Smith) were the most frequent visitors (Figure 3). Both *C. crassus* and *C. blandus* behaved very aggressively towards larvae of *U. spitzzi*, irrespective of larval size. Early larvae, however, were more vulnerable to ants ($G = 6.78$, d.f. = 2, $P < 0.0337$; Table 1). Generally, larvae under attack remained completely motionless (freezing, 55% of times), but both early and late larvae also regurgitated (35%) or performed beat reflex (to rear up the body, curling and wriggling vigorously, 22.5%). Ants took less time ($U = 3.00$, $P = 0.0012$) to attack early (7.60 ± 5.82 seconds, $n = 10$; mean \pm 1SD) than late larvae (181.62 ± 69.54 seconds, $n = 8$; mean \pm 1SD). Ant-exclusion experiments revealed that larval

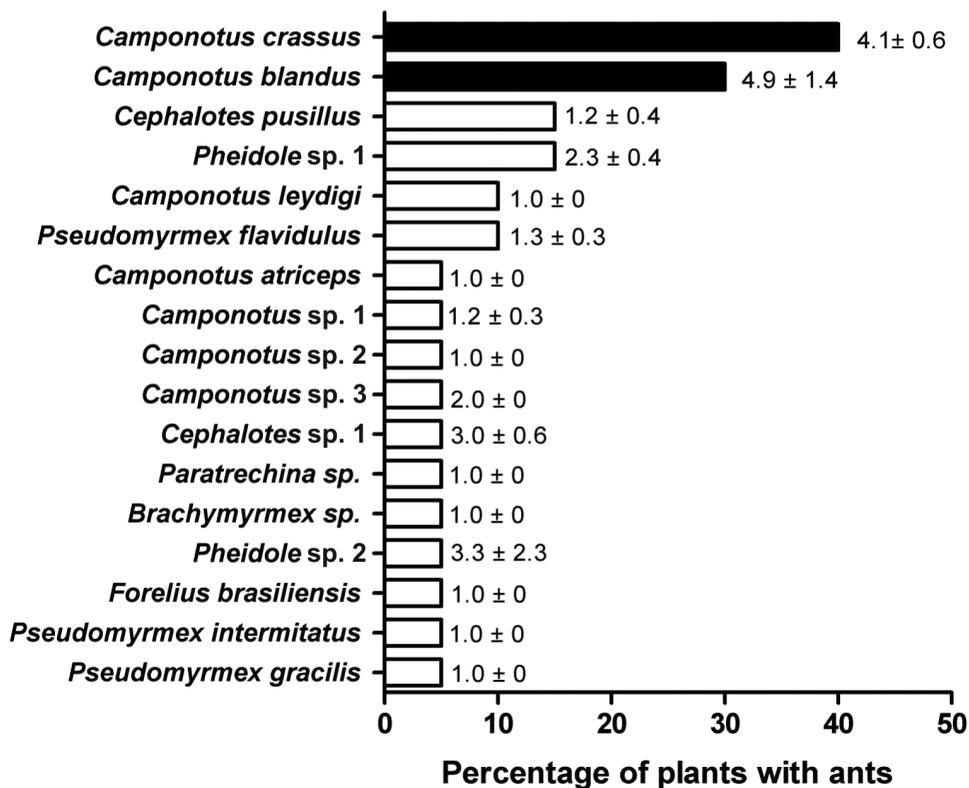


Figure 3. Frequency of ant species visiting *Ouratea spectabilis* plants ($n = 20$ individuals) in a cerrado area of Uberlândia, Brazil. Numeric values next to bars indicate mean number of ants per occupied plant (\pm SE).

Table 1. Behavioural interactions between larvae of *Udranomia spitzi* and ants on shrubs of *Ouratea spectabilis*.

Larvae	Ant response in encounters		
	Ignored	Attacked	Removed
Early (<i>n</i> = 20)	10 (50%)	10 (50%)	5 (25%)
Late (<i>n</i> = 20)	12 (60%)	8 (40%)	0 (0%)

Results are based on 10 min of observations of encounters between larvae and ants.

survival did not differ between ant-visited and ant-excluded plants of *O. spectabilis* (log-rank Mantel–Cox test, $\chi^2 = 1.048$, *P* = 0.3059; Figure 4).

Discussion

The general morphology and behaviour of *U. spitzi* are very similar to other HesperIIDae (Scoble 1995; Greeney and Warren 2003, 2004; Greeney and Sheldon 2008). As observed for other skippers (Lind et al. 2001), only one individual larva

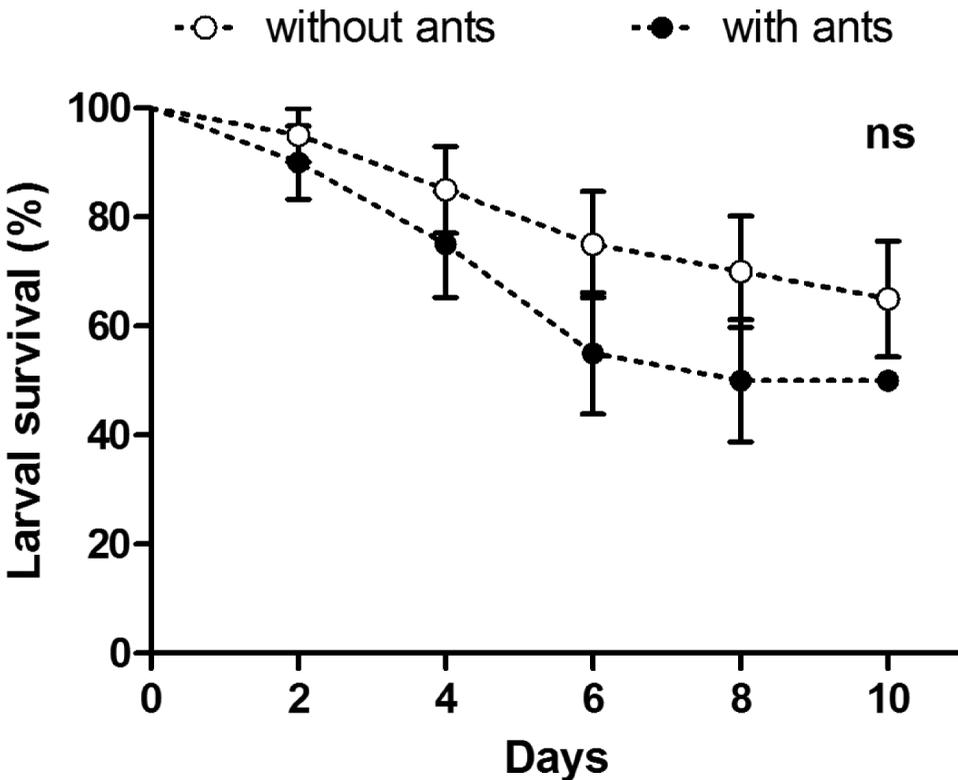


Figure 4. Survival curve of *Udranomia spitzi* larvae on paired branches of *Ouratea spectabilis* through time, as a function of the presence or absence of *Camponotus* ant in a cerrado area of Uberlândia, Brazil.

inhabits a shelter. The pattern of shelter building is in accordance with most studies involving immature skippers (see examples in Greeney and Jones 2003). In *U. spitzi*, two types of shelters are built during larval ontogeny, and up to five shelters can be built during the larval stages. These results are similar to those observed in other Pyrginae such as *Urbanus proteus* (Linnaeus), *Noctuana haematospila* (C. Felder and R. Felder) and *Eantis thraso* (Hübner) (Greeney and Warren 2003, 2004; Greeney and Sheldon 2008). Shelters built by Lepidoptera larvae may have several distinct functions, such as providing a favourable microclimate, reducing host plant chemical secondary compounds, and protecting against natural enemies (Marquis and Lill 2009).

Frass ejection is a behavioural trait seen in many lepidopteran species that build some kind of external shelter, and has been recorded in at least 17 families of Lepidoptera, including HesperIIDae (Scoble 1995; Weiss 2003). Some authors consider that frass may act as cues to natural enemies (Stamp and Wilkens 1993; Müller and Hilker 1999; Weiss 2003, 2006). For the skipper *Epargyreus clarus* (Cramer), frass ejection behaviour was suggested to be a defence against predatory wasps (Weiss 2003). Clearly, additional investigation is necessary to clarify the role of frass ejection in larval hesperIIDs (A.R. Moraes et al. in preparation).

Late larvae of *U. spitzi* were observed to be more efficient than early larvae at avoiding ant attacks, combining a series of strategies such as regurgitation, beat reflex and fleeing (Freitas and Oliveira 1992; Smedley et al. 1993; Gentry and Dyer 2002). Regurgitation is considered a type of chemical defence in Lepidoptera, and is usually associated with other behaviours such as beat reflex or biting (Dyer 1995; Salazar and Whitman 2001). Our results suggest that late larvae are less vulnerable to ants because of a combination of the above defensive traits. Early larvae, conversely, were more vulnerable to ant predation, as also observed for the nymphalid *Eunica bechina* (Hewitson) on an ant-visited cerrado plant (Freitas and Oliveira 1996).

Ants are considered the main predators of butterfly larvae on ant-visited plants (Smiley 1985). In *O. spectabilis*, however, ant visitation did not cause any negative effect on *U. spitzi* larval survival (see also Byk and Del-Claro 2010). Frequency and abundance of pugnacious ant visitors on plants is an important factor related to predation pressure on insect herbivores in the cerrado savanna (e.g. Del-Claro and Oliveira 2000; Byk and Del-Claro 2010; Sendoya et al. 2009; Silveira et al. 2010). This is the case for the butterfly *E. bechina*, whose larvae survive better on less frequently visited plants (Freitas and Oliveira 1996).

The current study illustrates how observational data and field experiments can contribute to a better understanding of the biology and ecology of a species of interest. In the case of *U. spitzi*, our study showed that predatory ants apparently are not as relevant as demonstrated for other systems in the cerrado (Del-Claro and Oliveira 2000; Oliveira and Freitas 2004; Sendoya et al. 2009; Kaminski et al. 2010). The pervasiveness of ant–plant–herbivores in cerrado suggests that combining natural history with manipulative experiments should improve our understanding of ant-based multitrophic interactions.

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