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Baronia brevicornis caterpillars build shelters to avoid predation

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ABSTRACT

In at least 18 Lepidoptera families, caterpillars build shelters that mainly serve to regulate microclimate (humidity, temperature) and/or to avoid predation. We aimed to explore the function of the tubular structures built with the leaves of the host plant, *Acacia cochliacantha* Humboldt and Bonpland ex Willdenow (Fabaceae), by a lepidopteran endemic to Mexico, *Baronia brevicornis* Salvin. We experimentally evaluated whether tubular structure building behaviour is induced by high temperature or predator odour, and if shelters reduce or enhance predation of *B. brevicornis* caterpillars. We used *Calosoma angulatum* as predator. Our analyses showed that caterpillars did not make the tubular structures in response to high temperature. We also found no difference in predators' visual recognition of sheltered versus unsheltered caterpillars. Caterpillars did not build shelters but they moved more often when exposed to predator odour. Unsheltered caterpillars were more frequently consumed when predators were allowed to interact with sheltered and unsheltered caterpillars. Hence, the tubular structures built by *B. brevicornis* are most likely a strategy for reducing predation, for example by *C. angulatum*.

Introduction

In the animal kingdom, shelters are constructed to avoid unfavourable environmental conditions and/or predators (Forsythe et al. 2003), and animals modify the size, form, texture and colour of these shelters to optimize their functionality (Alberstadt et al. 1995; Blank and Figler 1996; Gregory and Griffith 1996; Walters and Wethey 1996; Steele et al. 1997; Arsenault and Himmelman 1998; Antonelli et al. 1999; Forsythe et al. 2003). For example, Lepidoptera caterpillars in many basal families (Ditrysia: Tineoidea, Gracillarioidea, Yponomeutoidea, Gelechioidea) build individual shelters (Lima et al. 2013; Regier et al. 2013) or community shelters (e.g. Yponomeutiidae, Notodontidae, mainly among Thaumetopoeinae, and a few Lasiocampidae; Joos et al. 1988; Roessingh 1990; Romero and Benson 2004, 2005; Abarca and

Boege 2011), and it is considered that in Lepidoptera, the building of shelters is a plesio-morphic behaviour (Scoble 1992; Greeney 2009; Diniz et al. 2012). Functions of shelters have been explained as mainly to regulate microclimate and/or prevent predation (Loeffler 1996; Eubanks et al. 1997; Fukui 2001; Jones et al. 2002; Diniz et al. 2012), to lessen plant defences and to protect food sources (LoPresti and Morse 2013).

Butterflies, like other poikilotherms, must maintain an optimum body temperature based on environmental heat sources like sunlight (Huey 1982) to optimize numerous physiological processes, including metabolism. Shelters can provide an optimum micro-climate if the shade provided by the structure can avoid excessive heat (Henson 1958; Hunter and Willmer 1989; Larsson et al. 1997; Martín 2001; Romero and Benson 2004, 2005; Abarca and Boege 2011). The microclimate conservation hypothesis has been tested in community shelters, in which groups of caterpillars build and live in shelters together (these are called silk tents; Joos et al. 1988). In this case, the shelter may regulate the microclimate to be suitable for young caterpillars, for example, for over-wintering (Joos et al. 1988; Roessingh 1990; Romero and Benson 2004, 2005; Abarca and Boege 2011; Lima et al. 2013). Caterpillars of *Malacosoma americanum* (Lasiocampidae) build a communal shelter that provides a temperature 4°C above that found outside, so avoiding the cold temperatures (Joos et al. 1988).

To avoid natural enemies, including predators and parasitoids (Scoble 1992), Lepidoptera possess a great variety of adaptations (Wink and Legal 2001; Gentry and Dyer 2002; Hundsdoerfer et al. 2005; Diniz et al. 2012; Bermudez-Torres et al. 2013). To this end, shelter construction may avoid or reduce predation for their inhabitants. For example, *Michaelus ira* (Lycaenidae) caterpillars make two holes in buds of *Distictella elongata* (Bignoniaceae) flowers. One hole is used as an entrance, which is sealed with silk thread to block the way for natural enemies (e.g. the ants *Camponotus crassus* and *Ectatomma tuberculatum*), and the other is the exit by which caterpillars obtain food. Inside the shelter caterpillars are unnoticed by ants, which monitor the plant to repel herbivores. However, as soon as these ants detect a caterpillar outside its tent, they attack and kill it (Bächtold and Alves-Silva 2013).

Regarding shelter function, the main role of the individual structure is assumed to be protection against predators and, more rarely, to provide a temperature/humid-ity-regulated nest (Jones et al. 2002; LoPresti and Morse 2013). However, no matter which hypothesis may explain its function, it is also assumed that such constructions are costly because they may also attract predators (Loeffler 1996). This generates a controversy on the function of the shelters. Indeed, it has been observed that some birds (Robinson and Holmes 1982; Heinrich and Collins 1983; Greenberg 1987) and wasps (Steiner 1984; Raveret Richter 1988; Jones et al. 2002) open shelters to attack their occupants (Raveret Ritcher 1988, 2000; Loeffler 1996; Jones et al. 2002), and shelters may be attractive to other predatory arthropods as resting places (Frost 1959; Danthanarayana 1983; Fukui 2001; Lima et al. 2013). So, although shelters may provide protection, they may also be a trade-off because they are easy to detect by predators, as are larval movements during shelter construction, which increases the vulnerability of the inhabitants (Bernays 1997; Jones et al. 2002).

Here we used *Baronia brevicornis* Salvin, 1893 (Papilionidae) to test the function of tubular structures made using the foliage of their host plant. This butterfly comes from the oldest Papilionoidea lineage, which originated approximately 65–75 million years

ago (Hancock 1983; Heikkilä et al. 2012; Regier et al. 2013; Machkour-M'Rabet et al. 2014); it is endemic to Central Mexico and specialized to a local type of tropical dry forest called *Selva Baja Caducifolia* (Soberón and Townsend-Peterson 2005; Legal et al. 2015). In this habitat, species confront temperatures that range from 18°C to 38°C with an average of 24°C (Dorado et al. 2005; Legal et al. 2015). Between May and June, adult *B. brevicornis* emerge from the soil. After mating, females lay eggs on the underside of leaves of the host plant, *Acacia cochliacantha* (Fabaceae). After hatching, caterpillars feed individually and exclusively on the leaves of this plant or, exceptionally, on a closely related species – *Acacia pennatula* (Vázquez and Pérez 1961; Pérez 1967, 1972; Pérez-Espinoza 2001; León-Cortés et al. 2004). They complete their entire larval development on branches of *A. cochliacantha* and each one makes elaborate tubular structures by joining leaves with silk thread (Vázquez and Pérez 1961; Ramírez 2011). *Baronia brevicornis* is one of the few species within the Papilionidae that build tubular structures (Figure 1). These structures are 'simple', knitting together the foliage of their host plant with silk thread (Vázquez and Pérez 1961). They sometimes abandon one tube and build another, or eat the leaf structure when food is scarce (Vázquez and Pérez 1961). At the end of the fifth instar, caterpillars fall to the soil, bury themselves and pupate, emerging as adults at the beginning of the following summer (Vázquez and Pérez 1961; Pérez-Espinoza 2001).

The function of the tubular structures made by *B. brevicornis* is unclear because the caterpillars' high concentration of cyanogenic glycosides (metabolization/excretion strategy) acquired from its host plant may protect them from their natural enemies (Bermudez-Torres et al. 2013; Legal et al. 2015). Regarding their natural enemies, the only known parasitoid on the egg stage is *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae; Legal et al. 2015). *Calosoma sayi* (Carabidae; Legal et al. 2015), *Brochymena* sp. or *Parabrochymena* sp. (Heteroptera: Pentatomidae; Legal et al. 2015) are predators of caterpillars, and *Calosoma angulatum* attacks both larvae and adults (personal observation; Figure 2). Adults of *B. brevicornis* are also attacked by two species of lizards (*Aspidoscelis communis* and *Aspidoscelis deppei*; Chávez-Juárez et al. 2010; Legal et al. 2015); enemies of the chrysalis stage have not yet been documented.
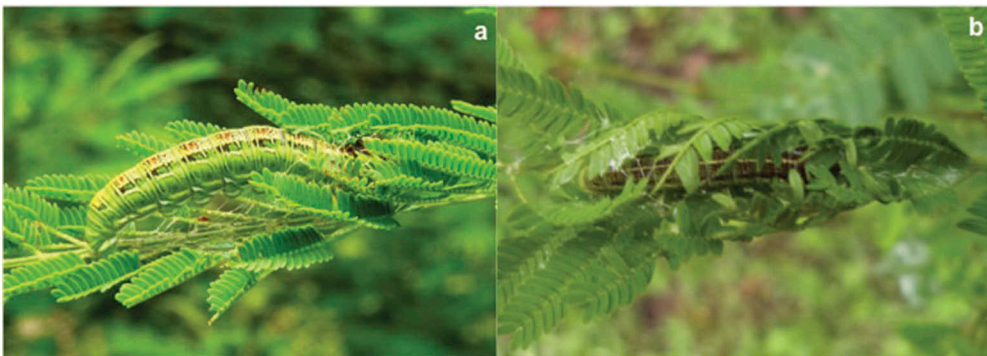
Figure 1. *Baronia brevicornis* caterpillar building a shelter on its host plant *Acacia* cochliacantha (a), and a caterpillar inside a builded shelter (b).

Figure 2. *Calosoma angulatum* eating a prey on an *Acacia cochliacantha* branch.

In this paper, we used *B. brevicornis* caterpillars to test if (1) tubular structures avoid excessive heat and/or (2) tubular structures are costly in that they attract the attention of predators; (3) caterpillars build their tubes after detecting the odour of predators; and (4) caterpillars are less vulnerable to predation when inside their shelters.

Material and methods

Study site and species

The study was conducted in Morelos state, Mexico in June–July 2014 and 2015. The study site is located 6 km from the Biosphere UNESCO Reserve Sierra de Huautla, and is approximately 6600 m^2 of post-agricultural terrain abandoned for 20 years, with *A. cochliacantha* as a predominantly woody species. The zone under conservation corresponds to the upper valley of the Balsas River and mainly consists of tropical dry forest (Miranda and Hernández-X 1963; Rzedowski and Calderón de Rzedowski 1987; Trejo-Vazquez 1999).

Caterpillars (*n* = 215: 196 fifth instar + 19 fourth instar) were collected within their tubular structures and were only pushed out if the experiment required it (see below). Instars were determined based on size and colour (Vázquez and Pérez 1961; Pérez 1967, 1972). Each caterpillar was placed in an individual round plastic container (11 cm in

diameter and 4.5 cm high, with an area of 95 cm^2) with small holes in the top. Containers were cleaned daily and fresh leaves of *A. cochliacantha* were provided each morning as food. Caterpillars remained in captivity until the end of the experiments and were then released in the field. *Calosoma angulatum* (Carabidae), a natural predator of *B. brevicornis*, was used to investigate the importance of predation on tubular structure construction. Caterpillars were not used more than once.

Effect of tubular shelters on predation

A pilot assay was conducted to assure that *C. angulatum* preys on *B. brevicornis* in captivity and we found that this beetle can ingest more than five caterpillars per day. In all tests, the beetles had undergone 72 h of fasting to stimulate their predatory behaviour. A different predator was used for each test.

Experiment 1: does high temperature induce shelter building?

To test this hypothesis, we opened the shelter and exposed the caterpillars to two temperatures. The control group (*n* = 25, fifth-instar caterpillars) was exposed to 25°C (corresponding to the average temperature in July), and the experimental group (*n* = 20, fifth-instar caterpillars) was exposed to a temperature of 40°C (the maximum recorded temperature in the area). We also carried out another experiment to discover how high temperatures (40°C) affect caterpillars inside (*n* = 15, fifth instar) or outside (*n* = 15, fifth instar) the tubular structure. The temperature of each group was kept stable with a heat lamp (OSRAM, 40W/125V), a Bionaire heater (minitower type, model BCH9210) and a digital thermometer (Control Company 4184 S/N 101793497). For all groups, humidity was maintained at a constant 30% with an ultrasonic humidifier (Vitallys, model VUH-3). In each condition, we observed whether the caterpillar built a shelter. If so, we recorded time elapsed from the moment the insect was exposed to the temperature (1) until the time that it finished building the shelter (2). Each assay lasted 8–10 minutes.

Experiment 2: do the shelters of B. brevicornis hide them from their predators or attract the predators' attention?

We tested predators' visual recognition of sheltered and unsheltered caterpillars by using a three-chambered choice arena. The total arena consisted of a plastic container (4.5 cm high, 11 cm in diameter, area of 95 cm^2) divided into three sections: two of the same size (5.5 × 5.5 cm, area of 23 cm^2) and a larger section that contained a predator (11 cm × 5.5 cm, area of 47 cm^2). Each small section was occupied by a caterpillar inside a tubular structure or without leaves and tube. A clear plastic barrier was placed between the caterpillars and the predator, such that they could see, but not access, each other. During 30 assays (employing 60 caterpillars in the fifth instar), the time that the predator spent in front of each of the two sections (sheltered and unsheltered caterpillars) during a 10-minute period was recorded.

Experiment 3: do caterpillars build their shelters after detecting the odour of their predators?

The third test determined if predator odour induced caterpillars to build their tubular structures. Two different plastic containers of the same size were used (4.5 cm high, 11 cm diameter, area of 95 cm^2). In one container, an individual of *C. angulatum* was left for 24 h and then removed (hereafter termed 'predator odour container'). In the other container, no predator had occupied the space (hereafter termed 'control container'). After the predator's odour had been established in one of the containers, we alternately placed 50 caterpillars (19 fourth instars and 31 fifth instars) in the predator odour container or control container for 10 minutes. The following behaviours were observed: immobility, movement (the caterpillar moved its head, ate or moved to a different location), and the construction of shelters. Predator odour is very characteristic, even for observers, and we assume that caterpillars can recognize it.

Experiment 4: are caterpillars less vulnerable to predation when inside their shelters?

The fourth test was conducted to find out if the tubes provided protection for the caterpillars against predation. We carried out this experiment using the same plastic three-section arena as experiment 1, except that there was no physical separation between sections. A caterpillar inside a tubular structure occupied one of the smaller sections, and a caterpillar without a tube or leaves occupied the other. A predator was then introduced into the larger middle section and we recorded which of the two caterpillars was attacked by the predator; this was performed 30 times (60 fifth-instar caterpillars).

Statistical analyses

We used Student's *t*-tests without variance homogeneity. In all cases we confirmed the assumption of normality and variance homogeneity. Mean ± standard error is reported. Given the small sample size in some experiments we used a bootstrap test ($n = 5000$) to know if our results are maintained after increasing the sample size. We also used a Chi-squared test to test significant differences between percentages. All of these analyses were carried out in IBM SPSS Statistics 20.

Results

Does high temperature induce shelter-building?

No caterpillar built a tube in either temperature, 25°C ($n = 25$) versus 40°C ($n = 20$), even though 15% of the caterpillars exposed to 40°C showed signs of damage due to the temperature and one died. We confirmed that tubes were not a barrier against desiccation because we did not record mortality in caterpillars that were inside or outside their tubular structure at 40°C; indeed, at this high temperature, caterpillars that were inside their tubular structure went out instead of remaining inside the tube.

Do shelters of *B. brevicornis* attract the attention of their predators?

There was no significant difference in the amount of time that *C. angulatum* spent in front of the area of the caterpillar without shelter (139.5 ± 38.6; $n = 30$) compared with the caterpillar with a shelter (194 ± 44.6; $n = 30$; $t_{27} = 0.163$, $p = 0.872$).

### Do caterpillars build their shelters after detecting the odour of their predators?

There was a significant difference in the time that caterpillars spent immobile or in movement in the study of *C. angulatum* odour ($t_{49} = 2.2$, $p = 0.026$). They were less mobile (216.4 ± 32.3 seconds) in the control treatment than in the experiment with odour (373.3 ± 32.6; $n = 50$) but tubular structures were not constructed. The bootstrap analysis confirms these results ($n = 5000$; $p = 0.02$).

Are these caterpillars less vulnerable to predation when inside their shelters?

Calosoma angulatum attacked unsheltered caterpillars more often (83%) than those with shelters (16%; $\chi^2 = 26.367$, $p < 0.0001$, $n = 30$; Figure 3), supporting the hypothesis that the function of the tubular structures is to provide protection for the caterpillars against this natural predator.

Discussion

According to our results, tubular structures made by caterpillars of *B. brevicornis* reduce the caterpillars' risk of predation by *C. angulatum*, probably by reducing visual recognition
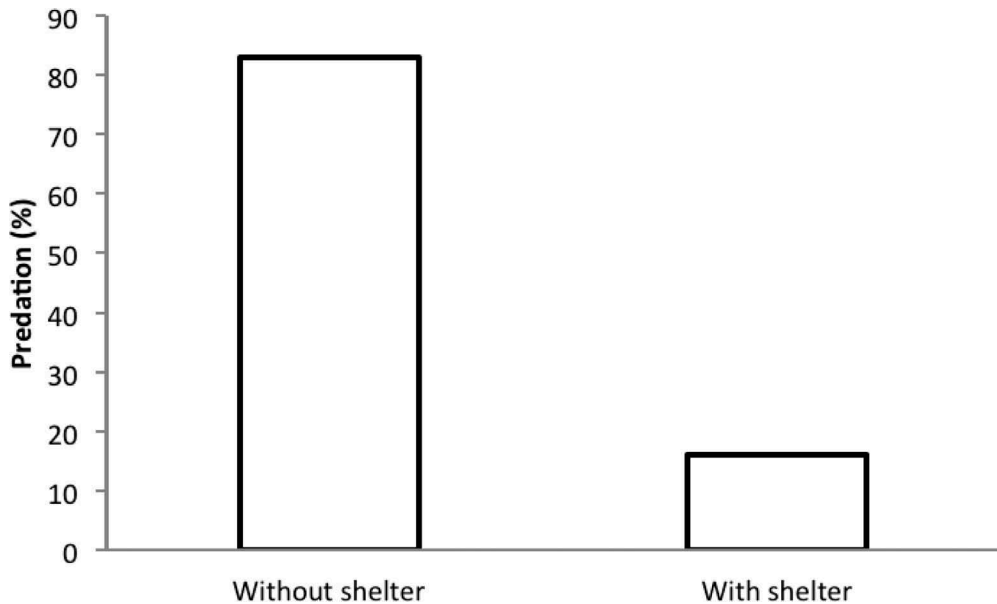
Figure 3. Percentage of predation by *Calosoma angulatum* on *Baronia brevicornis* caterpillars with shelter (16%) or without shelter (83%).

by this natural predator. In addition, our results showed that caterpillars may detect the chemical compounds of *C. angulatum* and possibly move to escape. In addition, we did not find support for the hypotheses that the caterpillars' buildings attract predators or that they made such buildings to confront temperature changes.

In our experiment, extreme heat did not induce shelter-building. More field observations are necessary to discern whether caterpillars build shelters only at certain hours of the day or if the experimental duration of our protocol was long enough to observe it. However, this is unlikely given that high temperatures induce caterpillars to leave the refuge rather than remain inside. In caterpillars, it has been proposed that inside shelters an optimal temperature favours resistance to desiccation (Huey 1982; Diniz et al. 2012), but our results suggest that tube-building behaviour in *B. brevicornis* is not favoured to resist high temperatures.

On the other hand, it has been suggested that shelters attract predators. For example, in *Epargyreus clarus* caterpillars (Pyrginae: Hesperiidae), their shelters are recognized and opened by *Polistes fuscatus* and *Polistes dominulus* wasps (Weiss et al. 2004). This was not the case with *C. angulatum*, a natural predator of *B. brevicornis*. This inability to recognize the shelter could be due to *Calosoma* being present in Mexico for a relatively short time (speaking ecologically), it was first reported in 1917 (Burgess and Collins 1917). So, they may not have been adapted to recognize *B. brevicornis* shelters. On the other hand, the visiual capability of *C. angulatum* may not favour such recognition. It would be interesting to investigate whether the shelters of *B. brevicornis* attract other predators such as stinkbugs, which also predate *B. brevicornis* (Legal et al. 2015). However, adults and larva of *C. angulatum* are among the main predators of *B. brevicornis* found in the field (personal observation in two consecutive seasons, 2014 and 2015), which leads us to propose that the construction of shelters probably has a strong protective effect for *B. brevicornis*.

Caterpillars are able to detect predators such as *Brenthia* caterpillars (Choreutidae). These caterpillars live in web shelters and chew an escape hole into the floor of their nests through which they dart when alarmed. They possess a sensory system with two grossly hypertrophied abdominal setae behind the body that remain intercalated into the silken lattice of the web shelter. With this, the caterpillar is able to monitor both sides of its host leaf simultaneously and avoid predators (Rota and Wagner 2008). In *B. brevicornis* there is no information about how they may detect predators, but our results suggest that chemical signals may be implicated to detect *C. angulatum* odour. Surprisingly, caterpillars increased mobility instead of building tubes, and this quick escape may be less costly and faster than shelter-building. Hence, it is possible that building behaviour is a way to avoid potential predators rather than an immediate escape from them. Building shelters may not be only costly and less effective than escape movements if caterpillars are confronted with predators, but also caterpillars are more attractive and vulnerable during refuge construction (Loader and Damman 1991), and hence, this may increase the risk of predation (Abarca and Boege 2011). Tubular structures may function as shelters to avoid predation rather than favouring a rapid escape.

Most studies about the function of communal shelters have tested the hypothesis of microclimate optimal conditions (for example: Henson 1958; Huey 1982; Joos et al. 1988; Hunter and Willmer 1989; Roessingh 1990; Larsson et al. 1997; Diniz et al. 2012) and most studies of individual shelters have tested the predator-avoidance function (for example:

Scoble 1992; Loeffler 1996; Fukui 2001; Jones et al. 2002; Romero and Benson 2004, 2005; Abarca and Boege 2011; Bächtold and Alves-Silva 2013; Lima et al. 2013), and the cost of predator attraction has also been tested (for example: Raveret Ritcher 1988, 2000; Bernays 1997; Jones et al. 2002). Here we tested all of these hypotheses in a species with individual shelters and our results support the predator-avoidance function hypothesis. We suggest taking into account these three hypotheses in single species with communal shelters to know if the cost of shelter elaboration is related to those species in which shelters provide optimal microclimate conditions. On the other hand, more studies in species with individual shelters may reveal if shelters provide protection against some but not all predators, leading to an arms race between predators and prey.

In conclusion, shelters did not attract *C. angulatum* and caterpillars did not build tubes when confronted with the predators' odour, sheltered caterpillars were attacked significantly less frequently than unsheltered caterpillars when predators were allowed direct access to them. So, shelters apparently provide protection against predators, such as *C. angulatum*. *Baronia brevicornis* builds its tubular structures as a strategy for reducing predation; interestingly their closest species, *Hypermnestra helios* (Parnassiinae) (Michel et al. 2008), does not build shelters but a more derived species, *Papilio glaucus*, does. Given the phylogenetic position of *B. brevicornis*, it is possible that shelter building is an ancestral trait in Papilionidae but has been lost in most derived species or has evolved independently in this clade.

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