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# Defensive Strategies of a Noctuid Caterpillar in a Myrmecophytic Plant: are *Dyops* Larvae Immune to *Azteca* Ants?

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**Abstract**
Immature stages of insects are generally susceptive to their natural enemies, but many species developed defensive and evasive mechanisms to circumvent predation. Gregarious larvae of the noctuid moth *Dyops* cf. *cuprescens* feed on leaves of young *Cecropia pachystachya* shrubs colonized by *Azteca* ants. Ants avoid contact with larval clusters, retreating to the nest when larvae are moving near the stems. Provoked encounters revealed that *Dyops* caterpillars present several specialized behaviors to avoid and overcome ant attacks, such as fleeing to under leaf, jumping off the leaf, curling and wriggling vigorously the anterior portion of the body, spitting droplets of oral fluids, or killing ants by pouncing them. These mechanisms allow the caterpillars to overcome ant attacks and consume leaves of ant-colonized plants. By feeding on a heavily protected plant, larvae can enjoy not only a competitor-free plant, but possibly also the enemy-free space created by the aggressive ants.

## Introduction

As most holometabolous insects, Lepidoptera, one of the most diverse insect orders (Aguiar et al., 2009; Zhang, 2011), split their lives in distinct stages, enabling them to exploit different environments and diets. However, while adults are mobile and can easily escape from predators, lepidopteran larvae (caterpillars) present low mobility and usually feed on foliage, where vulnerability to natural enemies is high (Bernays, 1997). Together with birds, ants are the main predators of lepidopteran larvae (Remmel et al., 2011; Singer et al., 2012; Sendoya & Oliveira, 2017), and adults and larvae both exhibit a large array of strategies to avoid ant encounters (Salazar & Whitman, 2001; Freitas, 1999; Freitas & Oliveira, 1992, 1996; Machado & Freitas, 2001; Gentry & Dyer, 2002; Greeney et al., 2012; Sendoya & Oliveira, 2015, 2017).

Anti-predator strategies may involve gregariousness (Turner & Pitcher, 1986; Lawrence, 1990; McClure & Despland 2011; Greeney et al., 2012), coloration such as camouflage and aposematism (Edmunds, 1974), morphological traits that make an enemy approach physically difficult, such as scoli, spines, and hairs (Frost, 1959), construction of protective shelters using plant tissue and faeces (Eubanks et al., 1997; Freitas, 1999; Freitas & Oliveira 1992, 1996; Machado & Freitas, 2001; Moraes et al., 2012), and the use of oral fluids to build circular barriers (DeVries, 1991).

Gregarious larvae of the moth *Dyops* cf *cuprescens* Hampson (Noctuidae) use several species of Urticaceae as larval hostplant (Wiltshire, 1962, see also Janzen and Hallwachs, 2017, for pictures of early stages and host plant records), including *Cecropia pachystachya* Trécul (present study), a common myrmecophytic plant usually harboring colonies of *Azteca* ants (Formicidae: Dolichoderinae) in their hollow stems (Müller, 1881; Ihering, 1907). *Azteca* ants are known to prevent vines from climbing *Cecropia* trunks (Janzen, 1969; Schupp, 1986; Longino, 1991), and to attack insect herbivores on leaves (Davidson 2005; Oliveira et al., 2015). Therefore, given that encounters between *Dyops* larvae and *Azteca* ants are expected to occur frequently on *Cecropia* foliage, we investigated the following questions: (1) Do *Azteca* ants attack *Dyops* larvae feeding on *Cecropia* leaves? (2) Do *Dyops* larvae present anti-predatory strategies to overcome ant attacks?

## Material and Methods

The noctuid moth *Dyops cf. cuprescens* is a species widely distributed in the Neotropical region, occurring on the dry and humid Central American forests, in the Amazon and in the Atlantic Forest. Their caterpillars are gregarious and were reported using host plants mainly of the family Urticaceae (Wiltshire, 1962; Janzen & Hallwachs, 2017; Discover Life, 2018).

Field observations and experiments were carried out in two areas of lowland dense ombrophilous forest (IBGE, 2012) on coastal São Paulo State, Southeastern Brazil: 1) Most of the study was undertaken at the "Vale do Rio Quilombo" (hereafter VQ), Santos municipality (further information in Francini 2010). Behavioral observations and simulated ant-caterpillar encounters in this site were carried out from April to May 2017. 2). Additional observations were carried out in the "Parque Estadual Xixová-Japui" (XJ), São Vicente municipality, from April to May 1992 (further information in Freitas, 1996).

Encounters between *Dyops* and *Azteca* ants (n = 10) were provoked by gently removing one caterpillar (from 8 to 13 mm) from its cluster (n = 2 clusters) using a tweezer. The larva was then placed on the upper leaf surface of different individuals of *C. pachystachya* colonized by ants, categorized as follows: (1) the same plant where the larva was found (n = 4); (2) a different plant (same size and colonized by *Azteca* ants), not infested by *Dyops* larval clusters (n = 6). Experimental plants were gently shaken before each provoked encounter to incite ant activity on leaves. Ant-caterpillar interactions were recorded using two photographic cameras (Nikon Coolpix L5 and Canon 7D) and two video cameras (Go-Pro Hero 3 and Sony DSC HX300).

## Results

Larvae of *Dyops* were always found in clusters containing 40 to 150 individuals (mean = 87.8, SD = 38.28, n = 7) on mature leaves of *C. pachystachya* (Fig 1A, B). All observed clusters were located on young plants (1 to 2 m tall) colonized by *Azteca* ants in both study sites, VQ (n = 2 clusters) and XJ (n = 5 clusters). In the beginning of our observations, despite the presence of larval clusters, all plants had most of their leaves intact. Ants appeared not to be disturbed by the presence of larval clusters, keeping distance as caterpillars fed and moved freely on foliage. Although larval clusters remained distant from the hollow *Cecropia* stems harboring the ant colonies most of the time, encounters with ants inevitably occurred whenever a cluster moved from one leaf to another. On these occasions, the larval cluster walked through the petiole and plant stem to reach a new leaf (Fig 1B). During these larval movements, ants retreated into the nest gallery and avoided contact with larvae. During the study period in VQ, *Dyops*-induced herbivory caused one *Azteca*-occupied *Cecropia* to have its leaves reduced from 10 to two in two weeks.

A single observation of ant attack to a torn larva was observed, but the ant withdrew to the nest soon after the attack. Behavioral strategies of *Dyops* caterpillars to avoid ant attacks are summarized in Table 1. Nine out of 10 provoked encounters resulted in attacks by the ants (one larva was ignored on a plant hosting a cluster). Evasive behavior was by far the most observed, with larvae moving to under leaf ceasing its movements (n = 6). On two occasions the caterpillars jumped off the leaf upon attack, and suspended themselves on the end of a silken thread (Fig 1C). When attacked by ants (n = 7), *Dyops* caterpillars exhibited a "beat reflex" (n = 3), curling and wriggling vigorously the anterior portion of the body to dislodge or keep ants away, and/or spit oral fluids (n = 4) that effectively repelled the ants (Table 1). Oral fluids are expelled as drops of a transparent liquid that turns dark

**Table 1.** Description of observed behavioral strategies of *Dyops* larvae to avoid attacks by *Azteca* ants on *Cecropia pachystachya* (from 10 provoked encounters). N = total number of observations of each behavior based on the 10 provoked encounters.

| Behavior | Description | N |
|---|---|---|
| Jumping off the leaf | Larva drops off the plant after successive bites or attacks, falling on the soil or on a lower leaf of the same plant, or hanging themselves by silken threads (see below). | 2 |
| Dislodgment | Larva moves to under leaf ceasing its movements; the larva usually is not followed by the ants. | 6 |
| Hanging from a silken thread | The jumping larva can suspend itself by silken threads, eventually climbing back to leaf after a few minutes. | 2 |
| Spiting oral fluids | Attacked larva raises the anterior portion of body and spits droplets of oral fluid towards the ants. | 4 |
| Safety zone | Oral fluid falling on leaf surface forms moist patches that keep ants momentarily away ("safety perimeter"); ants touching these fluids showed several signs of disturbance such as body trembling, lethargy, rubbing the mandibles on leaf surface, and withdrawing stunned. | 3 |
| "Beat reflex" | Curling and wriggling vigorously the anterior portion of the body can intimidate and temporarily keep ants away. | 3 |
| Pounce | Pounce the ant simultaneously releasing oral fluid; ant dies almost instantly. | 2 |

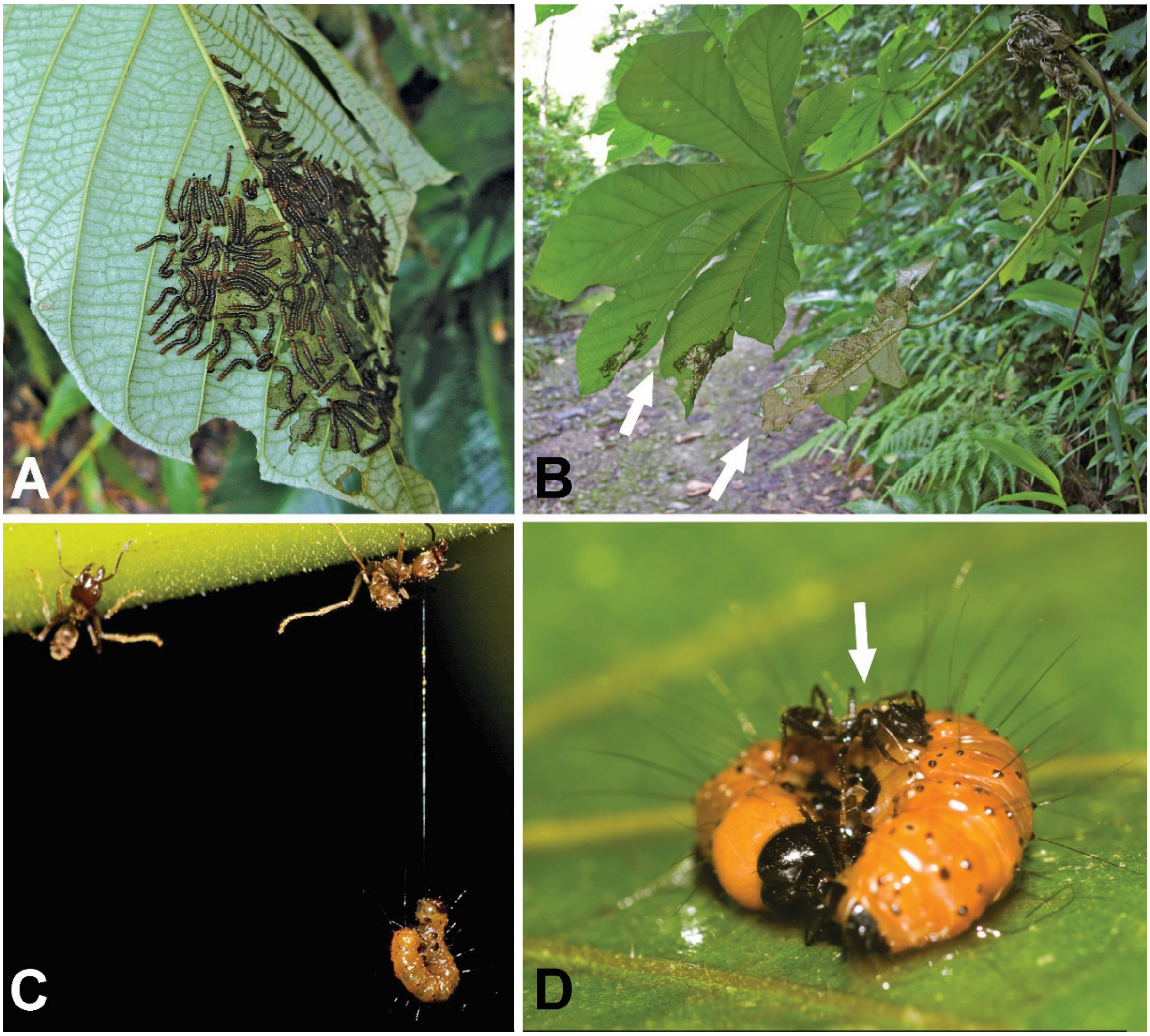


**Fig 1**. A. Cluster of about 150 larvae of *Dyops* cf. *cuprescens*; B. A large larval cluster feeding on a nearly entire leaf (left arrow) after completely consuming a leaf (right arrow); note that a larval cluster must reach the main stem to reach a new leaf; C. A small larva (ca. of 1 cm) suspended by a silken thread after being attacked by ants; D. A medium sized larva (ca. of 3.5 cm) attacked by an ant that died later (white arrow); note the presence of brownish oral fluids beneath the larva.

after some minutes. These oral fluids falling on leaf surface form moist patches that keep ants away for several minutes, in a sort of "safety perimeter" (n = 3). Ants soaked by these oral fluids vigorously cleaned their mandibles, antennae and head, and some of which died after few minutes. Interestingly, ants that attached the caterpillar body ended up dying in few minutes (Fig 1D) after biting them. In addition, two larvae were observed displaying a pounce behavior, simultaneously biting and spitting fluids towards the ant, causing immediate death of the aggressor (see additional data on table 1) (a video clip showing most of the anti-predator behaviors is available at the following link: https://youtu.be/yHYiOQthFKg).

See also a video as supplementary file:
http://periodicos.uefs.br/index.php/sociobiology/rt/suppFiles/2843/0
http://dx.doi.org/10.13102/sociobiology.v65i3.2843.s1892

## Discussion

By living on a plant usually sheltering ant colonies, *Dyops* caterpillars display a series of anti-predator behaviors, as observed in other species feeding on plants where encounters with ants are frequent (Heads & Lawton, 1985; Bentley & Benson, 1988; Freitas & Oliveira, 1992, 1996; Oliveira & Freitas, 2004; Sendoya & Oliveira, 2015, 2017; Bächtold et al., 2012; Moraes et al., 2012). Most of the observed behaviors are common in non-myrmecophilous caterpillars, such as the "beat reflex", biting, and jumping off the plant followed by hanging on a silken thread (Heads & Lawton, 1985; Salazar & Whitman, 2001; Sendoya & Oliveira, 2017). The behavior of spitting droplets of oral fluids against the aggressors is by far the most immediate anti-predation strategy observed in *Dyops* larvae. Regurgitation is a common anti-predation behavior in caterpillars in general (Freitas & Oliveira, 1992; Smedley et al., 1993; Gentry &

Dyer, 2002), and its effectiveness to deter ant attacks has been already tested (Peterson et al., 1987; Rostas & Blassmann, 2009). In addition to the sub lethal effects observed when ants are soaked with oral fluids, *Dyops* larvae also displayed a very specialized pounce behavior that cause immediate death of the aggressors. The observation of dead ants attached to the body of attacked caterpillars suggests that larval fluids can be poisonous to ants (see also Collins, 2013), a defensive strategy that could be enhanced by gregariousness. However, further observations and experiments are needed to determine more precisely if the death of the ants attached to caterpillars' bodies are caused by cuticle fluids, oral secretions, or bites by *Dyops* larvae upon attack. In short, although the present study do not include chemical analysis of the oral fluid of *Dyops*, the results strongly suggests that the oral fluids are not simple regurgitation of gut contents, as observed in other caterpillars and surely present noxious compounds that repel and protect the larvae against ants and other arthropod predators (Peterson et al., 1987; Rostas & Blassmann, 2009).

In addition to the potential improvement of chemically-based ant deterrence, gregariousness is a defensive behavior by itself, where the group size and movement enhance the efficacy of defensive behaviors (Lawrence, 1990; McClure & Despland, 2011; Greeney et al., 2012). In fact, clusters of *Dyops* larvae were observed freely moving through various parts of *C. pachystachya* without being disturbed by ants, which retreat to their nest in the stem galleries when caterpillars approach, or are displaced to patrol plant sectors away from *Dyops* larval clusters. Additional observations in both study sites showed that, except for *Dyops* larvae, all other *Cecropia* herbivores are eliminated from plants after *Azteca* colonization. Interestingly, another species of *Dyops* (*Dyops* cf. *cuprescens* (Walker), was also observed in small *Cecropia* plants colonized by *Azteca* ants in the XJ site. However, larvae of this species are isolated and build shelters by curling the leaf edge under the leaf blade to form a tube (see Greeney & Jones, 2003). Further studies and experiments should be carried out to investigate if this species also present deterrence or other elaborate behaviors to escape from ant attacks.

Our field observations indicate that gregarious larvae of *Dyops* can overcome the aggressiveness of *Azteca* ants inhabiting *C. pachystachya*, making it possible to feed on an ant-defended plant (Janzen, 1969; Schupp, 1986). In addition, by using a protected plant, larvae can enjoy not only a competitor-free plant, but possibly also an enemy-free space created by the aggressive ant inhabitants (see Price et al., 1980; Jeffries & Lawton, 1984; Kaminski et al., 2010; Dáttilo et al., 2016).

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