# Caterpillar Responses to Ant Protectors of Plants

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Sulphur butterfly caterpillar (*Phoebis* sp., Pieridae) on *Senna chapmannii* flower. (Photo by Brittany Harris)

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297

## Introduction

Adult butterflies emerge from their chrysalises to find mates and reproduce; however, during their caterpillar larval stage, time is spent feeding to gain enough mass and energy to form a chrysalis and successfully transform into an adult. During this comparatively sedentary larval stage, caterpillars are vulnerable to predation. Consequently, caterpillars have evolved a host of chemical, morphological, visual, and behavioral traits to defend themselves against diverse predators (Bernays 1997; Dyer 1997; Sugiura 2020).

When consuming plants, caterpillars are exposed to a variety of natural enemies, including predators and parasitoids (Singer et al. 2017; Sendoya and Oliveira 2017). A common defense of caterpillars against many natural enemies includes being poisonous or distasteful by sequestering plants' chemical defenses for their own defense (see Bowers, Chapter "Sequestered Caterpillar Chemical Defenses: From "Disgusting Morsels" to Model Systems"). The iconic monarch butterfly is well-known for feeding on milkweeds, making the caterpillars and adult butterflies distasteful (Brower and Glazier 1975; Calvert et al. 1979); many other Lepidoptera utilize other hostplants in this and other plant families to similar effects. Some of these defenses are carried over to the adult stage, providing defense in more than one phase of the life history.

In addition to the chemicals themselves, many Lepidoptera use aposematic coloration to warn predators that prey are distasteful (Skelhorn et al. 2016a). Other Lepidoptera have irritating hairs or spines to deter predators from consuming them or as a physical barrier to parasitoids' ovipositors (Murphy et al. 2010; Sugiura and Yamazaki 2014; Kageyama and Sugiura 2016) just as trichomes can protect plants from caterpillars (Kariyat et al. 2017).

Some caterpillars use colorful startle tactics, revealing eyespots or other warnings (osmeteria that look like snake tongues with a pungent odor) when harassed (Hossie and Sherratt 2012), and some have color patterns and behaviors that mimic larger predatory animals, a ruse for scaring away some predators. Many hide themselves within their host plant by spinning together plant parts and residing within or cutting leaves and silking them to construct shelters (Ito and Higashi 1991; Diniz et al. 2012; Lill et al. 2007; Marquis et al. 2019; Marquis et al. Chapter "The Impact Of Construct-Building By Caterpillars On Arthropod Colonists In A World Of Climate Change") to escape detection from certain enemies. Of those, some fling their frass (Weiss 2003, Moraes et al. 2012) or even make frass chains (Freitas and Oliveira 1992, 1996) to avoid detection when they climb out on the chains away from the leaf.

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Larval Lepidoptera may pose as inedible objects, a strategy described as masquerade (Skelhorn and Ruxton 2010). Caterpillars of Geometridae may pose as twigs, holding on to branches with their back prolegs and keeping their body erect, at angles with the stem during the day. Others deploy a combination of crypsis with parts they can exert or flash to startle predators when disturbed (Stevens et al. 2008).

Early instars of the giant swallowtail butterfly look like shiny bird droppings on their citrus (Rutaceae) hostplants (Minno and Emmel 1992), while later instars may resemble small snakes (McAuslane 2009). Many tropical Sphingidae caterpillars are also snake mimics, a ruse to scare away predators (Janzen 1980) rather than to attract birds to eat snakes (Castellano and Cermelli 2015); the caterpillars can display behavior that furthers the ruse such as changing their posture (Hossie and Sherratt 2014), advantageous if the predators encounter the same prey repeatedly during their lives (Skelhorn et al. 2016b).

The least studied of the caterpillars may be those that are assumed to be palatable, and cryptically colored, avoiding detection by staying still on the plant surface (Bernays and Cornelius 1989; Dyer 1997; Henrique et al. 2005; Skelhorn and Ruxton 2010; Gaitonde et al. 2018). Animals may escape visual detection by blending into their surroundings, a phenomenon termed "background matching" (Skelhorn and Ruxton 2010; Ruxton et al. 2018). Young caterpillars of many Sphingidae align themselves with the midrib on the abaxial side of the leaf, not feeding during the day, to avoid detection. Many moth caterpillars demonstrate colors and patterns that easily camouflage against plant surfaces, including leaves and bark. Some employ "disruptive coloration" that makes their body harder to detect on patterned surfaces, or compound leaves, making it difficult for predators to grab them (Ruxton et al. 2018).

Birds and ants are considered the main enemies of caterpillars on foliage (Remmel et al. 2011; Singer et al. 2012), though parasitoids may also have a large negative effect (Wanner et al. 2007). Since foliage-dwelling ants detect prey at close range using mostly substrate-borne vibration and/or chemical cues (Cerdá and Dejean 2011; Wüst and Menzel 2017), and parasitoids can locate their prey by detection of kairomones (Rutledge 1996; Dutton et al. 2000; Afsheen et al. 2008; Wölfling and Rostás 2009), visual camouflage in caterpillars likely results from selective pressure exerted by visually hunting insectivorous birds that spot prey from greater distances (Edmunds 1974; Heinrich and Collins 1983).

Ant foraging on vegetation can be an important source of mortality to lepidopteran caterpillars on host plants (Floren et al. 2002). Since caterpillars usually move slowly on foliage, host plant selection by adult butterflies is one of the most important factors affecting caterpillar survival, which can be markedly lower on plants with high levels of ant visitation (Thompson and Pellmyr 1991; Sendoya and Oliveira 2015, 2017). Some butterflies are able to detect the presence of ants and avoid certain host plants in response (Mota and Oliveira 2016). The presence of ant attractants on plants (extrafloral nectaries, food/pearl bodies, fleshy fruits, insect trophobionts) has been demonstrated to induce ant presence on leaves and promote ant-caterpillar antagonism, which can negatively affect infestation levels by lepidopterans in numerous plant species (Koptur 1984, 1992, 2005; Heil and McKey

2003; Oliveira and Freitas 2004; Dutra et al. 2006; Rico-Gray and Oliveira 2007). Recent meta-analyses have concluded that ants attracted to and maintained by plant rewards are beneficial to plants, providing biotic protection in most cases (Chamberlain and Holland 2009; Rosumek et al. 2009).

Despite their pugnacious bodyguards (Bentley 1977), plants with ant attractants are still eaten by herbivores. Most well-known are some caterpillars that themselves secrete honeydew, appeasing the ant defenders to include them in their patrols, and protect them from their parasitoids (Pierce and Mead 1981; Pierce et al. 2002; Pierce & Dankowicz Chapter "Specializations for Ant Association in Caterpillars"), sometimes utilizing plants with extrafloral nectaries as "enemy free space" (Atsatt 1981). Some ant-tended Lycaenidae caterpillars have exocrine secretions that tantalize their ant attendants (Hojo et al. 2015). Caterpillars without such features may avoid ants by dropping from the plant, usually suspended by a silk strand up which they may return later (Sugiura and Yamazaki 2006). Some may even repel the ant guards by working in groups to fight back, such as the gregarious larvae of the noctuid moth *Dyops* on *Cecropia* plants protected by *Azteca* ants in Brazil (Ramos et al. 2018).

## The Study System: Cryptic Caterpillars on Ant-Tended Plants

Many butterflies in the Pieridae family have green caterpillars, or otherwise blend into the color of plant parts on which they feed. Their eggs may be laid singly (e.g., *Phoebis* spp.) or in groups (e.g., *Ascia monuste).* Our experimental studies focused on pierid butterflies that oviposit on *Senna* spp. as hostplants. These butterflies have cryptically colored larvae that occur with a variety of patterns (Minno et al. 2005).

In southern Florida, native and ornamental species of *Senna* serve as host plants for *Phoebis philea*, *P. sennae*, and other Pieridae, including *Abaeis nicippe*. Ants are associated with all *Senna* spp., as these plants provide extrafloral nectar. Native *Senna* spp. associate with more species of native ants than do exotic species, though associations involve more species in urban areas than in natural areas (Koptur et al. 2017). Experimental exclusion of native ants from *Chamaecrista (*syn. *Cassia) fasciculata* in natural areas in northern Florida demonstrated that ants were effective in reducing numbers and damage to the plants by *P. sennae* larvae (Barton 1986); ant exclusion experiments in Iowa revealed that ants were important in reducing damage from another sulphur butterfly, *Pyrisitia (*syn. *Eurema) lisa* (Kelly 1986). In human-disturbed habitats, invasive species are more common than in natural areas, and fire ants, in particular, readily recruit to and occupy space near plants providing food rewards. The protective ability of imported fire ants was dramatically demonstrated by Fleet and Young (2000), who excluded red imported fire ants from *Senna occidentalis* in Texas and found that plants suffered much more herbivory from *P. sennae* and *A. nicippe* caterpillars in their absence, resulting in shorter plants that produced fewer and lighter fruits, and fewer seeds.

Extrafloral nectaries (EFNs) of *Senna mexicana* (Jacq.) H.S. Irwin & Barneby var. *chapmanii* (Isely) H.S. Irwin & Barneby (hereafter referred to as *Senna chapmanii*) attract ants and other predators that provide protection against herbivores (Koptur et al. 2015). When ants are excluded from plants, there are more caterpillars on the plants, and the nectaries attract numerous other predators and parasitoids. Artificial defoliation experiments showed that *S. chapmanii* plants produce more extrafloral nectar (EFN) in response to leaf damage (Jones and Koptur 2015a). Greenhouse experiments showed that plants produce more nectar at higher light intensities (Jones and Koptur 2015b), and field experiments showed that ant protection is most effective in sunny locations, where plants with ants received less herbivore damage, grew larger, and produced more flowers and fruits (Jones et al. 2017). More than eight species of ants have been observed at the foliar nectaries of *S. chapmanii* (Koptur et al. 2015; Jones et al. 2017), with two of the most common being the native Florida carpenter ant (*Camponotus floridanus* Buckley) and the invasive red imported fire ant (*Solenopsis invicta* Buren). Carpenter ants make their nests in fallen wood on soil or decaying wood in standing trees; conversely, fire ants nest in the ground, sometimes even at the base of *S. chapmanii* plants (Koptur et al. 2015). We have observed sulphur caterpillars (*Phoebis* spp.) on plants with both ant species in the field, sometimes being bothered or attacked by ants, other times ignored by the ants (Fig. 1).
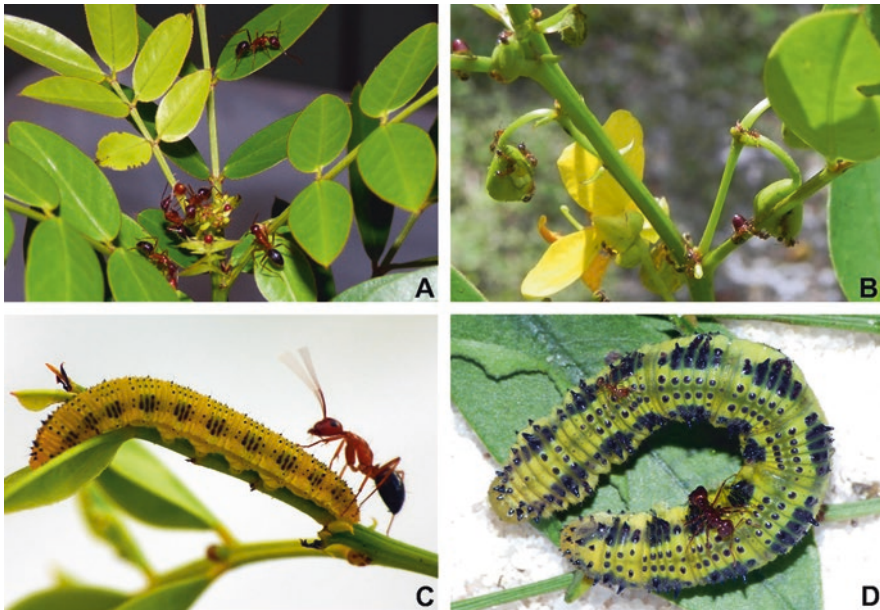


**Fig. 1** Typical interactions between carpenter ants, nectaries, and sulphur butterfly caterpillars. (**a**) *Camponotus floridanus* ants at extrafloral nectaries of *S. chapmanii* in an experimental colony (photo M.C. Pimienta); (**b**) *Solenopsis invicta* at extrafloral nectaries on a field-growing plant (photo I.M. Jones); (**c**) *C. floridanus* worker touching caterpillar with its antennae (photo M.C. Pimienta); (**d**) *S. invicta* workers attacking large sulphur caterpillar (photo M.C. Pimienta)

The efficacy of defense mechanisms by caterpillars may be crucial for their survival chances on ant-visited plants (Bernays 1997; Salazar and Whitman 2001; Sendoya and Oliveira 2017). On the other hand, ant-induced deterrence of caterpillars may also depend on the ant species' weaponry and aggressiveness (e.g., Sendoya et al. 2009). Consequently, ant-derived benefits to EFN-bearing plants may be conditioned by traits on either side of the ant-caterpillar interaction (Koptur 1992; Rico-Gray and Oliveira 2007, and references therein). Here, we sought to compare the interactions between sulphur butterfly caterpillars and the two main ant species visiting *Senna chapmanii* (*Camponotus floridanus* and *Solenopsis invicta*) to better understand the dynamics of the ant-herbivore interactions and gain insight into how so many caterpillars live to pupation on plants in nature.

## Methods

To compare the response of these two ants to the caterpillars, we created captive colonies in the laboratory. In this way, we could control for environmental variables, allowing us to examine the effects of only caterpillar size and ant species in the interactions.

*Senna chapmanii* plants were grown from seeds collected from pine rockland natural areas in south Florida the previous year. Seeds were scarified with a razor blade, soaked overnight, and planted individually in soil-filled germination trays. After seedlings were large enough (and their roots protruded from the bottom of the seedling cell), they were potted up into 4″ pots where they grew for at least 4 months prior to being used in our experiments.

The plastic containers housing the ants were fashioned into mesocosms for the study. Six mesocosms were set up the same way before the ant colonies were introduced: one potted *Zanthoxylum coriaceum* plant was partially buried and centered in the container, two potted *Senna chapmanii* plants were partially buried and equidistant from the central plant, and six sticks were placed around each partially buried, potted plant as a pathway to ascend and descend. Periodically, plants were pruned to avoid touching edges, shelves, and lights above each box (so they would not serve as pathways for ant escapes). Grow-lights were suspended from the ceiling above the mesocosms to keep the plants healthy and to provide semi-natural light. Grow-lights were kept on a 12/12 light schedule.

In the spring of 2016, we collected native carpenter ants (*Camponotus floridanus*, Fig. 1a, c) from woodlands in city parks and gardens in Miami, Florida, by following workers to their nesting site, usually a rotting log lying on the ground surrounded by leaf litter. We collected the suspected colony into a large plastic tub, and in the laboratory opened it up enough to see if it contained a queen. We then put the colony in an open-topped plastic container filled with several inches of sandy loam soil, leaf litter, and pieces of decaying wood. The edges of the plastic container were coated with Fluon® Insect-a-Slip, a slippery surface that prevents ants from

escaping. Three carpenter ant colonies were established and used throughout the duration of experiments.

Invasive red imported fire ants (*Solenopsis invicta*, Fig. 1b, d) were also collected in city parks and gardens in Miami, Florida. Fire ant nests are typically located in open areas with low vegetation and demonstrate a small, slightly raised, oval-shaped mound appearance. Once mounds were detected, a portion of it was dug up and transferred to a 5-gallon bucket. In the lab, fire ants were collected from the substrate by taking advantage of their rafting abilities against floods. A slow-drip technique was applied that inundates the substrate over a period of several days (Banks et al. 1981); afterwards, the floating raft of ants was transferred to a plastic container containing a sandy loam soil, leaf litter, and pieces of decaying wood. As for the carpenter ants, the edges of the plastic container were coated with Fluon® Insect-a-Slip. Three fire ant colonies were established and used throughout the duration of experiments.

Ant colonies were provided test tubes filled with sugar water and plain water using cotton wool to stop the liquids from spilling out. For protein and lipids, ant colonies were provided chunks of hard-boiled eggs and potted meat (Spam) every other day on small plastic dishes, which were cleaned every 2–3 days. Test tubes were replaced and cleaned every 3 days. Prior to experimentation with caterpillars, all food was removed for 2 days, so ants would be more likely to forage for solid food and collect foliar nectar produced by *Senna chapmanii*.

Caterpillars of the cloudless sulphur butterfly (*Phoebis sennae* (L.)) and the orange-barred sulphur butterfly (*P. philea* (L.)) were field-collected in Miami, Florida, and used for experimentation. The two caterpillar species are very similar in appearance and size in their earlier instars, and both occur in many different patterns, and are therefore difficult to distinguish prior to adult emergence. Therefore, we grouped both species together as "sulphur caterpillars." In our experiments we used a variety of patterns, though all the caterpillars we used were green and not yellow (green caterpillars are found eating foliage, yellow ones on flowers).

To measure the ants' responses to caterpillars, a single caterpillar was placed on the distal part of the plant's leaf with a small paintbrush or leaf fragment, observing it until ants discovered it. Ant colonies were randomly selected each day and rotated until approximately equal numbers of caterpillars (small and large, < 1.5 cm vs. > 1.5 cm) were tested against carpenter and fire ants. Small caterpillars represented 2nd instars, while large caterpillars included 4th and 5th instars.

For each trial, the caterpillar was introduced slowly onto the plant using a paintbrush or a leaf fragment. The placed caterpillar was observed for 15 min; if there was no encounter between caterpillar and ant then the trial was terminated, and no other data were recorded that day for that particular ant colony. If an encounter occurred, we recorded the time and observed all subsequent activity for 30 min or until the caterpillar was removed from or left the plant. Time to discovery was measured as the time at which an ant came into direct contact with the caterpillar after the caterpillar had settled on the leaf, irrespective of their behavioral response. The observer then recorded the behavioral responses of ants, categorizing them as ignore, inspect (Fig. 2), attack (Fig. 3), and/or removal from plant. Behavioral
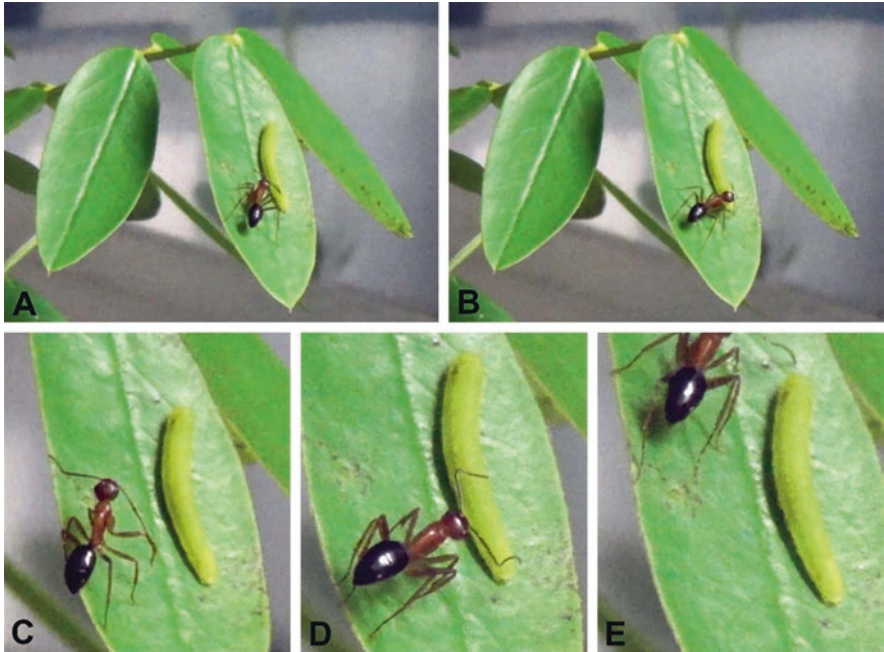
**Fig. 2** Carpenter ant touching then ignoring a sulphur caterpillar (photos J.T. Clayborn): (**a**) ant encounters caterpillar; (**b**) ant investigates with its mouthparts and antennae; (**c**) ant grooming antenna from material picked up from the caterpillar's surface; (**d**) ant investigates further; (**e**) ant departs

responses of caterpillars were also recorded such as twitch, flick, bite, bleed, thrash, or drop from the plant. We recorded time to discovery, time to attack, caterpillar behavior, and caterpillar fate for each trial. We summarized the behavioral interactions between the ants and caterpillars using the following categories:

1. Contact without violence (inspect and ignore/inspect and investigate).
2. Contact with agitation (ant inspects the caterpillar and the caterpillar moves—head flick or head butt)
3. Violence and agitation (ant bites the caterpillar and the caterpillar responds with a head butt or tail flick)
4. Caterpillar regurgitating after ant attack
5. Caterpillar bleeding after attack
6a. Caterpillar drops on silk strand from the leaf
6b. Ants remove and kill the caterpillar

We repeated a smaller number of placement experiments using a caterpillar that does not eat *Senna*, the long-tailed skipper (*Urbanus proteus* (L.); Hesperiidae). The goal was to see if these might be more easily detected than the sulphur caterpillars that normally eat the plants. These butterflies oviposit on butterfly pea (*Centrosema virginiana* (L.) Benth.) as well as on weedy species of *Desmodium* (*D. incanum*

**Fig. 3** Carpenter ant attacking a caterpillar that moved when touched—a fatal flaw (photos J.T. Clayborn). (**a–f**) ant struggling with wriggling caterpillar, biting, wrestling; (**g**) ant attempts to carry caterpillar down plant; (**h**) help is on the way as another ant approaches

(Sw.) DC, *D. tortuosum* (Sw.) DC), and garden beans (*Phaseolus vulgaris* L.). Garden bean plants were the sole food source for the caterpillars used in these experiments. As in the other caterpillar trials, small caterpillars were less than 1.5 cm in length, and the large were greater than 1.5 cm in length.

We compared average time to discovery for each ant/caterpillar size combination using t-tests for independent samples, with Bonferroni probability corrections for multiple t-tests. Time to attack (post-discovery) was also compared using the same statistical tests.

We compared caterpillar fate in the presence of each ant species (proportions alive, dropped, or dead) using contingency table Chi-squared tests. We further explored caterpillar fate (dead or alive) using logistic regression of several variables (time to discovery, time to attack, and number of ants on plants).

We developed flow diagrams summarizing the sequences of behaviors and outcomes observed for caterpillars of each size in the presence of each ant species. These flow diagrams compare the proportions of caterpillars that conformed to each pathway.
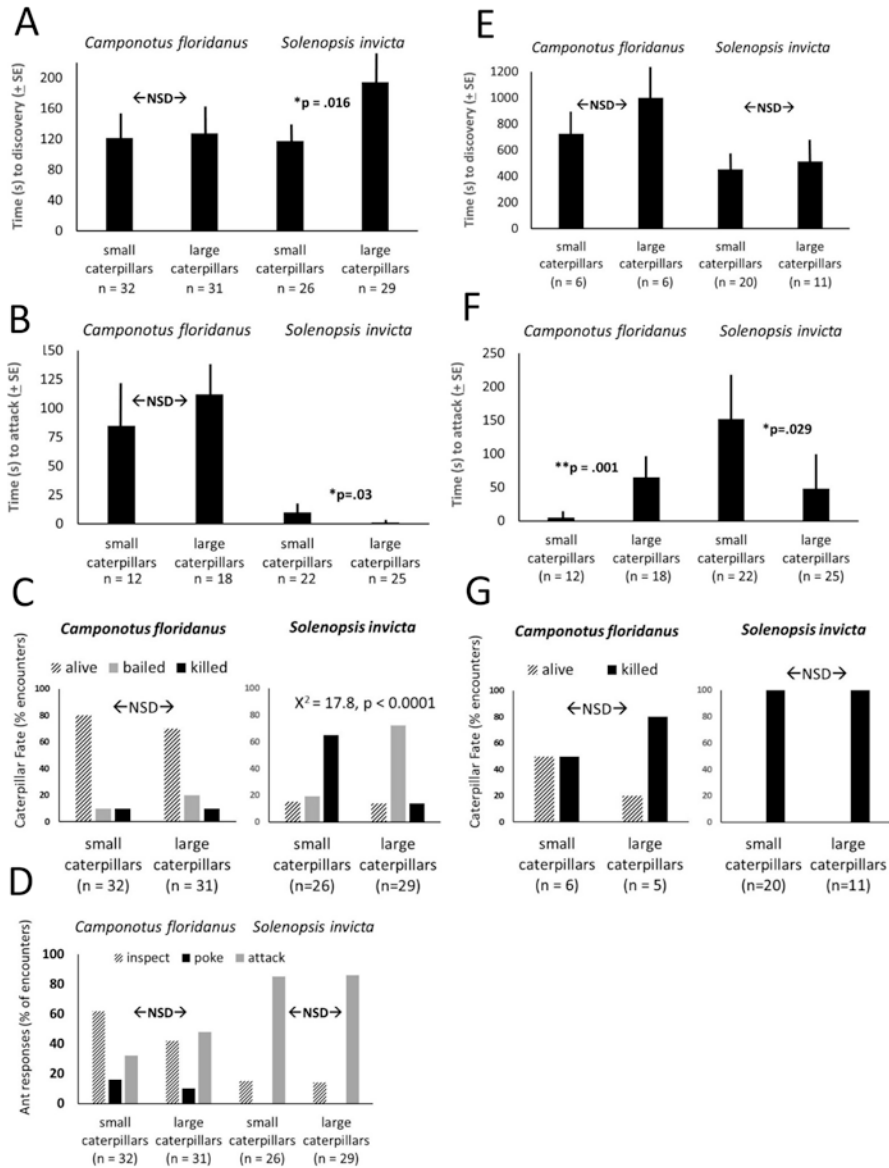
## Results

Many of the trials resulted in no encounters, and those data were not part of the behavioral responses. Of the 94 trials we attempted with carpenter ants, 33% of them were discarded, as the ants never contacted the caterpillars placed on the plant. Of the 63 trials attempted with fire ants, 14% of them were discarded as no shows.

The average time-to-discovery (i.e., the time when ants come into contact with the caterpillar), in those trials where an encounter was observed, showed no significant difference between caterpillar sizes for carpenter ants, but it took fire ants substantially longer to find the large caterpillars than the small ones (Fig. 4a). Time-to-attack (post-discovery) was nearly instantaneous for fire ants (within 5 s), whereas carpenter ants took much longer if they did attack the caterpillar (Fig. 4b). Carpenter ants did not differ in their attacks on small and large caterpillars, but fire ants attacked large caterpillars more quickly than small caterpillars (Fig. 4b). A logistic regression analysis revealed that attack time was the only variable correlated with caterpillar survival (p = 0.037); ants that attacked more quickly were more likely to kill and remove caterpillars from the plants.

The fate of sulphur caterpillars differed markedly between carpenter ant and fire ant encounters (Fig. 4c). In the presence of carpenter ants, more large caterpillars dropped from the plant than did small caterpillars (16% vs. 10%), and a similar proportion of caterpillars of both sizes were killed by the carpenter ants (10%). Most of the caterpillars detected remained alive and in place, with no significant differences in any of these responses between small and large caterpillars. In contrast, few caterpillars remained alive on the plants in the presence of fire ants (4%). As with carpenter ants, larger caterpillars were much more likely to drop off the plant than smaller caterpillars, but this difference was much larger in the presence of fire ants (72% vs. 19%). Most remaining ants that did not drop were killed by the fire ants (14% of the large caterpillars vs. 65% of the small caterpillars). The mortality rate of small sulphur caterpillars was significantly higher than that of large sulphur caterpillars from encounters with fire ants, but similar numbers of both sizes remained on the plants alive (15% and 14%). The ant responses to caterpillars of different sizes differed (Fig. 4d): carpenter ants were more likely to inspect, then poke or touch the caterpillars, and only sometimes attack, whereas fire ants were less likely to inspect before attacking the caterpillars.

Non-*Senna* eating skipper caterpillars placed on plants also sometimes went undetected by both ant species, although rates differed between ants. Half (50%) of these caterpillars were undetected by carpenter ants (n = 26), and 16% were undetected by fire ants (n = 38). The sample sizes of trials with these caterpillars with carpenter ants were therefore small, but we report them here for descriptive comparison.

Though half of the long-tailed skipper (*Urbanus proteus)* caterpillars placed on the plants were not detected by carpenter ants, those that were found took considerably longer to be detected (more than 10 min) than those found by fire ants (less than 5 min on average) (Fig. 4e). Once discovered by carpenter ants, however, the

**Fig. 4** Caterpillar placement experiment results: (**a**) Average time to discovery of small and large sulphur caterpillars (*Phoebis* spp.) placed on *Senna chapmanii* plants in mesocosms by carpenter ants (*Camponotus floridanus)* and fire ants (*Solenopsis invicta*). NSD indicates no significant difference between small and large caterpillars; (**b**) average time to attack of caterpillars, as in A; (**c**) fate of sulphur caterpillars placed on plants; (**d**) response of ants to sulphur caterpillars on encounter; (**e**) average time to discovery by carpenter ants and fire ants of small and large skipper caterpillars (*Urbanus proteus*) placed on *Senna chapmanii* plants in mesocosms; (**f**) average time to attack of caterpillars, as in E; (**g**) fate of skipper caterpillars placed on plants, as in E

caterpillars were attacked in less than 5 s. Fire ants took longer on average to attack a detected skipper caterpillar (Fig. 4f). The fate of skipper caterpillars encountered by fire ants was more dire than that of sulphur caterpillars. Some of them began to silk together leaves, in which they might have evaded detection, but none were observed to silk off or bail from plants. When compared with sulphur caterpillars, more of these skipper caterpillars were removed from the plants by carpenter ants, especially the smaller caterpillars (Fig. 4g), though the small sample sizes precluded statistical comparisons. With fire ants, the fate of every skipper caterpillar encountered was the same; all (small and large) were removed or killed by fire ants (Fig. 4g).

Comparing the sequence of events in the observed interactions reveals some differences in the ants' responses to small and large sulphur caterpillars (Fig. 5). A large proportion of the small caterpillars were ignored after encounter by carpenter ants (Fig. 5a), while those that were discovered were attacked and dispatched (a few dropped from the plant). Carpenter ants recognized most of the large caterpillars, but many of those resisted ant attack and a large proportion of them dropped from the plant (Fig. 5b). Fire ants found nearly all the caterpillars, both small (Fig. 5c) and large (Fig. 5d). Most small caterpillars succumbed to ant attack (Fig. 5c), while a substantial number of the larger caterpillars escaped by dropping from the plant (Fig. 5d).

## Discussion

### *Size Matters*

As in many other experimental studies (Tilman 1978; Smiley 1985, 1986; Koptur 1984; Freitas and Oliveira 1996; Fleet and Young 2000), we found that sulphur caterpillar mortality from ant predation is size-dependent: larger caterpillars were more likely to take evasive action by silking off and dropping from the plant and have higher survival. With carpenter ants, if the sulphur caterpillar did not move, it was not usually detected. It may be that individual caterpillars that hold still in the presence of ants are those likely to survive to larger sizes.

### *All Ants Are Not Created Equal*

Ant species vary widely in size, behavior, and food preferences and exist as a mosaic throughout natural habitats interacting with the plant communities (Bluethgen et al. 2004; Leston 1978; Sendoya and Oliveira 2015). Experiments have revealed that some species are better than others in providing protection for plants (Horvitz and Schemske 1984; Letourneau 1983; Koptur 1984; Rico-Gray and Thien 1989; Mody and Linsenmair 2004; Sendoya and Oliveira 2015, 2017; Melati and Leal 2018).
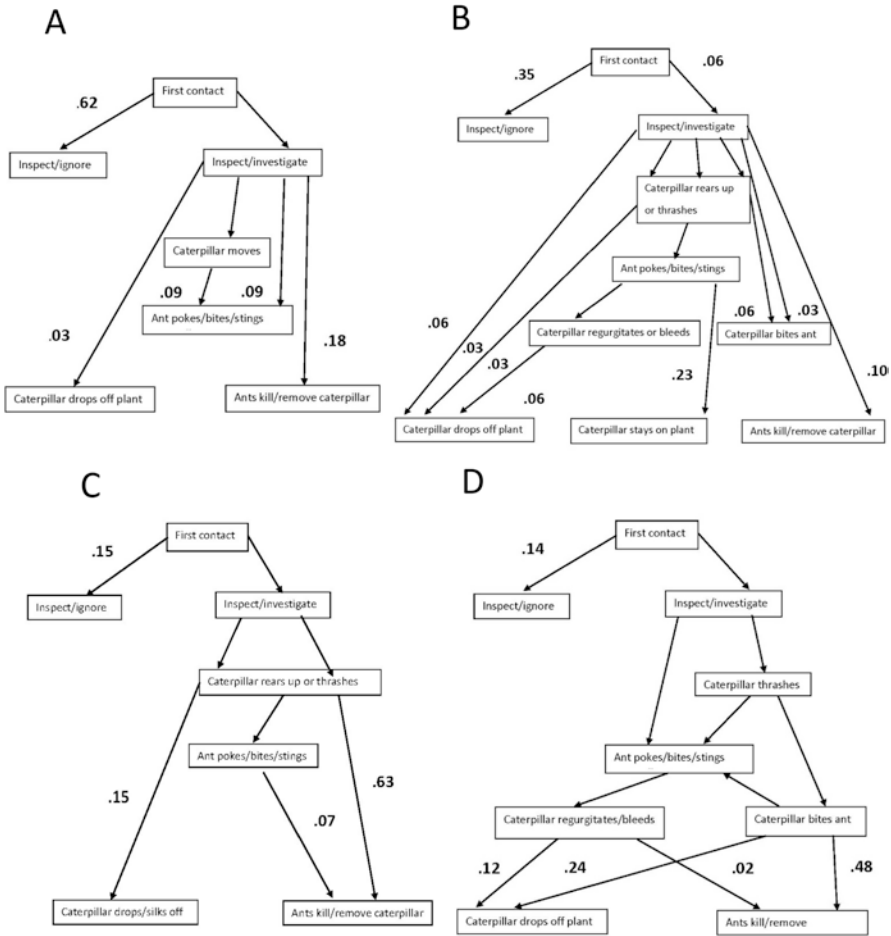
**Fig. 5** Pathways of different ant/caterpillar interactions. (**a**) Carpenter ants and small sulphur caterpillars; (**b**) carpenter ants and large sulphur caterpillars; (**c**) fire ants and small sulphur caterpillars; (**d**) fire ants and large sulphur caterpillars. Numbers on lines are the proportion of interactions that follow that pathway

*Camponotus* spp. respond to both extrafloral nectar and homopteran produced honeydew (Sendoya et al. 2016) and are found more abundantly where those resources are available (Bluethgen and Feldhaar 2010). In the Brazilian cerrado, *Camponotus* spp. are attracted to these liquid plant rewards and are effective plant bodyguards (Del-Claro and Oliveira 2000; Oliveira and Freitas 2004), not only harassing caterpillars but also discouraging oviposition by butterflies (Sendoya et al. 2009). Several species of *Camponotus* associated with *Pseudocedrela* in Cote d'Ivoire differed in their ability to repel herbivores (Mody and Linsenmair 2004), as did those on *Inga* in Costa Rica (Koptur 1984).

*Solenopsis invicta*, an invasive species, can facilitate establishment of invasive plant species by protecting them against herbivores (Ackerman et al. 2014). However, sometimes the most aggressive ant species are not the most beneficial to the plant bearing extrafloral nectaries (Melati and Leal 2018). They may repel pollinators as well as herbivores (Ness 2006), thwarting a plant's reproduction. In addition, they can displace native ants and attack other beneficial insects, such as parasitoids (Ness 2003). Imported fire ants have been recognized as having some benefits in agriculture as their aggressive behavior has the potential to repel and eliminate many pest species (Reagan 1986), including the cotton boll weevil (Jones and Sterling 1979) and the sugarcane borer (Adams et al. 1981), though also potentially harmful to agricultural workers.

Fire ants were quick to find the caterpillars in our experiments, and poked and prodded them until they flinched and were mercilessly attacked with bites and stings. After 2 days with no food supplied, they were ready for more than just nectar, they needed caterpillar meat (the "tenderloin of the insect world," to quote David Wagner). Their ravenous attacks resulted in the dropping off or demise of nearly all the caterpillars in the experiments. In the field, we have occasionally observed these ants eating the seeds from the developing fruits of *Senna chapmanii*, another way in which an overly voracious bodyguard may harm plant fitness.

## *Appearance May Not Matter to Ants, But What Does?*

It is thought that many lepidopteran species use cryptic coloration to evade visual predators, but few studies have explored the possible mechanisms by which such species avoid predation by insects (but see Henrique et al. 2005). Ants, for example, use largely tactile and olfactory senses to discover prey and orient themselves in the environment (Cerdá and Dejean 2011). What appears as visual camouflage may be effective against birds and other visual predators, but not be important to predators using tactile or olfactory cues to detect prey.

*Phoebis sennae* have been described as having "common, aposematic caterpillars" (Quicke 2017) and the US Forest Service states on its website (Cole 2017) that "Both *Senna* and *Cassia* are poisonous, which allows the caterpillars to accumulate a toxic deterrent to would-be predators." These reports are surprising, as we have often observed caterpillars of this species, and of *P. philea*, to be consumed by birds, lizards, spiders, and large wasps during our field studies. In addition, *Senna* is also consumed by humans as a laxative, so it is not very toxic to those primates. Another legume-consuming Pieridae tested for palatability with *Paraponera* ants (*Anteos clorinde*, hostplant *Cassia fruticosa*) was considered neither tasty nor nasty, but neutral (Dyer 1995). As the *Phoebis* spp. caterpillars in our experiments eat a similar legume hostplant, we assume they do not have chemicals in their bodies that make them unpalatable to ants. Indeed, those individuals that dropped into the captive ant colonies in our mesocosms were readily consumed.
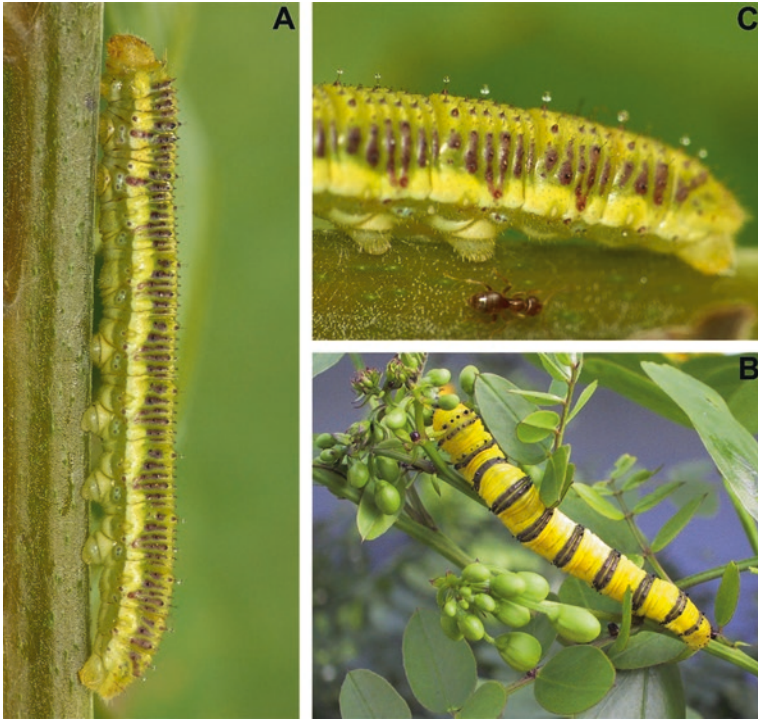
**Fig. 6** Sulphur caterpillars feeding on *Senna* flowers are yellow; here are two of several contrasting pattern morphs. (**a**) Yellow sulphur caterpillar with longitudinal black stripes; tiny droplets are visible along its body (Photo M.C. Pimienta). (**b**) Yellow sulphur caterpillar with black rings around its body in an inflorescence of *S. chapmanii* (photo S. Koptur). (**c**) Closer view of the tiny droplets on the sulphur caterpillar surface (photo M.C. Pimienta)

Given the lack of visual and chemical defenses exhibited by *Phoebis* spp. caterpillars, the question remains: how do so many beat the odds, surviving to maturity in the presence of motivated predatory ants? The answer to this question may lie in the sequestering of host-plant chemicals after all, not for the accrual of distasteful chemicals, but to develop a form of chemical camouflage. Photographers have documented tiny droplets at the ends of setae covering the bodies of *Phoebis* caterpillars (Fig. 6). It is likely that these droplets contain compounds similar to their hostplants, allowing the caterpillars to avoid detection by non-visual predators by blending in with the surrounding foliage. Chemical camouflage has been observed in Ithomiidae caterpillars, whose consumption of their hostplant led to their bodies expressing epicuticular waxes similar to those of the host plant, making them less likely to be found by *Camponotus* ants (Henrique et al. 2005). In our study, the more aggressive nature of the fire ants led them to prod anything they encountered, and once the caterpillars moved, they attacked. With carpenter ants, if the caterpillars remained motionless, the ants walked over them, occasionally grooming their antennae as if they had encountered some substance they needed to clean off, but not

apparently detecting the caterpillars, and not attacking them. Future experiments using freeze-dried caterpillars and hexane extracts of these compounds are planned to determine if this phenomenon is a defense in these caterpillars against some of their ant predators (Henrique et al. 2005). In addition, repeating the present study, but placing the sulphur caterpillars on a non-host plant with extrafloral nectaries and ants, might reveal if the caterpillars can quickly discover caterpillars with cuticular chemicals that do not match the non-host plant.

## Sulphur Butterfly Caterpillars and Ants in a Changing World

Temperature is apparently the most important variable predicting the diversity of ants in a given location (Jenkins et al. 2011), and ant ecologists agree there is much we still need to know about how changes in the warmest parts of the earth, both wet and dry, will be affected by climate change. These parts of the world are currently where the greatest ant diversity exists. The same is true for plant diversity, and species that are not tolerant of warmer temperatures may migrate higher in elevation or further north or south of the equator if connections exist and habitat is available for migration (Feeley 2012; Feeley and Rehm 2012).

Development encroaching on natural areas means less wildlife habitat and fewer native plants available for species that depend upon them. The host plant range of *Phoebis philea* and *P. sennae* butterflies includes a number of genera in the Fabaceae, and they utilize both native and introduced species (Koptur et al. 2017), making them one of the best ambassadors for butterfly gardening in urban areas (Minno and Minno 1999). Areas where people live often have more pest control (spraying for mosquitoes, fleas, ticks, etc.) that can reduce the numbers of butterflies as well as their natural enemies, particularly parasitoid wasps and flies. Depending on the timing of these chemical controls, the numbers of butterflies may increase when parasitoids and predators are suppressed, and at such times the butterflies can be numerous and a beautiful sight on city streets. When the timing is wrong, the urban landscape can be devoid of not only butterflies but other beautiful and beneficial insects, as few insecticides target only problem species.

While *P. sennae* is native to Florida and the southeastern USA., *P. philea* is naturalized to Florida, having become established around 1920 from its native range further south (Minno and Minno 1999). It is likely that as conditions warm up along the east coast of the USA, the range of tolerance of the hostplants will extend further north. Perhaps hostplants that require more tropical conditions may move northward and provide new alternative hosts for these butterflies; but likewise, a wider variety of Fabaceae-consuming Pieridae may also follow northward.

*Camponotus floridanus* is native but abundantly present in areas of human habitation, nesting in dead wood on trees and sometimes in man-made structures. *Solenopsis invicta* is an invasive species, outcompeting many native ants and occurring especially around the edges of many natural areas. They are frequent pests of developed areas, including home gardens and lawns, and people take many

measures to limit their presence as their stings are painful and long-lasting. Wherever the sulphur butterfly caterpillars occur in southern Florida, they are likely to encounter both ant species; as the climate warms, *S. invicta* is spreading across the southern USA and may continue northward over the coming years (Fitzpatrick et al. 2007). Perhaps *C. floridanus* will do the same, as their populations are likely limited by freezing temperatures.

## Conclusion

Caterpillars exhibit a broad spectrum of defensive traits, ranging from aposematic coloration and the sequestering of plant toxins to aggressive flicks and the flashing of osmeteria. Nevertheless, *Phoebis* spp. maintain large populations, seemingly in the absence of any such defenses. It is possible that evasion of ants is due to cuticular chemicals sequestered from their hostplants that function as chemical camouflage to the ants, but this suggestion requires further examination and experimentation.

## References

Ackerman JD, Falcon W, Molinari J, Vega C, Espino I, Cuevas AA (2014) Biotic resistance and invasional meltdown: consequences of acquired interspecific interactions for an invasive orchid, *Spathoglottis plicata* in Puerto Rico. Biol Invasions 16:2435–2447

Adams CT, Summers TE, Lofgren CS, Focks DA, Prewitt JC (1981) Interrelationship of ants and the sugarcane borer *Diatraea saccharalis* in Florida USA sugarcane fields. Environ Entomol 10:415–418

Afsheen S, Wang X, Li R, Zhu CS, Lou YG (2008) Differential attraction of parasitoids in relation to specificity of kairomones from herbivores and their byproducts. Insect Sci 15:381–397

Atsatt PR (1981) Lycaenid butterflies and ants: selection for enemy-free space. Am Nat 118:638–654

Banks WA, Lofgren CS, Jouvenaz DP, Stringer CE, Bishop PM, Williams DF, Wojcik PD, Glancey BM (1981) Techniques for collecting, rearing, and handling imported fire ants. US Department of Agriculture Technician AAT-S-21. 9 p

Barton AM (1986) Spatial variation in the effect of ants on an extrafloral nectary plant. Ecology 67:495–504

Bentley B (1977) Extrafloral nectaries and protection by pugnacious bodyguards. Annu Rev Ecol Syst 88:407–427

Bernays EA (1997) Feeding by lepidopteran larvae is dangerous. Ecol Entomol 22:121–123

Bernays EA, Cornelius ML (1989) Generalist caterpillar prey are more palatable than specialists for the generalist predator *Iridomyrmex humilis*. Oecologia 79:427–430

Bluethgen N, Feldhaar H (2010) Food and shelter: how resources influence ant ecology. In: Lach L, Parr CL, Abbott KL (eds) *Ant ecology*, pp 115–136

Bluethgen N, Stork NE, Fiedler K (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. Oikos 106:344–358

Brower LP, Glazier SC (1975) Localization of heart poisons in the monarch butterfly. Science 188:19–25

Calvert WH, Hedrick LE, Brower LP (1979) Mortality of the monarch butterfly (*Danaus plexippus* L.) due to avian predation at five overwintering sites in Mexico. Science 204:847–851

Castellano S, Cermelli P (2015) Preys' exploitation of predators' fear: when the caterpillar plays the gruffalo. Proc R Soc Biol Sci Ser B 282:20151786

Cerda X, Dejean A (2011) Chapter 3: Predation by ants on arthropods and other animals. In: Polidori C (ed) Predation in the Hymenoptera: an evolutionary perspective, pp 39–78. ISBN: 978-81-7895-530-8

Chamberlain SA, Holland JN (2009) Quantitative synthesis of context dependency in ant-plant protection mutualisms. Ecology 90:2384–2392

Cole E (2017) U.S. Forest Service webpage pollinator of the month – cloudless Sulphur butterfly. https://www.fs.fed.us/wildflowers/pollinators/pollinator-of-the-month/cloudless-sulphur-butterfly.shtml

Del Claro K, Oliveira PS (2000) Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity. Oecologia 124:156–165

Diniz IR, Hay JD, Rico-Gray V, Greeney HF, Morais HC (2012) Shelter-building caterpillars in the cerrado: seasonal variation in relative abundance, parasitism, and the influence of extra-floral nectaries. Arthropod Plant Interact 6:583–589

Dutra HP, Freitas AVL, Oliveira PS (2006) Dual ant attraction in the Neotropical shrub *Urera baccifera* (Urticaceae): the role of ant visitation to pearl bodies and fruits in herbivore deterrence and leaf longevity. Funct Ecol 20:252–260

Dutton A, Mattiacci L, Dorn S (2000) Plant-derived semiochemicals as contact host location stimuli for a parasitoid of leafminers. J Chem Ecol 26(10):2259–2273

Dyer LA (1995) Tasty generalists and nasty specialists? Antipredator mechanisms in tropical lepidopteran larvae. Ecology 76:1483–1496

Dyer LA (1997) Effectiveness of caterpillar defenses against three species of invertebrate predators. J Res Lepidop 34:48–68

Edmunds M (1974) Defence in animals. Longman, Harlow

Feeley KJ (2012) Distributional migrations, expansions, and contractions of tropical plant species as revealed in dated herbarium records. Glob Chang Biol 18:1335–1341

Feeley KJ, Rehm EM (2012) Amazon's vulnerability to climate change heightened by deforestation and man-made dispersal barriers. Glob Chang Biol 18:3606–3614

Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Glob Ecol Biogeogr 16:24–33

Fleet RR, Young BL (2000) Facultative mutualism between imported fire ants (*Solenopsis invicta*) and a legume (*Senna occidentalis*). Southwest Nat 45:289–298

Floren A, Biun A, Linsenmair KE (2002) Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia (Berlin) 131:137–144

Freitas AVL, Oliveira PS (1992) Biology and behavior of the neotropical butterfly *Eunica bechina* (Nymphalidae) with special reference to larval defence against ant predation. J Res Lepidop 31:1–11

Freitas AVL, Oliveira PS (1996) Ants as selective agents on herbivore biology: effects on the behaviour of a non-myrmecophilous butterfly. J Anim Ecol 65:205–210

Gaitonde N, Joshi J, Kunte K (2018) Evolution of ontogenic change in color defenses of swallowtail butterflies. Ecol Evol 8:9751–9763

Heil M, McKey D (2003) Protective ant-plant interactions as model systems in ecological evolutionary research. Annu Rev Ecol Syst 34:425–453

Heinrich B, Collins S (1983) Caterpillar leaf damage, and the game of Hide-and-seek with birds. Ecology 64(3):592–602. https://doi.org/10.2307/1939978

Henrique A, Portugal A, Trigo JR (2005) Similarity of cuticular lipids between a caterpillar and its host plant: a way to make prey undetectable for predatory ants? J Chem Ecol 31:2551–2561

Hojo MK, Pierce NE, Tsuji K (2015) Lycaenid caterpillar secretions manipulate attendant ant behavior. Curr Biol 25:2260–2264

Horvitz CC, Schemske DW (1984) Effects of nectar-harvesting ants and an ant-tended herbivore on seed production of a neotropical herb. Ecology 65(5):1369–1378

Hossie TJ, Sherratt TN (2012) Eyespots interact with body colour to protect caterpillar-like prey from avian predators. Anim Behav 84:167–173

Hossie TJ, Sherratt TN (2014) Does defensive posture increase mimetic fidelity of caterpillars with eyespots to their putative snake models? Curr Zool 60:76–89

Ito F, Higashi S (1991) Variance of ant effects on the different life forms of moth caterpillars. J Anim Ecol 60:327–334

Jenkins CN, Sanders NJ, Andersen AN, Arnan X, Brühl CA, Cerda X, Ellison AM, Fisher BL, Fitzpatrick MC, Gotelli NJ, Gove AD, Guénard B, Lattke JE, Lessard J, McGlynn P, Menke SB, Parr CL, Philpott SM, Vasconcelos HL, Weiser MD, Dunn RR (2011) Global diversity in light of climate change: the case of ants. Divers Distrib 17:652–662

Jones D, Sterling WL (1979) Manipulation of red imported fire ants in a trap crop for boll weevil suppression. Environ Entomol 8:1073–1077

Janzen DH (1980) Two potential coral snake mimics in a tropical deciduous forest. Biotropica 12(1):77–78.

Jones IM, Koptur S (2015a) Dynamic Extrafloral nectar production: the timing of leaf damage affects the defensive response in *Senna mexicana* var. *chapmanii* (Fabaceae). Am J Bot 102:58–66

Jones IM, Koptur S (2015b) Quantity over quality: light intensity, but not red/far-red ratio, affects extrafloral nectar production in *Senna mexicana* var. *chapmanii*. Ecol Evol 5:4108–4114

Jones IM, Koptur S, Gallegos HR, Tardanico JP, Trainer PA, Peña J (2017) Changing light conditions in pine rockland habitats affect the intensity and outcome of ant-plant interactions. Biotropica 49:83–91

Kageyama A, Sugiura S (2016) Caterpillar hairs as an anti-parasitoid defence. Sci Nat 103:86

Kariyat RR, Smith JD, Stephenson AG, De Moraes CM, Mescher MC (2017) Non-glandular trichomes of *Solanum carolinense* deter feeding by *Manduca sexta* caterpillars and cause damage to the gut peritrophic matrix. Proc R Soc Biol Sci Ser B 284:20162323

Kelly CA (1986) Extrafloral nectaries: ants, herbivores and fecundity in *Cassia fasciculata*. Oecologia 69:600–605

Koptur S (1984) Experimental evidence for defense of *Inga* saplings (Mimosoideae) by ants. Ecology 65:1787–1793

Koptur S (1992) Extrafloral nectary-mediated interactions between insects and plants. In: Bernays E (ed) Insect–plant interactions, vol 4. CRC, Boca Raton, pp 81–129

Koptur S (2005) Chapter 3: Nectar as fuel for plant protectors. In: Wäckers FL, van Rijn PCJ, Bruin J (eds) Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press, Cambridge, pp 75–108

Koptur S, Jones IM, Liu H, Diaz-Castelazo C (2017) Playing the system: the impacts of invasive ants and plants on facultative ant-plant interactions. In: Oliveira PS, Koptur S (eds) Ant-plant interactions - impacts of humans on terrestrial ecosystems. Cambridge University Press, Cambridge, pp 249–266

Koptur S, Jones IM, Peña J (2015) The influence of host plant extrafloral nectaries on multitrophic interactions: an experimental investigation. PLoS One 10:e0138157

Leston D (1978) A neotropical ant mosaic. Ann Entomol Soc Am 71:649–653

Letourneau DK (1983) Passive aggression an alternative hypothesis for the *Piper Pheidole* association. Oecologia (Berlin) 60:122–126

Lill JT, Marquis RJ, Walker MA, Peterson L (2007) Ecological consequences of shelter sharing by leaf-tying caterpillars. Entomol Exp Appl 124:45–53

Marquis RJ, Lill JT, Forkner RE, LeCorff J, Landosky JM, Whitfield JB (2019) Declines and resilience of communities of leaf chewing insects on Missouri oaks following spring frost and summer drought. Front Ecol Evol 7:396. https://doi.org/10.3389/fevo.2019.00396

McAuslane HJ (2009) Giant swallowtail, orangedog, *Papilio cresphontes* Cramer (Insecta: Lepidoptera: Papilionidae). EDIS 2009:4. Archival copy, update of EENY-008

Melati BG, Leal LC (2018) Aggressive bodyguards are not always the best: preferential interaction with more aggressive ant species reduces reproductive success of plant bearing extrafloral nectaries. PLoS One 13:e0199764

Minno MC, Butler JF, Hall DW (2005) Florida butterfly caterpillars and their host plants. University of Florida Press, Gainesville

Minno MC, Emmel TC (1992) Larval protective coloration in swallowtails from the Florida Keys (Lepidoptera: Papilionidae). Trop Lepidop Res 3:47–49

Minno MC, Minno M (1999) Florida butterfly gardening. A complete guide to attracting, identifying, and enjoying butterflies of the lower south. University Press of Florida, Gainesville

Mody K, Linsenmair KE (2004) Plant-attracted ants affect arthropod community structure but not necessarily herbivory. Ecol Entomol 29:217–225

Moraes AR, Greeney HF, Oliveira PS, Barbosa EP, Freitas AVL (2012) Morphology and behavior of the early stages of the skipper, *Urbanus esmeraldus*, on *Urera baccifera*, an ant-visited host plant. J Insect Sci 12:52

Mota LL, Oliveira PS (2016) Myrmecophilous butterflies utilize ant–treehopper associations as visual cues for oviposition. Ecol Entomol 41:338–343

Murphy SM, Leahy SM, Williams LS, Lill JT (2010) Stinging spines protect slug caterpillars (Limacodidae) from multiple generalist predators. Behav Ecol 21:153–160

Ness JH (2003) Contrasting exotic *Solenopsis invicta* and native *Forelius pruinosus* ants as mutualists with *Catalpa bignonioides*, a native plant. Ecol Entomol 28:247–251

Ness JH (2006) A mutualism's indirect costs: the most aggressive plant bodyguards also deter pollinators. Oikos 113:506–514

Oliveira PS, Freitas AVL (2004) Ant-plant-herbivore interactions in the neotropical cerrado savanna. Naturwissenschaften 91:557–570

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu Rev Entomol 47:733–771

Pierce NE, Mead PS (1981) Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. Science (Washington D C) 211:1185–1187

Quicke DLJ (2017) Mimicry, crypsis, masquerade and other adaptive resemblances. Wiley Blackwell, Hoboken

Ramos RR, Freitas AVL, Francini RB (2018) Defensive strategies of a noctuid caterpillar in a myrmecophytic plant: are *Dyops* larvae immune to *Azteca* ants? Sociobiology 65(3):397–402

Reagan TE (1986) Beneficial aspects of the imported fire ant: a field ecology approach. In: Lofgren CS, VanderMeer RK (eds) Fire ants and leaf-cutting ants. Westview Press, Boulder, pp 58–71

Remmel T, Davison J, Tammaru T (2011) Quantifying predation on folivorous insect larvae: the perspective of life-history evolution. Biol J Linn Soc 104:1–18

Rico-Gray V, Oliveira PS (2007) The ecology and evolution of ant-plant interactions. The University of Chicago Press, Chicago, 331 pp

Rico-Gray V, Thien LB (1989) Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). Oecologia 81:487–489

Rosumek FB, Silveira FAO, de Neves SF et al (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. Oecologia 160:537–549. https://doi.org/10.1007/s00442-009-1309-x

Rutledge CE (1996) A survey of identified kairomones and synomones used by insect parasitoids to locate and accept their hosts. Chemoecology 7(3):121–131

Ruxton GD, Allen WL, Sherratt TN, Speed MP (2018) Avoiding attack: the evolutionary ecology of crypsis, aposematism, and mimicry, 2nd edn. Oxford University Press, Oxford

Salazar BA, Whitman DW (2001) Defensive tactics of caterpillars against predators and parasitoids. In: Ananthakrishnan TN (ed) Insect and plant defense dynamics. New Hampshire Science Publisher, pp 161–207

Sendoya SF, Blüthgen N, Tamashiro JY, Fernandez F, Oliveira PS (2016) Foliage-dwelling ants in a neotropical savanna: effects of plant and insect exudates on ant communities. Arthropod Plant Interact 10:183–195

Sendoya SF, Freitas AVL, Oliveira PS (2009) Egg-laying butterflies distinguish predaceous ants by sight. Am Nat 174:134–140

Sendoya SF, Oliveira PS (2015) Ant-caterpillar antagonism at the community level: Interhabitat variation of tritrophic interactions in a Neotropical savanna. J Anim Ecol 84:442–452

Sendoya SF, Oliveira PS (2017) Behavioural ecology of defence in a risky environment: caterpillars versus ants in a Neotropical savanna. Ecol Entomol 42:553–564

Singer MS, Clark RE, Lichter-Marck IH, Johnson ER, Mooney KA (2017) Predatory birds and ants partition caterpillar prey by body size and diet breadth. J Anim Ecol 86:1363–1371

Singer MS, Farkas TE, Skorik CM, Mooney KA (2012) Tritrophic interactions at a community level: effects of host plant species quality on bird predation of caterpillars. Am Nat 179:363–374

Skelhorn J, Halpin CG, Rowe C (2016a) Learning about aposematic prey. Behav Ecol 27:955–964

Skelhorn J, Holmes GG, Hossie TJ, Sherratt TN (2016b) Multicomponent deceptive signals reduce the speed at which predators learn that prey are profitable. Behav Ecol 27:141–147

Skelhorn J, Ruxton GD (2010) Predators are less likely to misclassify masquerading prey when their models are present. Biol Lett 6:597–599

Smiley J (1985) *Heliconius* caterpillar mortality during establishment on plants with and without attending ants. Ecology 66:845–849

Smiley J (1986) Ant constancy at *Passiflora* extrafloral nectaries: effects on caterpillar survival. Ecology 67:516–521

Stevens M, Stubbins CL, Hardman CJ (2008) The anti-predator function of 'eyespots' on camouflaged and conspicuous prey. Behav Ecol Sociobiol 62:1787–1793

Sugiura S (2020) Predators as drivers of insect defenses. Entomol Sci 23:316–337

Sugiura S, Yamazaki K (2006) The role of silk threads as lifelines for caterpillars: pattern and significance of lifeline-climbing behaviour. Ecol Entomol 31(1):52–57

Sugiura S, Yamazaki K (2014) Caterpillar hair as a physical barrier against invertebrate predators. Behav Ecol 25:975–983

Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. Annu Rev Entomol 36:65–90

Tilman D (1978) Cherries, ants, and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. Ecology 59:686–692

Trager MD, Bhotika S, Hostetler JA, Andrade GV, Rodriguez-Cabal MA, McKeon CS, Osenberg CW, Bolker BM (2010) Benefits for plants in ant-plant protective mutualisms: a meta-analysis. PLoS One 5(12):e14308. https://doi.org/10.1371/journal.pone.0014308

Wanner H, Gu H, Hattendorf B, Günther D, Dorn S (2007) Tracking parasitoids with the stable isotope [44]CA in agroecosystems. Agric Ecosyst Environ 118:143–148

Weiss MR (2003) Good housekeeping: why do shelter-dwelling caterpillars fling their frass? Ecol Lett 6:361–370

Wölfling M, Rostás M (2009) Parasitoids use chemical footprints to track down caterpillars. Commun Integr Biol 4:353–355

Wüst M, Menzel F (2017) I smell where you walked - how chemical cues influence movement decisions in ants. Oikos 126:149–160