

Eavesdropping on cooperative communication within an ant-butterfly mutualism

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Abstract Signalling is necessary for the maintenance of interspecific mutualisms but is vulnerable to exploitation by eavesdropping. While eavesdropping of intraspecific signals has been studied extensively, such exploitation of interspecific signals has not been widely documented. The juvenile stages of the Australian lycaenid butterfly, *Jalmenus evagoras*, form an obligate association with several species of attendant ants, including *Iridomyrmex mayri*. Ants protect the caterpillars and pupae, and in return are rewarded with nutritious secretions. Female and male adult butterflies use ants as signals for oviposition and mate searching, respectively. Our experiments reveal that two natural enemies of *J. evagoras*, araneid spiders and braconid parasitoid wasps, exploit ant signals as cues for increasing their foraging and oviposition success, respectively. Intriguingly, selection through eavesdropping is unlikely to modify the ant signal.

Keywords *Jalmenus evagoras* · *Iridomyrmex* · Araneidae · Exploitation · Chemical signals · Foraging · Mating costs · Kairomone

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Introduction

Communication is crucial for many interspecific mutualisms, yet theoretical models of mutualism (e.g., Doebeli and Knowlton 1998; Foster and Wenseleers 2006) typically stress fitness benefits for each partner, such as nutritional rewards or protection from enemies, and pay less attention to the signaling systems required to generate or sustain these relationships. Such a perspective is critical because individuals must produce and receive signals to identify and alert individuals to the presence of their mutualistic partners, as well as to modify investment in mutualistic activities. Importantly, while selection will favor an efficient signaling system, the signals maintaining the mutualism may also be subject to exploitation by unintended receivers, because signals have a source, and hence can reveal the location of the signaler as well as provide information intended for the receiver (see also Goodale et al. 2010).

Signal exploitation by eavesdroppers, which include predators, parasitoids, and parasites, has been reported for most sensory modalities and among diverse taxa (Stevens 2013). The majority of studies document specialized eavesdroppers that locate their victims by detecting intraspecific signals involving courtship or social behavior, typically exerting a selection pressure on signal design (e.g., Cade 1975; Tuttle and Ryan 1981; Zuk and Kolluru 1998; Peake et al. 2001; Kim et al. 2009; Brandley et al. 2013; Siemers et al. 2012, but see Beckers and Wagner 2012). Defense against eavesdropping may include changing the timing of signaling (e.g., Lewkiewicz and Zuk 2004), modifying signal intensity (e.g., Endler 1980), changing the signal modality (e.g., Belwood and Morris 1987), employing private signals (e.g., Nakano et al. 2008), or even mimicry (Igic et al. 2015). Interspecific signals are not likely to be any less vulnerable to eavesdropping, but have received less attention (e.g., Ranganathan and Borges 2009; Schatz and Hossaert-McKey

2010; Vergara et al. 2011; Hsieh et al. 2012; Baigrie et al. 2014).

Associations between ants and lycaenid butterfly larvae provide remarkable examples of symbioses (Pierce et al. 2002). In mutualistic contexts, lycaenid caterpillars provide ants with nutrient-rich secretions (Pierce and Nash 1999; Daniels et al. 2005) in exchange for protection against predators and parasites (Pierce and Mead 1981; Pierce et al. 1987; Fiedler et al. 1996). Signaling between ants and lycaenids is required to assemble these relationships: the lycaenid larvae have specialized glands that secrete substances capable of attracting and appeasing ants (Kitching 1983; Agrawal and Fordyce 2000; Axén et al. 1996; Hojo et al. 2008; but see Oliver and Stein 2011), while adult lycaenids may use the volatile intraspecific chemical signals of their ant partners as cues for oviposition (e.g., Pierce and Elgar 1985; Wagner and Kurina 1997; Fraser et al. 2002; but see also Fürst and Nash 2010; Patricelli et al. 2015), thereby increasing the likelihood that eggs and young larvae are discovered by the tending ants.

The Imperial hairstreak, *Jalmenus evagoras* (Donovan), forms an obligate mutualism with its tending ant *Iridomyrmex mayri* (Forel). The ants acquire nutrients from the larvae and pupae, and in return provide essential protection (Pierce et al. 1987). Larvae and pupae aggregate, attracting myriad attending ants, and numerous adult males are attracted to these aggregations as pupae are about to eclose (Elgar and Pierce 1988). The adult butterflies use volatile pheromones from the ants as cues when searching for mates (Elgar and Pierce 1988) or oviposition sites (Pierce and Elgar 1985). Several lines of evidence suggest that predators and parasitoids of *J. evagoras* may similarly use the ants as cues to locate the lycaenid larvae. First, several species of orb-weaving spiders construct webs on food plants infested with the juveniles of *J. evagoras* and their tending ants, often positioning their webs adjacent to the larval and pupal aggregations: opportunistic surveys (over 6 days, with 10–68 webs per survey) reveal that 5 % ($\pm 2\%$) of the observed spiders had recently captured an adult *J. evagoras*. Studies of field populations also reveal higher levels of mortality by *Apanteles* (Braconidae) wasps on larvae that were tended by ants than on those that had attendant ants experimentally excluded (Pierce and Nash 1999).

We investigate whether these spiders and parasitoids eavesdrop on the chemical communication system that maintains the mutualism between *J. evagoras* and its attending ants. Specifically, we ask the following: (1) is the distribution of spider webs, both between and within food plants, associated with the distribution of aggregations of *J. evagoras*; (2) is the persistence of orb-webs on food plants influenced by the presence of ants; and (3) is the searching behavior of *Apanteles* parasitoids influenced by the presence of tending and non-tending ants?

Methods

Spider predators

We observed *J. evagoras* at two sites separated by approximately 10 km: Panton's Gully and Cathedral Rock, both located near the town of Ebor in northeastern NSW, Australia. The butterflies at these sites feed predominantly on *Acacia melanoxylon* (R. Br.), and rarely on *Acacia decurrens* (Willd.) and *Acacia mearnsii* (De Wild.) host plants. All observations made here were with individuals feeding on *A. melanoxylon*. At least three species of orb-weaving spiders are commonly found on the *Acacia* host plants of the butterflies. These spiders include *Plebs eburnus* (Keyserling), “*Cyclosa*” *fuliginata* (Koch), and another unidentified species, probably closely related to “*C.*” *fuliginata*. Since we were unable to distinguish confidently between the species while in the field, we incorporated all of the spiders into a single category.

Site surveys

In each site, we located and tagged an individual plant (average height 1.4 m, range 0.7–2.2 m) that was host to juvenile stages of *J. evagoras*, and then located another host plant (typically less than 10 m away) that was matched for height but was not host to *J. evagoras*. We located 18 pairs of plants at Cathedral Rock, and 15 pairs of plants at Panton's Gully. We censused each plant, recording the number of larvae and pupae of *J. evagoras*, the total number of orb-weaving spider webs, and the body length of the resident spider. Webs were included in our census only if they contained a resident spider.

Additionally, we noted the number of webs that were located within 50 cm of each cluster of larvae and pupae of *J. evagoras* on six large (>3 m in height) host plants. A “cluster” contained a minimum of three pupae and/or larvae of *J. evagoras* that were within 5 cm of each other, and we identified 74 clusters (range 7–20 clusters per plant). We then selected, at the same height on the same plant, a random location by dividing the plane (horizontal) view of the plant into eight sectors, randomly selecting a sector (by choosing a numbered piece of paper from a hat), and then locating that sector on the plant. We recorded the number of spider webs located within 50 cm of that location.

Field experiment

We selected 36 host plants, which had not been previously censused and were >3 m apart that contained juvenile stages of *J. evagoras*, and recorded the plant height and number of larvae and pupae. We then designated pairs of plants that were matched for both size and number of juveniles. For each pair of host plants, we designated one as the control and the other

as the experimental. We wrapped a band of plastic marking tape around the base of each plant and cut away any vegetation that touched the plant. We then removed all of the ants found on the experimental plant and prevented ants from regaining access to the plant by smearing BirdOff™ onto the plastic band at the base of the plant. We collected all of the spiders ($N = 108$) from these plants and marked each spider with a dot of acrylic paint applied to the cephalothorax. In the late afternoon, we released three spiders onto each of the 36 plants, ensuring that no spider was released back onto the same plant from which it had been collected. We subsequently recorded the presence of painted (resident) and unpainted (immigrant) spiders on each plant three times over the next 6 days. Missing larvae or pupae were replaced to ensure that all host plants had juvenile stages of *J. evagoras*.

Wasp parasitoids

Laboratory experiment

Ten *Apanteles* parasitoids were obtained from caterpillars of *J. evagoras* collected from Stanthorpe, Queensland. These wasps produce distinctive silk pupal cocoons under the body of the fourth instar larvae from which they emerge, and it was these cocoons that were collected. After eclosion (which usually happened in the late afternoon or evening), each adult parasitoid was kept in a small plastic container with ad libitum water and 10 % honey solution. Parasitoids were introduced into a circular choice chamber provided with three arms: one contained a worker of *Iridomyrmex mayri*, the second held two workers of *I. rufoniger* (Lowne) (*I. rufoniger* is approximately half the mass of *I. mayri*) and the third contained no ants (Fig. 1). Air was drawn through each of the arms to the

centre of the choice chamber by a hose leading to a low flow rate pump.

The chamber was marked into six equal sized sectors, reflecting the content of the arms (Fig. 1). The chamber was illuminated from above by a ring light, which minimized any directional biases due to light intensity. Each wasp was placed, as far as possible, into the center of the choice chamber and allowed to equilibrate for 5 min. The sector that it occupied, together with its activity (walking, resting, or grooming), was then recorded at 20-s intervals for 30 min. The positions of the ant species involved were changed systematically between each test. Wasps were tested once a day from the day after they eclosed for 3 days or until they died, whichever was longer. The data for each wasp was then combined across trials to avoid pseudo-replication. Five wasps were tested, two of which died on the day of first testing and one on the second day of testing. Five additional wasps failed to eclose or died within 12 h of eclosion and were not tested. Sexing of the wasps was not possible, and all were kept in isolation after eclosion, so that mating was prevented.

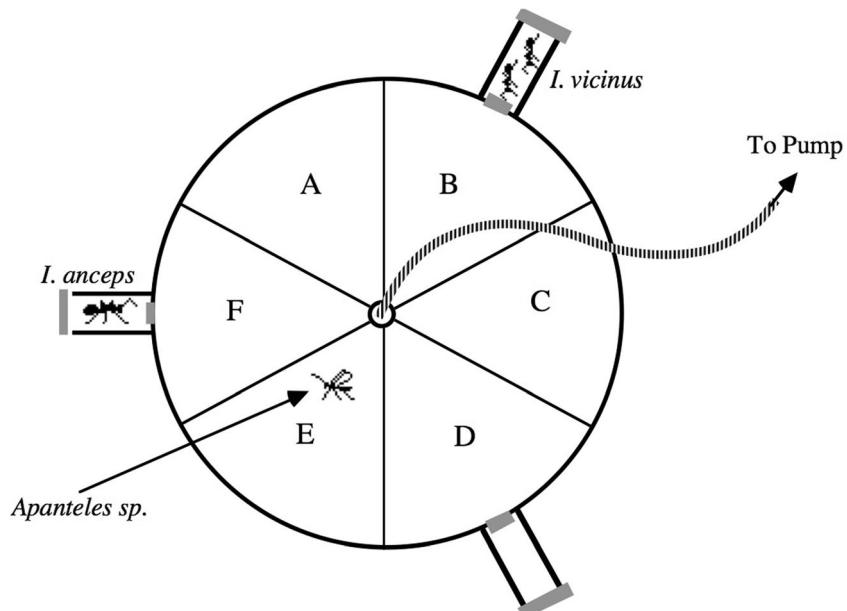
The attractiveness of the two ant species was compared by examining the proportion of the total amount of time the wasp spent walking in each sector relative to the positions of the different ant species. Resting or grooming was deemed to be not associated with host-searching behavior.

Analysis

Spiders

We used ANOVA to examine the natural variation in the number (log transformed) and size of spiders per plant, with population, height of plant, and either presence/absence or total

Fig. 1 Experimental arrangement to test for ant-dependent oviposition by the *Apanteles* parasitoid. The different sectors of the arena are labeled according to the olfactory cues provided: M = *Iridomyrmex mayri* (host ant), R = *Iridomyrmex rufoniger* (non-host ant), and E = empty. Intermediate sectors are labeled accordingly (e.g., R-E = Between *I. rufoniger* and the empty arm). The arena, worker ants and the parasitoid wasp are shown approximately to scale



number of juvenile stages (larvae and pupae) as fixed effects. Nonsignificant ($P > 0.1$) interaction terms were sequentially removed, and we report the reduced model. A mixed-effects model was used to investigate spatial variation in spider numbers (log transformed), with location (aggregation or random location) as a fixed effect and plant identity as a random effect, with the variance partitioned using restricted maximum likelihood (REML). For the field experiment, we used repeated measures ANOVA to examine the variation in spider numbers, with treatment (control or ants removed) and the initial number of larvae and pupae as fixed effects, and sampling time (1, 3, and 6 days from the start of the experiment) as the repeated measure. Reported values are untransformed means \pm SE.

Parasitoids

We used a Friedman test to examine whether the parasitoid spent different relative amounts of time in each of the sectors, given that the variances were not homogenous.

Results

Spider predators

Larger numbers of spiders were found on *Acacia* plants with juvenile stages of *J. evagoras* (ANOVA: $F_{1,61} = 13.38$, $P = 0.0005$; Fig. 2) and on taller plants ($F_{1,61} = 4.96$, $\beta = 0.43 \pm 0.19$, $P = 0.03$). There were no between-site differences in the number of spiders on *Acacia* plants ($F_{1,61} = 0.508$, $P = 0.48$). Among host plants that were infested with *J. evagoras*, the number of spiders also increased

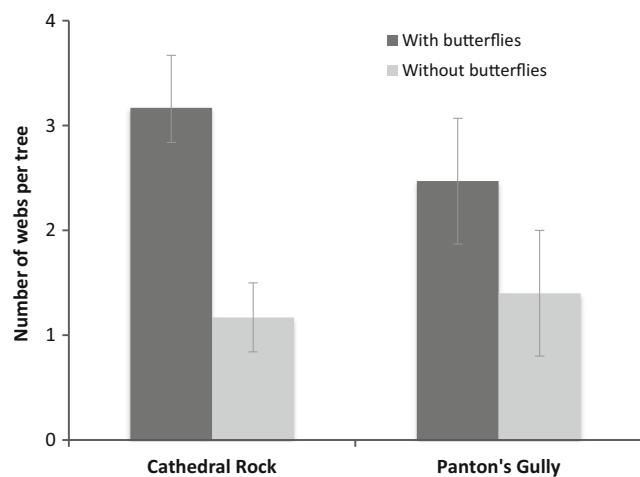


Fig. 2 The number of orb-weaving spiders on *Acacia* when the juvenile stages of *J. evagoras* were or were not present on the plants. The number of spiders was significantly higher on plants with juveniles of *J. evagoras*, but there was no significant between site differences or site by presence interaction term (see text for details)

with increasing numbers of larvae and pupae ($F_{1,32} = 8.53$, $r^2 = 0.22$, $\beta = 0.02 \pm 0.01$, $P = 0.006$). The average size of the spiders in the webs was not related to the height of the plant (ANOVA: $F_{1,49} = 0.077$, $P = 0.78$) or the presence of juveniles of *J. evagoras* ($F_{1,49} = 0.001$, $P = 0.98$), although the spiders at Cathedral Rock tended to be larger (7.4 ± 0.7 mm) than those at Panton's Gully (5.8 ± 0.6 ; $F_{1,49} = 4.07$, $P = 0.08$).

The spiders not only preferred plants with juveniles of *J. evagoras* and their attendant ants but also preferred to place their orb-webs near aggregations of the larvae and pupae. The mean number of spiders surrounding aggregations of the larvae and pupae of *J. evagoras* (1.5 ± 0.20 , $N = 74$) was significantly greater than the number found in a random position at an equivalent height on the same plant (0.3 ± 0.05 ; ANOVA (REML): $F_{1,143} = 39.47$, $P < 0.001$). These aggregations of *J. evagoras* comprised, on average, 6.8 ± 0.7 juveniles (2.5 ± 0.4 larvae and 4.3 ± 0.4 pupae). Several of the randomly selected locations on the plant were also adjacent to aggregations of *J. evagoras* and, when considering only these data, the presence of spiders was strongly associated with proximity to an aggregation: random locations were more likely to have spiders if they were adjacent to an aggregation (94 %, $N = 17$) than if not (9 %, $N = 57$; test for independence: $\chi^2 = 40.9$, $P < 0.001$).

The ant exclusion experiment revealed that the presence of ants alone influenced where the orb-weaving spiders located their webs (Fig. 3). More spiders were found on plants with ants compared with plants without ants (ANOVA: $F_{1,32} = 8.248$, $P = 0.007$), but the number was not associated with the initial number of larvae and pupae located on the plant ($F_{1,32} = 0.001$, $P = 0.98$). The number of spiders on the plants varied significantly between sampling times ($F_{2,31} = 4.778$, $P = 0.016$).

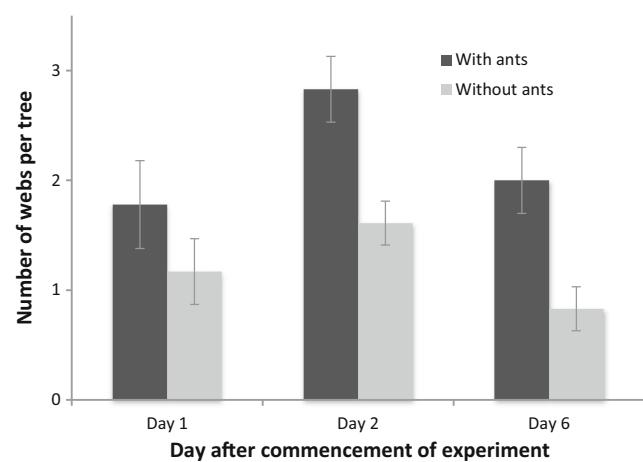


Fig. 3 The number of spiders on *Acacia melanoxyylon* plants in the presence and absence of ants. The number of spiders was significantly higher on plants with juveniles of *J. evagoras*, and also varied across the three sampling times, but there was no significant time by treatment interaction

Wasp parasitoids

The *Apanteles* parasitoids spent roughly 15 % of the time stationary, 45 % of the time grooming, and 40 % of the time walking. There was significant variation across the sectors in the proportion of time walking (Friedman test: $Q = 11.07$, $P = 0.046$) with the most time spent in the sector containing *I. mayri*, and the least in the sector with *I. rufoniger* (Fig. 4).

Discussion

This study provides several lines of evidence that orb-web spiders and braconid parasitoids exploit ant-derived chemical signals used to maintain a mutualistic association between the ants and the larvae of a lycaenid butterfly. The choice-chamber experiments revealed that *Apanteles* sp., a braconid parasitoid of *J. evagoras*, was attracted to the ant *I. mayri*, which tends *J. evagoras* where it was collected, and apparently repulsed by *I. rufoniger*, which tends *J. daemeli* and not *J. evagoras* in the area from which they were collected. These parasitic wasps emerge exclusively from ant-tended larvae in the field (Pierce et al. 1987; Pierce and Nash 1999). The orb-weaving spiders, which capture adult *J. evagoras*, increase their foraging success by using the chemical volatiles released by *I. mayri* to build their webs in areas where there is increased adult flight activity: the ant exclusion experiments demonstrated that spiders were more likely to settle (and remain)

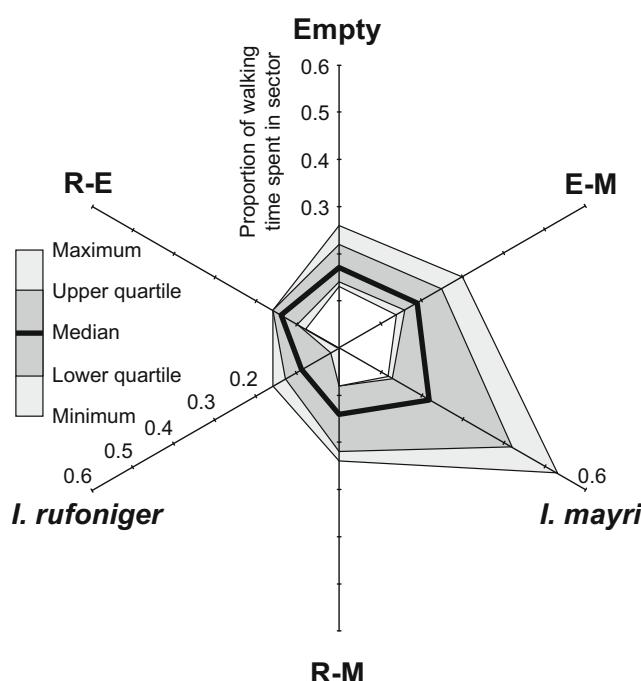


Fig. 4 The proportion of time spent by the *Apanteles* parasitoid in the different sectors. See Fig. 1 for an explanation of the labeling of sectors. The parasitoid spent more time in the sector with the butterfly tending ant *I. mayri* than the non-tending ant *I. rufoniger*

on *A. melanoxyton* plants with ants than on plants without ants, and field observations revealed that the abundance of spider webs on plants was positively correlated with the number of larvae and pupae of *J. evagoras* and thus with the number of tending ants (see Pierce et al. 1987; Axén and Pierce 1998). Finally, these spiders located their webs adjacent to aggregations of *J. evagoras* and their attendant ants, which are frequently visited by flying adults.

These data reveal an intriguing and novel example of an eavesdropping predator that improves its foraging success by exploiting the communication channels that maintain an interspecific mutualism. Adult females and males of *J. evagoras* use olfactory signals from their mutualistic partner ants for oviposition (Pierce and Elgar 1985; Fraser et al. 2002) and mate search (Elgar and Pierce 1988), respectively, apparently using the volatile signals for long- and medium distance orientation. Typically, females spend more time fluttering around plants with ants, eventually alighting on them to oviposit, sometimes near aggregations of pupae and larvae. Males similarly pay more attention to plants with ants, as they search for imminently eclosing adults, typically alighting on or adjacent to solitary or aggregating pupae. These pupal aggregations can attract large numbers of males (Elgar and Pierce 1988). The spiders increase their foraging success by using the volatile chemical odors of the ants to locate their webs in plants with considerable ant activity, corresponding with areas with substantial adult *J. evagoras* flight activity. Thus, the interspecific signals that are crucial for the reproductive success of the adults are the same as those used by their spider predators. Given the proximity of the spider webs to larval and pupal aggregations, it seems that males are the more likely victims of spider predation, although we have insufficient data to confirm this.

Our data support the hypothesis that braconid wasps *Apanteles* sp. use the tending ant species as a host-finding cue. Thus, parasitism of the juvenile stages by highly specialized parasitoid wasps can represent a true cost to the association between larvae of *J. evagoras* and workers of *I. mayri*. Nevertheless, adult females of *J. evagoras* use workers of *I. mayri* as cues in oviposition (Pierce and Elgar 1985), and all exclusion experiments involving the juvenile stages of *J. evagoras* indicate that the magnitude of this cost to adults is apparently small compared with the benefits to the juvenile stages of protection by ants from other parasitoids and predators (Pierce et al. 2002). Eavesdropping on host signals by parasitoids is widely reported (e.g., Rutledge 1996; Fatouros et al. 2008), but these signals are typically intraspecific, revealing the location of mates and/or aggregations. This novel example of eavesdropping on an interspecific signal between mutualistic partners has been implicated in parasitoid host-finding and contrasts with other studies on parasitism of ant-associated lycaenids. Two other parasitoids, an egg parasitoid (Family Trichogrammatidae) and a pupal parasitoid (Family

Chalcidae) attack *J. evagoras* whether the ants are present or experimentally excluded, but both cause much greater mortality in their absence (mortality with ants excluded vs ants present: 48 vs 11 % and 10 vs 2 %, respectively; Pierce and Nash 1999). The same pattern occurs in several parasitoid species that attack facultatively ant-associated lycaenids, including *Glauopsyche lygdamus* (Pierce and Mead 1981), *Drupadietheda*, *D. ravindra*, *Cheritra freja* (Seufert and Fiedler 1996), and *Hemiarthus isola* (Weeks 2003). The only other case so far reported where ants are used by a parasitoid of a myrmecophilous lycaenid is *Ichneumon eumerus*, which attacks caterpillars of the parasitic lycaenid butterfly *Maculinea alcon* (=rebeli) inside the nests of its host *Myrmica* ants. This species can distinguish between the odors produced by the host ants and non-host *Myrmica* ants in the initial stage of host-finding, but uses additional cues produced by the caterpillars after entering the *Myrmica* nests to oviposit (Thomas and Elmes 1993). Intriguingly, newly emerged parasitoid wasps of several species from the braconid subfamily Microgastrinae (which includes *Apanteles*) readily find and feed on the dorsal nectary organ of their lycaenid butterfly hosts (Schurian et al. 1993), although this appears to be related to nutrition rather than using the ant-directed signals produced by this gland.

The role of olfactory cues for spider foraging is not widely appreciated. The myrmecophile zodarid spider *Habronestes bradleyi* uses the alarm pheromone of its *Iridomyrmex purpureus* ant prey as a foraging cue (Allan et al. 1996), and there is increasing evidence that other myrmecophilous spiders can similarly detect volatile odors from ants (*Zodarion rubidum* (Zodaridae), Cardenas et al. 2012; *Phintella piantensis* (Salticidae) and *Scytodes* sp. (Scytodidae), Nelson and Jackson 2014, *Habrocestum pulex* (Salticidae), Clark et al. 2000). Western black widow spiders (*Latrodectus hesperus*) are more likely to locate their webs in microhabitats previously inhabited by their prey (Johnson et al. 2011), while lycosid spiders *Pardosa milvina* and *Trochosa ruricola* avoid microhabitats previously inhabited by a common predator (Schonewolf et al. 2006; see also Mestre et al. 2014)). The legs of both juvenile and adult male and female orb-weaving spiders are covered in sensilla that function in mechano-chemical cue reception (Foelix 2010). Adult males locate females via the volatile sex pheromones produced by sexually receptive females (Gaskett 2007), and also use silk-bound chemicals to further distinguish between females of different populations (Henneken et al. 2016) and mating status (e.g., Gaskett et al. 2004). Which pheromones of *I. mayri* the spiders use are unknown, but these data raise the intriguing possibility that web site selection in orb-weaving spiders can be mediated by olfactory cues, including prey odors (see also Johnson et al. 2011).

Once the spiders have arrived on a tree inhabited by ants and lycaenid butterflies, they may utilize more local cues to locate their webs adjacent to the larval aggregations and/or

pupal clusters. Vibratory cues are likely candidates for the spiders at this close range. While chemical signals play a primary role in mediating lycaenid/ant interactions, lycaenids and ants also communicate via substrate borne stridulation (e.g., Devries 1990; Travassos and Pierce 2000; Barbero et al. 2009). The larvae and pupae of *J. evagoras* generate vibrational signals that are important in attracting and maintaining an ant guard, suggesting that these substrate-borne vibrations form part of the cooperative communication system. Given the sensitivity of orb-web spiders to vibrations, it seems likely that the spiders can detect these stridulations and respond accordingly. In particular, they may be particularly sensitive to the vibrations of pupae, ensuring that their webs are located near the flight paths of both males and females.

Avoiding being attacked by the myriad numbers of ant workers that tend the larvae and pupae of *J. evagoras* and patrol the surrounding areas is a significant issue for the spiders. One potential line of defense for the spiders is to remain on the web: Zhang et al. (2012) discovered that the surface of the silk of the golden orb-weaver *Nephila antipodiana* contains a pyrrolidine alkaloid, 2-pyrrolidinone, which acts as a repellent to workers of three species of myrmecine ants (*Monomorium pharaonis*, *Pheidole angulicollis*, and an unidentified species of *Monomorium*). The presence of this chemical on the silk of orb-web spiders is taxonomically widespread (e.g., Henneken et al. 2016; Daiqin Li, personal communication) and appears to repel the workers of species from other subfamilies, including smaller, unidentified species of *Iridomyrmex* (MA Elgar, personal observation). Of course, the spider must initially spend some time on the substrate of the plant while it releases the first strands of silk that form the initial, web-supporting bridge. However, a spider that encounters a worker ant can quickly leap off the vegetation, while still suspended by a silk thread. Thus, the workers are unlikely to be able to mount a strong defense against orb-web spiders that prey on their mutualistic partners.

In theory, eavesdropping can exert a considerable selection pressure on the nature of the signaling system, resulting in modifications of the signal, or even favoring alternative private channels (Stevens 2013). This is especially likely in signaling systems where both signaler and receiver suffer similarly strong negative effects of eavesdropping. For example, eavesdropping on sexual signals may result in fitness losses for both sexes, through mortality for the signaler and/or loss of reproductive success for the receiver (Stevens 2013). Adaptive responses to these costs are less likely in the lycaenid/ant mutualism, because the relationship is asymmetric: the survival of the larvae and pupae of *J. evagoras* depends critically on the presence of tending ants (Pierce et al. 1987). However, while the ants benefit from the association (Pierce and Nash 1999), their colonies can still thrive in the absence of the butterflies. As a consequence, there is little opportunity for selection to favor changes in both the signal

produced by the ant and the capacity for the butterfly to detect and act on that signal. This asymmetric opportunity for selection is not likely in parasitic lycaenids, such as *Maculinea*, because the evolutionary interests of the ants and parasitoid wasps are aligned.

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