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Phoretic specialization on insect herbivores facilitates mite transportation to host plants

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Abstract

Phoresy, the use of another organism for dispersal, is one of the most intriguing commensalistic interactions. The selection of a correct host is fundamental for phoretic organisms to ensure arrival to suitable habitats and to encounter potential mates. This study focuses on a group of phoretic mites in the genus *Lasioseius* (Acari: Blattisociidae). In La Selva Biological Station, a tropical wet forest in Costa Rica, *Lasioseius* mites feed on nematodes inside the scrolls formed by the young leaves of their hosts, plants in the order Zingiberales. When leaves expand and unfurl, mites disperse to another rolled leaf by clinging onto 'rolled-leaf beetles', a group of insect herbivores specialized on Zingiberales (genera *Cephaloleia* and *Chelobasis*; Coleoptera: Chrysomelidae). In this study, we determined whether *Lasioseius* mites associated with *Cephaloleia belti* Baly are specialized on this beetle species as a phoretic host. Mites may also be attracted to *Chelobasis perplexa* Baly, sharing the same host plant. Another possibility is that *Lasioseius* mites are opportunistic generalists and attach to rolled-leaf beetle species (e.g., *Cephaloleia dorsalis* Baly) that never share host plants with either *C. belti* or *Ch. perplexa*. In a laboratory setting, we tested whether mites preferred scents from and/or attached to particular beetle species. Scent attraction experiments showed that *Lasioseius* mites collected from *C. belti* were attracted to scents from *C. belti* and *Ch. perplexa*, but were not attracted to scents from *C. dorsalis*. Mites collected from *C. belti* attached to both *C. belti* and *Ch. perplexa,* but never to *C. dorsalis*. In conclusion, *Lasioseius* mites are not strict specialists, but are able to detect and attach to beetle species that inhabit their host plant.

KEYWORDS
Acari, Blattisociidae, *Cephaloleia*, *Chelobasis*, chemical cues, commensalism, dispersal, host recognition, *Lasioseius*, phoresy, scent attraction, symbiosis

INTRODUCTION

Phoresy, the use of another organism for dispersal among habitats or resource patches, is one of the most intriguing types of commensalistic interactions (Houck & OConnor, 1991). Host recognition and choice are fundamental steps in the life history of organisms that strongly depend on others to complete their life cycles. Phoretic organisms must recognize and choose appropriate hosts to ensure their dispersal to suitable habitats. Perhaps the most ubiquitous phoretic organisms are mites (Acari). In this group of small and wingless arthropods, phoresy has evolved multiple times, likely as an adaptation to overcome challenges associated with long-distance dispersal (Binns, 1982).

For phoretic mites, the selection of a suitable phoretic host results in effective transport to optimal habitats in which to feed and encounter potential mates (Binns, 1982; Walter & Proctor, 1999). The mechanism by which mites recognize their phoretic hosts remains largely understudied (Bartlow & Agosta, 2021). Mites are equipped with olfactory receptors on the tip of the tarsi of the first pair of legs, which are used to detect chemical cues (Hunter & Rosario, 1988; Bartlow & Agosta, 2021). These structures are known to be used by phoretic mites associated with dung beetles to recognize host beetle species (Niogret et al., 2006). Studies of mites that feed on cockroaches also concluded that these specialist parasites use scent to recognize their hosts (Schaefer & Peckham, 1968; Egan et al., 1975).

The genus *Lasioseius* (Acari: Blattisociidae) is a diverse group of mites that includes at least 206 described species (Lindquist & Moraza, 2014; Moraza & Lindquist, 2015, 2016; De Moraes et al., 2016). At our study site, La Selva Biological Station in Costa Rica (hereafter La Selva), five *Lasioseius* species are associated with plants of the order Zingiberales, a charismatic group of tropical plants that includes gingers and bananas (Kress, 1990; Lindquist, 2001; Moraza & Lindquist, 2018).

Lasioseius mites hunt for nematodes living on the wet surface of young leaves of their host plants (Lindquist, 2001). Inside the scroll formed by the young leaves of Zingiberales plants, *Lasioseius* mites interact with 'rolled-leaf beetles' (genera *Cephaloleia* and *Chelobasis*; Coleoptera: Chrysomelidae), a group of insect herbivore specialists that feed almost exclusively on plants of this order (Lindquist, 2001).

At La Selva, 33 plant species in the order Zingiberales are hosts to 22 species of rolled-leaf beetles (Garcia-Robledo et al., 2017). The diet breadths of rolled-leaf beetles range from extreme specialization on a single host plant, to generalization, with some beetle species feeding on more than 17 plant species (Garcia-Robledo et al., 2017). When young leaves mature and unfurl, rolled-leaf beetles fly in search of a new host plant (Garcia-Robledo et al., 2017). *Lasioseius* mites must climb on a beetle to colonize new young rolled leaves. If a mite is unable to ride to a new host plant to find a new young rolled leaf, it will desiccate and die.

This study, conducted in a laboratory setting, explores the role of scent and tactile cues in the recognition and choice of beetle hosts in *Lasioseius* mites. Using two species of rolled-leaf beetles that share the same host plant, and a third species that never shares host plants with the other two beetle species, the objective of this study was to determine the degree of specialization of phoretic behavior in *Lasioseius* mites.

It is possible that mites are generalists that disperse on any species of rolled-leaf beetle and are attracted by its scents. One disadvantage of such extreme generalization is that this behavior increases the probability of arriving to unsuitable environments where mites cannot find food or mates. A second possibility is that mites are specialized on a single beetle species. Although this extreme specialization will increase the probability of arrival to particular plant species, it also reduces the probability of finding a beetle for transportation when a rolled leaf expands. Finally, we hypothesized that a more advantageous behavior could be for mites to specialize on a subset of rolled-leaf beetle species that share the same host plants to maximize opportunities for transport to suitable habitats. If this is the case, mites may be indirectly specialized on particular host plants by selecting insect herbivore species that share the same diets.

MATERIALS AND METHODS

Study area and species

This study was conducted during the rainy season (July–October) 2008 at La Selva Biological Station, Puerto Viejo de Sarapiquí, Heredia, Costa Rica (10°26′N, 83°59′W). La Selva is a lowland tropical wet forest, located at 35–150 m above sea level in the northeastern Caribbean slopes of Costa Rica. It is characterized by two main seasons: a wet and a dry season, with an average annual rainfall of 4000 mm (McDade et al., 1994).

For all experiments, we selected *Lasioseius* mites collected from *Cephaloleia belti* Baly (Figure 1A). Using molecular markers (DNA barcode CO1), we determined that *C. belti* is the host of three cryptic species of *Lasioseius* (C Garcia-Robledo, unpubl. data). In our experiments, we used a mix of these three species. Although collecting mites from this beetle species ensures that *C. belti* is a host, we have no information regarding host use of other beetle species by mites collected from *C. belti*. At La Selva, *C. belti* feeds on 17 Zingiberales host plants (Garcia-Robledo et al., 2017). Most individuals of *C. belti* at La Selva are found inside the scrolls formed by young leaves of *Heliconia latispatha* Benth. (Heliconiaceae) (Figure 1A; Garcia-Robledo et al., 2017).

Chelobasis perplexa Baly is a rolled-leaf beetle specialized on plants in the genus *Heliconia* (Staines, 2009). At La Selva, *Ch. perplexa* shares five host plants with *C. belti* (Garcia-Robledo et al., 2017). *Chelobasis perplexa* and *C. belti* are usually found inside rolled leaves of *H. latispatha* (Figure 1A; Garcia-Robledo et al., 2017).

Cephaloleia dorsalis Baly is specialized on plants in the genus *Costus* (Costaceae). At La Selva, *C. dorsalis* feeds on five native species of *Costus*, and one exotic species introduced to Costa Rica from Southeast Asia [*Cheilocostus speciosus* (J. Konig) C.D. Specht, Costaceae]. The host plant in which *C. dorsalis* is most frequently found at La Selva is *Costus malortieanus* H. Wendl (Figure 1B). *Cephaloleia dorsalis* never shares host plants with *C. belti* or *Ch. perplexa* (Figure 1; Garcia-Robledo et al., 2017).

Field collections of beetles and mites

For all experiments, live beetles were collected from their most frequently used host plants (i.e., *H. latispatha* or *C. malortieanus*, Figure 1). We used small type-0 paint brushes to carefully remove mites from the beetles' bodies. We used different clean paintbrushes for each beetle species to reduce the risk of scent cross-contamination among species. Mites removed from *Ch.*

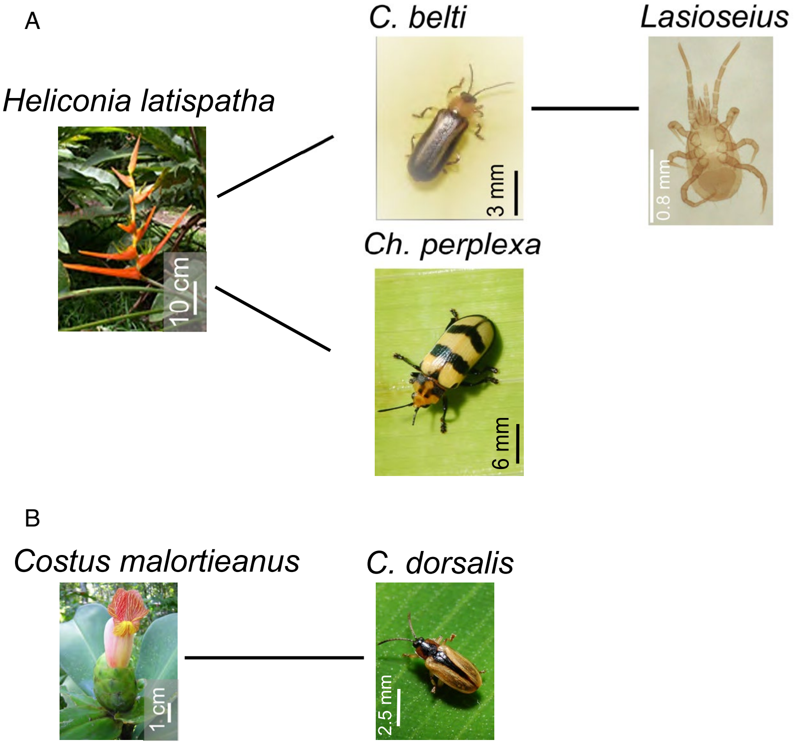

FIGURE 1 Neotropical gingers host a diverse community of arthropods in their rolled leaves. (A) *Cephaloleia belti* and *Chelobasis perplexa*, two species of rolled-leaf beetles, feed on the young leaves of *Heliconia latispatha*. Phoretic mites in the genus *Lasioseius* feed on nematodes found in surface water in young rolled leaves of *H. latispatha*. In this study we focus on three cryptic *Lasioseius* species collected from *C. belti*. (B) A third species of rolled-leaf beetle, *Cephaloleia dorsalis*, feeds on *Costus malortieanus*. This beetle never shares host plants with *C. belti* or *Ch. perplexa*

perplexa and *C. dorsalis* were released. Mites collected from *C. belti* were individually placed in 1.5-ml microcentrifuge tubes (Eppendorf, Hamburg, Germany). To maintain relative humidity close to 100%, each tube was lined with a 0.5 × 1.5 cm wet filter paper. Each beetle was handled with featherweight entomology forceps, rinsed with distilled water, and once dry, placed alive inside a microcentrifuge tube modified to be attached to the olfactometer (see next section).

Laboratory setup – scent attraction using an olfactometer

We tested mite attraction to beetle scents using custom-made four-chamber olfactometers (Figure S1A). The olfactometer consisted of a 2.5 × 2.5 cm Plexiglas arena, with a 0.5 cm radius central chamber. The top of the central chamber was covered with a slide cover slip after a mite was placed inside the olfactometer. The central chamber was connected to the sides of the arena by a 2-mm-diameter channel. We inserted one 5 µl, 2.5 cm long capillary tube to each side of the olfactometer (Figure S1A). The other side of each capillary tube was inserted into a 2-mm hole at the tip of the microcentrifuge tube, which was either empty (control) or contained a live beetle. We punched five 0.5-mm-diameter holes on the lid of each microcentrifuge tube to facilitate airflow from the microcentrifuge tube to the olfactometer chamber. Capillary and microcentrifuge tubes were only used once to avoid scent cross-contamination. Plexiglas arenas were rinsed with distilled water, then with 95% ethanol after each trial.

Can mites detect scents from rolled-leaf beetles?

To determine whether mites can detect the scents of any of the three beetle species selected for this study, each mite collected from *C. belti* was given a choice between scents from a beetle species or an empty microcentrifuge tube ('air' treatment, Figure S1A). We tested scent detection with each of the three beetle species included in this study (Figure 1). For each trial, we placed two microcentrifuge tubes holding the same species of beetle, and two empty tubes. The position of each tube relative to the central chamber in the olfactometer was selected using a random number generator. We recorded a choice if a mite walked and entered one of the lateral tubes. We scored no choice if mites failed to enter a lateral tube after 5 min of starting the trial. Each individual beetle or mite was used for a trial only once, then released.

Can mites distinguish between the scents of beetle species?

To determine whether mites have a preference for the scents between their known phoretic host beetle species (*C. belti*, Figure 1A), a beetle species sharing the same host plant as their known host beetle (*Ch. perplexa*, Figure 1A), or a beetle species never encountered on the same plant with either *C. belti* or *Ch. perplexa* (*C. dorsalis*, Figure 1B), we gave each mite a choice between *C. belti* and either *Ch. perplexa* or *C. dorsalis* (Figure S1B). As in the previous experiment, each mite was used only once for each trial, then released or collected for further identification.

Do mites display preferences in attaching to rolled-leaf beetle species?

Host recognition may occur when mites have direct physical contact with beetle hosts. We conducted phoresy experiments to determine whether (1) direct contact elicits phoretic behavior only when in contact with the beetle species from which mites were collected, (2) mites attach to other beetle species sharing host plants with the original phoretic hosts, or (3) mites are phoretic generalists and will attach to a beetle species never encountered in the same plant with the other two beetle species. For these experiments, one *Lasioseius* mite was collected from *C. belti* and placed in a glass vial containing a *C. belti* beetle and another beetle, either *Ch. perplexa* or *C. dorsalis* (Figure S1C). After 5 min, we recorded the beetle species selected by the mite, as evidenced by mite attachment to the host's body. In all three experiments, differences in the numbers of mites that selected one option vs. the other (e.g., beetle vs. an empty tube in the first experiment) were analyzed using two-tailed binomial tests (Zar, 1999).

RESULTS

Mites can detect scents from rolled-leaf beetles

Mites were attracted to scents from the rolled-leaf beetle species present in their original host plant (*C. belti* and *Ch. perplexa*), but not to the scent of *C. dorsalis*, the beetle species that never shares host plants with the other two beetle species (Figure 2). This result suggests that *Lasioseius* mites can detect beetle species present in *H. latispatha* using scent cues, and that they are not attracted to the beetle species that occurs on a different host plant.

Mites can distinguish between the scents of different beetle species

When given the option to choose between its original phoretic host and the beetle species present in the same host plant (i.e., *C. belti* vs. *Ch. perplexa*; Figure 1A), mites showed no preference for either beetle (Figure 3A). Mites significantly preferred the original phoretic host (*C. belti*) over *C. dorsalis* (Figure 3A). This result again supports that *Lasioseius* mites use scent cues to detect beetle species that share their host plant.

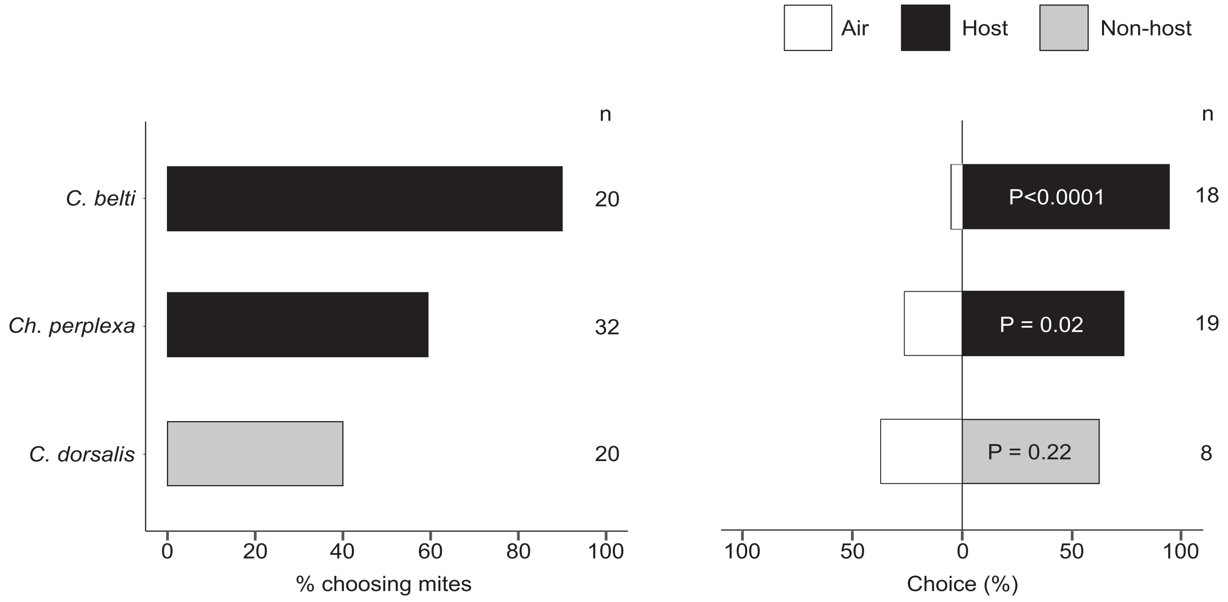

FIGURE 2 Percentage of phoretic *Lasioseius* mites collected from *Cephaloleia belti* attracted to an empty olfactometer chamber (air), to the scents of rolled-leaf beetles (*C. belti* or *Chelobasis perplexa*) found in their host plant (*Heliconia latispatha*), or to the scent of *Cephaloleia dorsalis*, a rolled-leaf beetle that never shares host plants with *C. belti* or *Ch. perplexa*. On the left the percentage of mites that had made a choice after 5 min of exposure. On the right the choices these mites had made, between each of the rolled-leaf beetles vs. air. 'n' represents sample sizes. The P-values inside the bars are based on two-tailed binomial tests

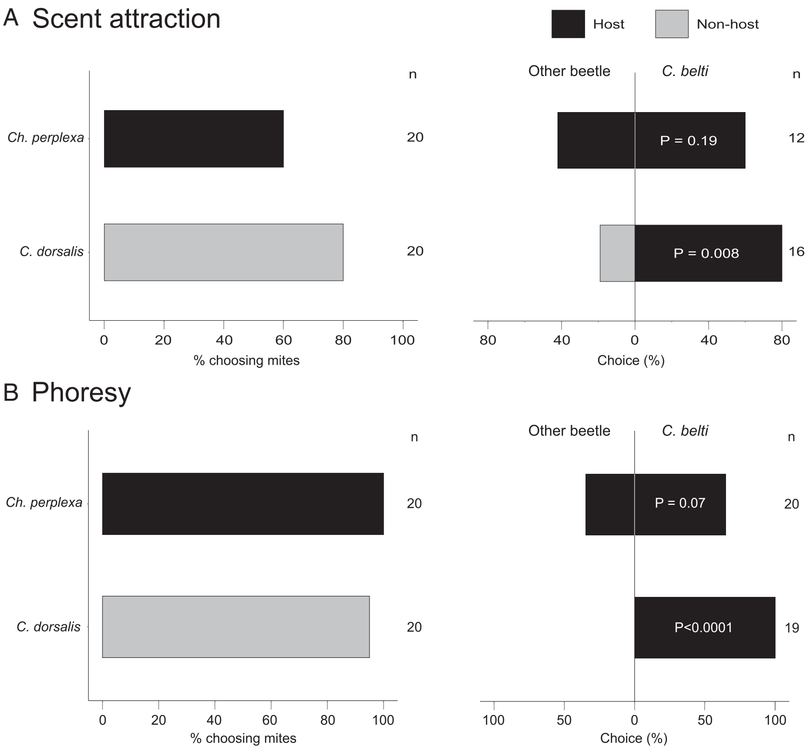

FIGURE 3 Percentage of phoretic *Lasioseius* mites collected from *Cephaloleia belti* (A) attracted to the scent of *C. belti* when tested vs. the scent of *Chelobasis perplexa* (a beetle sharing host plants with *C. belti*) or vs. the scent of *Cephaloleia dorsalis* (never sharing host plants with *C. belti* or *Ch. perplexa*), and (B) choosing to cling to *C. belti* when tested vs. *Ch. perplexa* or vs. *C. dorsalis*. On the left the percentage of mites that had made a choice after 5 min of exposure. On the right the choices these mites had made, between *C. belti* vs. the other beetles. 'n' represents sample sizes. The P-values inside the bars are based on two-tailed binomial tests

Mites display preferences in attaching to different rolled-leaf beetle species

When mites were given a choice between *C. belti* and *Ch. perplexa*, mites displayed no preference (Figure 3B). When given a choice between *C. belti* and *C. dorsalis*, mites rapidly attached to *C. belti* – none of the mites attached to *C. dorsalis* (Figure 3B). These results also support that *Lasioseius* mites have a strong preference for beetle species present in *H. latispatha*.

DISCUSSION

Our results strongly suggest that *Lasioseius* mites are specialized on the beetle community present in their host plant. This specialization on beetles that are herbivores of *H. latispatha*, increases the probability that mites will arrive at the optimal host plant when embarking on a phoretic beetle host. Mite specialization on specific phoretic hosts has previously been recorded in multiple mite taxa associated with burying beetles, carabid beetles, and dung beetles (Krantz & Mellott, 1973; Schwarz, 1996; Niogret et al., 2006). We propose that specialization on a community of phoretic hosts rather than a single species is the product of adaptation. However, plastic responses may also play an important role on phoretic host selection.

To supplement scent attraction experiments, our third experiment aimed to determine whether *Lasioseius* mites are preferentially phoretic on certain beetle species over others. We found that *Lasioseius* mites preferentially attached to *C. belti* beetles, when given a choice between *C. belti* and *C. dorsalis* but did not prefer *C. belti* over *Ch. perplexa*, the two beetle species that share *H. latispatha* host plants with the mites. These results provide further evidence of specialization in *Lasioseius* mites on the assemblage of beetle species that share the same host plant as the mites. In this study we were unable to differentiate among the three *Lasioseius* mite species based on morphology. Taxonomic identification to species is required to discern whether *Lasioseius* species differ in their preferences for *C. belti* over *Ch. perplexa*.

The main aim of this study was to investigate mechanisms of host-finding in phoretic *Lasioseius* mites. Our results support the involvement of chemical and, specifically, scent cues in the detection and recognition of phoretic hosts by various phoretic mite species (Krantz & Mellott, 1973; Huck et al., 1998; Soroker et al., 2003; Niogret et al., 2006). The exact chemicals that mediate this function are still unknown. In our study system, rolled-leaf beetles are herbivores of Zingiberales plants, and consume leaf tissue from the young rolled leaves that *Lasioseius* mites also utilize as their feeding grounds. Rolled-leaf beetles, similarly to mites, utilize cues from plant secondary metabolites to locate their preferred host plants (García-Robledo & Horvitz, 2009). It is reasonable to assume, that in the consumption of plant leaf tissues, chemical compounds from the plant are assimilated into the beetles' bodies (Levin, 1976), giving them specific scents that allow phoretic mites to recognize beetles that have been feeding on their preferred host plant. Alternatively, traces of plant tissue may remain on beetles, giving them specific scents that allow mites to detect and recognize the beetles that will take them to their preferred feeding grounds. Nearly all insect species are known to possess cuticular hydrocarbons, compounds that help prevent desiccation (Menzel et al., 2017). However, cuticular hydrocarbons are also thought to play a role in insect communication, particularly in the context of mate recognition or conspecific recognition in social insects (Howard & Blomquist, 2004; Everaerts et al., 2010). Although no studies have yet investigated the presence of hydrocarbons in rolled-leaf beetles, we hypothesize their potential role as chemical cues for phoretic mites, especially at close range.

Certain mite taxa, including parasitic trombidiid mites, have been suggested to use auditory cues for host finding or predator avoidance (Zhang, 1998). Auditory cues could potentially be used by mites phoretic on organisms that emit sounds, such as leaf beetles that stridulate (Schmitt, 1994). However, there is to date no evidence that the rolled-leaf beetle species included in this study stridulate.

This study represents a first step in understanding the role of scent cues in the detection, recognition, and phoresy of mites associated with rolled-leaf beetles. At least three genera of mites, in addition to *Lasioseius*, are known to be phoretic on rolled-leaf beetles at La Selva (Lindquist & Moraza, 2014; Moraza & Lindquist, 2015). Thus far, no other studies have explored the role that chemical cues might play in host choice by mites associated with rolled-leaf beetles, or whether mites display similar degrees of phoretic host specialization to the ones we report in this study.

Arthropods rely on chemical cues to make fundamental decisions, from finding mates, locating food resources, and avoiding predators (Pasteels et al., 1983; Dicke, 2000; Dicke & Grostal, 2001; Wertheim et al., 2004). Our experiments provide support for another role of chemical cues: phoretic host location and recognition in phoretic mites. The abundance and importance of commensalistic interactions is increasingly evident, yet there is a disproportionate lack of studies investigating the underlying mechanisms and resulting patterns of these types of interactions. This lack of information, coupled with a lack of knowledge of the ecology and behavior of many mite taxa, provide a fertile ground for future studies on these fascinating interactions.

In conclusion, this study showed that phoretic *Lasioseius* mites use scent cues to detect and recognize their preferred phoretic rolled-leaf beetle hosts. *Lasioseius* mites specialize on the assemblage of rolled-leaf beetles that share their host plants, rather than on individual beetle species. The specialization of *Lasioseius* mites on an assemblage of rolled-leaf beetles suggests that specialization on a few phoretic host species, rather than on individual species, can increase resource finding success for phoretic organisms. Future studies will need to determine whether this pattern of specialization holds when taking into consideration species level identifications within *Lasioseius*. Additionally, comparable data to ours are needed to determine the degree of phoretic host specialization in other genera of mites phoretic on rolled-leaf beetles. Although more research is needed to determine the exact cue or suite of cues that allows mites to detect and recognize their hosts, our study supports the role of olfactory cues in host recognition among phoretic mites.

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AUTHOR CONTRIBUTIONS

Laura Bizzarri: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (supporting); Writing – original draft (lead); Writing – review & editing (lead). **Erin K. Kuprewicz:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review & editing (equal). **Megana Varma:** Formal analysis (supporting); Writing – original draft (supporting); Writing – review & editing (equal). **Carlos Garcia-Robledo:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review & editing (equal).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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