Title: Are ants botanists? Ant associative learning of plant chemicals mediates foraging for carbohydrates

Running title: Ants associatively learn plant chemicals

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Abstract

1. Although associative learning is widespread across animals, its ecological importance is difficult to assess because learning is rarely studied in the field where informative cues are juxtaposed against complex backgrounds of uninformative noise.
2. Ants rely heavily on chemical cues for foraging and engage in many ecologically important interactions with plants. Nevertheless, little is known about the role of associative learning of plant chemicals in ant foraging for carbohydrates.
3. In a field setting, we investigated whether the distantly related ant species *Formica podzolica* (Formicinae subfamily) and *Tapinoma sessile* (Dolichoderinae subfamily) exhibited associative learning of the chemical cues from two co-occurring plant species that are taxonomically and chemically distinct (Asteraceae: *Helianthella quinquenervis* and Apiaceae: *Ligusticum porteri*).
4. For two consecutive summers, we trained ants to forage from artificial sugar-rich baits associated with the leaf chemicals from either *H. quinquenervis* or *L. porteri* for 24 h, after which we deployed a two-choice test to assess whether ants would be more likely to select baits associated with the same (vs. different) plant chemicals on which they had been trained.
5. We demonstrate associative learning of chemicals from both plant species, and these effects were consistent between ant species and years; training increased bait occupancy from 42% on the untrained scent to 66% on the trained scent. These results indicate that associative odor-learning may be widespread across ants and serve as an important mechanism mediating ant selection of resources.

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Keywords: ant foraging behavior, ant mutualism, associative learning, olfactory cues, plant chemicals

Introduction

Associative learning, the formation of predictive relationships between contingent stimuli in the environment, is widespread across animals and likely has far-reaching ecological and evolutionary consequences (Giurfa, 2007; Ginsburg & Jablonka, 2010; Morand-Ferron, 2017). Associative learning can result in adaptive behavioral changes and increased foraging efficiency, such as when birds develop search images for cryptic moth prey (Tinbergen, 1960; Pietrewicz & Kamil, 1979), bees form associations between floral color and nectar rewards (Frisch, 1914; Gumbert, 2000), and parasitoid wasps learn to locate prey based on olfactory cues (Ishii & Shimada, 2010). In turn, associative learning is believed to result in the evolution of new traits (e.g., anti-predator defenses in prey) (Ginsburg & Jablonka, 2010) and to structure populations and communities of associated species (Ishii & Shimada, 2010). For example, search images in birds can result in frequency-dependent foraging, with birds increasing their consumption of abundant prey but decreasing their consumption of rare prey, thus maintaining color polymorphisms and species coexistence in cryptic moths (Bond & Kamil, 1998).

However, because most studies of associative learning are conducted in the laboratory, we often lack information about the ecological and evolutionary relevance of associative learning under field conditions (Pritchard *et al.*, 2016; Morand-Ferron, 2017). Although laboratory tests of learning allow for greater experimental control, animals have access to different information and are under different selective pressures in the wild (Pritchard *et al.*, 2016; Muth *et al.*, 2018). As a result, estimates of learning performance in the laboratory may not translate to the field.

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While recent studies provide field-based evidence for associative learning in both vertebrates (Morand-Ferron *et al.*, 2015) and invertebrates (Huber & Knaden, 2018), additional field studies are needed to understand the extent to which associative learning influences species interactions in the wild.

Because ants rely heavily on chemical cues when foraging and engage in many ecologically important interactions with plants, associative learning of plant chemicals could mediate ant discovery and selection of plant-associated resources (Nelson *et al.*, 2019). Ants have widespread effects in most terrestrial ecosystems, where they engage with plants by visiting flowers, dispersing and preying on seeds, cutting leaves, protecting plant and insect-herbivore mutualists from their natural enemies, and serving as prey for carnivorous plants (Nelson *et al.*, 2019). Such encounters with plants are likely the result of ants using both pheromonal (Morgan, 2009) and non-pheromonal (hereafter "ambient") chemicals in the environment to navigate and locate resources (Knaden & Graham, 2016). Compared to other insects such as honeybees, for which associative odor-learning has been extensively studied (Giurfa & Sandoz, 2012), ants are known to have larger and more complex olfactory regions of the brain, highlighting the centrality of chemical detection to ant foraging (Gronenberg, 1996). All below- and above-ground plant tissues are known to produce ambient chemicals, including both volatile and non-volatile compounds on tissue surfaces, and ants could exhibit both innate (Edwards *et al.*, 2006; Dáttilo *et al.*, 2009) and learned responses to these chemicals. Interestingly, since ants live in colonies, associative learning by individual ant foragers could be socially transmitted not only through the recruitment of additional foragers with pheromone trails, but also through mouth-to-mouth food exchange (trophallaxis) in which otherwise naïve foragers learn to associate rewards with the chemical cues of the exchanged food (Provecho & Josens, 2009; Hayashi *et al.*, 2017). Thus,

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although associative odor-learning in ants has received less attention compared to in other animals (Giurfa, 2007), it may commonly mediate ant interactions with plants.

Past studies provide evidence for visual and olfactory learning by ants (e.g., Roces, 1994; Harris *et al.*, 2005; Dupuy *et al.*, 2006; Narendra *et al.*, 2007; Bos *et al.*, 2010), but to our knowledge, no studies have tested whether associative learning of natural blends of plant chemicals by ants mediates their associations with plants in the field. Associative learning has only been studied in a few ant species (*Acromyrmex lundi*, *Camponotus* spp., and *Cataglyphis fortis*) (e.g., Roces, 1994; Helmy & Jander, 2003; Huber & Knaden, 2018), thus making it unclear whether learning is widespread across ants. Most of these studies have been conducted in the laboratory, in which ants have been shown to form positive and negative associations with pure chemical compounds (Dupuy *et al.*, 2006; Josens *et al.*, 2009), artificial odors (Roces, 1990, 1994), and the cuticular hydrocarbon profiles of other ants (Bos *et al.*, 2010). Such experiments provide opportunity for controlled tests of ant associative learning and its underlying mechanisms (e.g., individual versus social learning) but lack ecological complexity and realism. Field-based studies have also shown that ants learn food odors (Helmy & Jander, 2003; Huber & Knaden, 2018) and use scents as landmarks for navigation (Wolf & Wehner, 2000; Steck *et al.*, 2009; Buehlmann *et al.*, 2015). However, most of these studies tested for associative learning using single chemical compounds, rather than natural blends of chemicals present in the environment (Steck *et al.*, 2009; Buehlmann *et al.*, 2015; Huber & Knaden, 2018). While several studies indicate that ants may associatively learn natural blends of plant chemicals, evidence is scant and inconclusive. For example, one study provides preliminary evidence that ants associatively learn plant odors (Helmy & Jander, 2003), but foragers were assayed from only two replicate colonies, and training was performed on the colony surface where competing chemical

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stimuli were likely minimal. Similarly, while several field-based studies have shown that ants recruit faster and forage more efficiently on plant-based resources (seeds or leaves) that are more familiar, the mechanisms (e.g., ant odor-learning) driving these patterns were not assessed (Fowler, 1982; Johnson, 1991; Howard *et al.*, 1996). Thus, additional studies are needed to determine whether associative learning of plant odors by ants mediates ecologically important interactions between ants and plants.

In this study, we assessed whether ants associatively learn plant chemicals when foraging for sugar-rich resources in the field. To do so, we tested whether ants exhibited associative learning when trained to forage for baits associated with leaf chemicals from two co-occurring taxonomically and chemically distinct plant species (Asteraceae: *Helianthella quinquenervis* and Apiaceae: *Ligusticum porteri*) that both naturally produce sugar-rich rewards for ants (extrafloral nectar and honeydew excreted by aphids, respectively) (Inouye & Taylor, 1979; Mooney *et al.*, 2016). By testing for associative learning of chemicals from both plant species by two ecologically and taxonomically distinct ant species (Dolichoderinae: *Tapinoma sessile* and Formicinae: *Formica podzolica*) across two years, we provide evidence that associative odor-learning may be an important mechanism mediating ant foraging in the field.

Materials and methods

Study sites and natural history

This study was conducted in July 2017 and 2018 near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO (38.96°N, -106.99°W). In 2017 and 2018, we worked in seven and eight (respectively) separate open, rocky meadows distributed within a 4 km radius (15 total sites; coordinates in Appendix S1). In these sites *Helianthella quinquenervis*

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(Asteraceae; "aspen sunflower") and *Ligusticum porteri* (Apiaceae; "osha") are the two dominant herbaceous, perennial plants that are both naturally associated with sugar-rich rewards for ants (extrafloral nectar and honeydew excreted by aphids, respectively) (Inouye & Taylor, 1979; Mooney *et al.*, 2016). Plants in the Apiaceae and Asteraceae family share many secondary compounds in common, including some aromatic essential oils and terpenoids in leaves and other plant tissues (Berenbaum, 2001). However, Apiaceae plants are known to have particularly distinctive odors and produce compounds such as furanocoumarins that are not present in the Asteraceae (Berenbaum, 2001). In the field, *H. quinquenervis* and *L. porteri* are distinguishable by scent (Nelson, personal observation).

The five taxonomic groups of ants that commonly occur in these sites are *Camponotus* spp., *Formica podzolica*, and the *Formica rufa* species group (subfamily Formicidae), *Myrmica* spp. (subfamily Myrmicinae), and *Tapinoma sessile* (subfamily Dolichoderinae). Ants in these three subfamilies have independently evolved to rely on sugar-rich liquid rewards (e.g., extrafloral nectar and honeydew produced by hemipterans) as main components of their diets (Hölldobler & Wilson, 1990). Of the taxa in this community, *F. podzolica* and *T. sessile* are the most abundant (Mooney *et al.*, 2016) and were most frequently observed in this study. *Formica podzolica* and *T. sessile* have contrasting colony structures; *F. podzolica* forms large colonies (approximately 5,000-40,000 workers) with multiple queens that often occupy multiple nests (Deslippe & Savolainen, 1994; DeHeer & Herbers, 2004), whereas *T. sessile* forms small colonies (approximately 70 workers) with single queens that occupy single nests (Buczkowski, 2010). While *F. podzolica* is a non-aggressive, competitively subordinate species (Savolainen, 1990; Mooney, 2006), *T. sessile* is more behaviorally and numerically dominant (Nelson et al., unpublished data).

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Experimental design

To test for ant associative learning of plant chemicals, we first trained ants to forage from artificial baits associated with leaf chemicals from either *H. quinquenervis* or *L. porteri*, and we then tested whether ants would subsequently be more likely to select resources scented with the same (vs. different) plant chemicals in a two-choice test (experimental setup shown in Fig. 1). To train ants, we deployed 10-14 artificial baits (hereafter "training baits") along a transect in each of the 15 sites on one to three separate occasions (n = 200 total baits in 160 separate transect locations), with each bait separated by at least 10 m to avoid repeatedly sampling ants from the same colony. To confirm that the 10 m (minimum) bait spacing was sufficient to assay unique ant colonies, we measured ant foraging distances. In July 2018, baits (1 mm diameter crumbs of pecan sandies; Kellogg Foods, Battle Creek, MI, USA) were randomly distributed within a meadow actively foraged by both *F. podzolica* and *T. sessile*, the two most abundant ants in this study. When a bait was discovered (n = 17 and 10 total discoveries by *F. podzolica* and *T. sessile*, respectively), the foraging ant was then followed until it entered an active ant nest, and the linear distance from the bait location to the nest was recorded. On average, *F. podzolica* and *T. sessile* foragers traveled 1.3 $\pm$ 1.1 m and 0.9 $\pm$ 0.3 m (mean $\pm$ 1 SD) from the nest, respectively. Accordingly, we assume that we assayed separate ant colonies at all locations along the transects. Ants were observed at 35 of the 70 total locations in 2017 and 71 of the 110 total locations in 2018. When we recorded ant species identities in the baits (done in 2018 but not 2017; described in more detail below), we observed two ant species at 19 of the locations and three ant species at 13 of the locations. Thus, we assume that we assayed a minimum of 151 unique ant colonies (although multiple species were likely also present at some transect locations in 2017).

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To test for associative odor-learning, we used baits that were intended to imitate the composition of mutualist-produced resources associated with plants (i.e., extrafloral nectar or honeydew) and consisted of 10 mL of a 20% solution by mass of forest honey (honey produced by bees that foraged on hemipteran honeydew [Langnese Forest Honey, Bargteheide, Germany]) in 15 mL plastic centrifuge tubes fitted with cotton wicks. We attached training baits to the top of 10-cm sanded and lacquered bamboo sticks, which were used as artificial plant stems. We rubbed the sticks once with fresh leaves from either *H. quinquenervis* or *L. porteri* (alternating between species along the transect) when baits were first deployed. Leaves were locally collected from plants that visually appeared to be undamaged by herbivores. Because leaves were crushed in the process of rubbing them along bamboo sticks, they may have released additional chemical compounds compared to undamaged leaves. However, because plants often release additional chemical compounds in response to natural herbivore damage (Dicke & Baldwin, 2010), these chemical compounds would likely still be naturally available to be detected by ants. Moreover, we used bamboo sticks (that were presumably odorless) rather than natural plant stems so that other non-olfactory cues (e.g., textural or visual) from *H. quinquenervis* and *L. porteri* would not affect ant behavior.

After training baits were deployed for 24 h, we deployed a two-choice test within 50 cm of each training bait to assess whether ants would be more likely to select baits associated with leaf chemicals from the same (vs. different) plant species on which they had previously been trained (Fig. 1). The base and arms of the two-choice test consisted of 10 cm bamboo sticks, with the arms positioned at a 90° angle. We placed one honey bait at the end of each arm of the two-choice test, randomly selecting one arm to rub with *H. quinquenervis* leaves and the other to rub with *L. porteri* leaves. The base of the two-choice test was unscented. We removed any

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vegetation that was touching the two-choice test so that ants could only access the baits by ascending the base and subsequently selecting one of the arms. Every 10-20 min for the subsequent 2-3 h, we recorded whether ants were present (in both years) and their identities (in 2018 only), both in the baits and ascending the arms of the two-choice test. We considered baits to have been occupied by ants if ants were ever observed feeding in the baits. While any ant could ascend the two-choice test (whether or not it had previously been trained), it is likely that ants in most locations had received prior training (with 94% of the training baits having been discovered by ants).

Statistical analyses

We used two separate models to test for associative learning (1) by two ant species (*F. podzolica* and *T. sessile*) that were most commonly observed in 2018 and (2) by all ant taxa combined in both 2017 and 2018 (after excluding locations where ants were never observed feeding from any baits). For both tests, we used generalized linear models (GLM) with binomial distributions to assess whether bait selection depended on the main effects of bait scent and whether ants had been trained on the same (vs. different) scent (hereafter "same-odor training"), as well as the bait scent x same-odor training interaction. A significant positive main effect of same-odor training would demonstrate associative learning. A significant main effect of bait scent would indicate that there were different responses to the two plant species, regardless of experimental training. Finally, a significant bait scent x same-odor training interaction would indicate that associative learning of one plant species was stronger than of the other. The model testing for learning in the two ant species in 2018 also included the main effect of ant species as well as all two- and three-way interactions to test whether learning was ant species-dependent.

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231 The model testing for learning in all ant taxa combined across both years included the main
232 effect of year as well as all two- and three-way interactions to test whether learning varied
233 between years.
234 All analyses were conducted in R 3.3.2 (R Core Team, 2016). We constructed GLMs
235 using the 'glm()' function in the 'stats' package (R Core Team, 2016). To test for the
236 significance of effects, we conducted Wald chi-square tests with type III sums of squares using
237 the 'Anova()' function in the 'car' package (Fox & Weisberg, 2010).
238
239 **Results**
240 In the model testing for learning by *F. podzolica* and *T. sessile* in 2018, there was a
241 significant positive effect of same-odor training (GLM: $\chi^2 = 5.31$, $P = 0.021$), where ants
242 selected a greater proportion of baits scented with the plant chemicals on which they had been
243 trained; for both ant species combined, same-odor training increased bait occupancy from 45% to
244 66% (Fig. 2). The main effects of bait scent and ant species were not statistically significant ($P >$
245 0.10 in both cases), and neither were any of the two- or three-way interactions ($P > 0.65$ in all
246 cases). Accordingly, we found evidence for associative learning that did not detectably differ
247 with ant species or plant scent.
248 We in turn tested for inter-annual variation (2017 vs. 2018) in associative learning across
249 all ant taxa in the community combined. There was a significant main effect of same-odor
250 training (GLM: $\chi^2 = 16.19$, $P < 0.001$), demonstrating associative learning across both years;
251 same-odor training increased bait occupancy from 42% to 66% (Fig. 3). There was also a
252 significant main effect of year (GLM: $\chi^2 = 11.49$, $P < 0.001$) and a marginally significant three-
253 way bait scent x same-odor training x year interaction (GLM: $\chi^2 = 3.72$, $P = 0.054$), with same-

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odor training increasing ant selection of *H. quinquenervis* more strongly in 2017 and *L. porteri* more strongly in 2018 (Fig. 3). None of the two-way interactions were statistically significant ($P > 0.15$ in all cases).

Discussion

We have demonstrated that associative learning of natural blends of plant chemicals mediates the selection of carbohydrates by two ant species across two years in the field. In 2018, two taxonomically and ecologically distinct ant species were both more likely to select artificial sugar-rich rewards associated with the same (vs. different) plant leaf chemicals on which they had previously been trained, and such effects did not detectably differ with ant or plant species; overall, same-odor training increased bait occupancy by these two ant species from 45% to 66%. Moreover, we found consistent evidence for associative learning with all ant taxa in the community combined across two years (2017 and 2018); overall, same-odor training increased bait occupancy by the ant community from 42% to 66%. Thus, we provide evidence for associative learning of plant odors as a previously uninvestigated but likely widespread mechanism mediating ant associations with plants in a chemically complex field setting.

Despite *F. podzolica* and *T. sessile* being taxonomically and ecologically distinct, we found no evidence for differences in learning between these two species (2018 data only). These ants occupy separate subfamilies that independently evolved to rely on plant-based sugar-rich rewards (Hölldobler & Wilson, 1990). Compared to *F. podzolica*, *T. sessile* ants have smaller brains (cross-sectional widths approximately 1 and 0.35 mm, respectively) (Muscedere *et al.*, 2014; Sulger *et al.*, 2014) and live in smaller colonies (Deslippe & Savolainen, 1994; Buczkowski, 2010), although they also often recruit more workers to baits (Nelson et al.,

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unpublished data). Such differences in brain and colony size as well as recruitment to resources could have potentially altered the capacity for both individual and social learning in these ants. For example, ants from larger colonies are predicted to rely more on chemical communication (Beckers *et al.*, 1989), and social learning could also thus be more important. However, no published papers to our knowledge have compared the neurophysiological bases of learning or the importance of social learning in these two species. Nonetheless, we found evidence for associative learning of natural blends of plant chemicals by both ant species (2018 only), as well as by all ant taxa present in the community combined (2017 and 2018). Thus, our results contribute to a growing number of studies of associative odor-learning in ants (e.g., Roces, 1990, 1994; Helmy & Jander, 2003; Dupuy *et al.*, 2006; Bos *et al.*, 2010; Huber & Knaden, 2018), which together show that associative learning of plant chemicals may be widespread across ant species.

There was a significant difference in learning across years (all ant species combined in 2017 and 2018) with respect to the two plant species, with associative learning being stronger for *H. quinquenervis* in 2017 but stronger for *L. porteri* in 2018. This bias in associative learning might have been due to the ambient resource environment within which the experiment was embedded. Rewards associated with *H. quinquenervis* are more consistent throughout the season and across individual plants; all flowering *H. quinquenervis* produce extrafloral nectar in both June and July (Inouye & Taylor, 1979), whereas not all flowering *L. porteri* plants host aphids, and they do so in July only (Nelson, personal observation). Training from the ambient resource environment is possible, as ant associative learning can be rapid (Huber & Knaden, 2018) and long term (e.g., up to 18 weeks; Saverschek *et al.*, 2010). Nevertheless, there were no obvious differences in the relative abundance of *H. quinquenervis*- or *L. porteri*-associated resources

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between the two years. Alternatively, the bias in associative learning might also have been due to inter-annual changes in the nutritional demands of these ants. Ultimately, the difference in associative learning with respect to plant species is weak (e.g., too weak to be detected in the 2018 analysis) compared to the overall finding of strong associative learning for both plant species across both years.

Additional research is needed to determine whether and which plant traits mediate the strength of ant associative learning. For example, honeybees have been shown to be able to better discriminate between odors that are more dissimilar (Paldi *et al.*, 2003), and it is possible that ants also exhibit stronger associative odor-learning of plants with more dissimilar blends of chemical compounds. In co-evolved ant-myrmecophytic plant associations, ant queens have been shown to use plant chemical compounds to distinguish between high and low quality host plants, both within and among species, and select optimal hosts based on the amount of food rewards, nesting space, and previous damage from herbivores and pathogens (Torres and Sanchez 2017; Razo-Belman et al. 2018). However, it is unclear whether such responses to plant chemicals are innate or learned. In addition, the quality (i.e., composition of sugars and amino acids) and volume of sugar rewards can determine the strength of ant attraction (Blüthgen *et al.*, 2004; Blüthgen & Fiedler, 2004) and could mediate the strength of associative learning, as has similarly been shown for honeybees (Wright *et al.*, 2009). Thus, future studies should test for associative learning by ants of multiple plant-associated rewards (e.g. extrafloral nectar and honeydew) of different qualities. Because ants also use visual landmarks and tactile cues when navigating (Seidl & Wehner, 2006; Steck *et al.*, 2011), future studies should test whether associative learning of multiple cues in combination mediates ant foraging for plant-associated resources (Fernandes *et al.*, 2018).

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In summary, we have shown that ants associatively learn chemicals from distinct plant species, and such learning may be widespread across ant taxa in the wild. In addition to associating with mutualist plants and insect herbivores, ants associate with plants in the contexts of floral visitation, seed dispersal and predation, leaf cutting, and plant predation of ants by carnivorous plants (Nelson *et al.*, 2019). Thus, ant associative learning of plant chemicals may occur in many contexts (e.g., Roces 1990; Roces 1994) and mediate ant population- and community-level effects on plants and the multi-trophic communities in which they are embedded (Styrsky & Eubanks, 2007). As a result, ant associative learning likely has far-reaching yet unrecognized effects on plant and insect evolutionary dynamics and community structure.

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Contribution of authors

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All authors designed the project; ASN, GDZ, and KTS collected the data; ASN analyzed the data and wrote the paper; ASN and KAM contributed substantially to paper revisions.

Data accessibility statement

Upon acceptance of the manuscript, we will archive our data with the Dryad Digital Repository.

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548 **Figure legends**

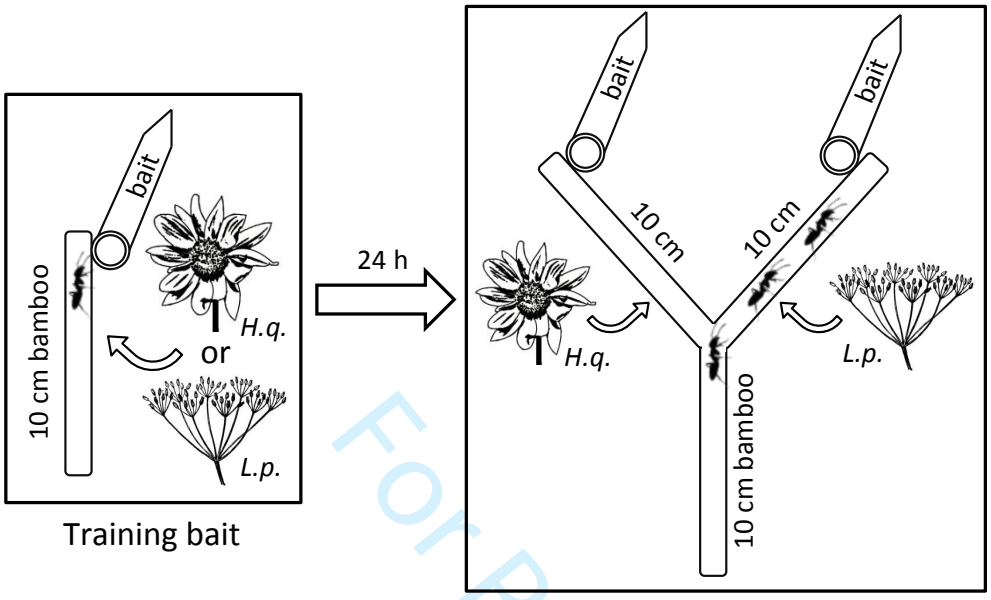
549 **Fig. 1.** First, ants were trained to forage for resources from baits ("training baits") associated
550 with chemicals from either *Helianthella quinquenervis* ("H.q.") or *Ligusticum porteri* ("L.p.")
551 leaves, which were rubbed on bamboo sticks to which the baits were attached. After 24 h we
552 deployed a two-choice test within 50 cm of the training baits. We placed one bait at the end of
553 each arm of the two-choice test, and we rubbed one arm with *H. quinquenervis* leaves and the
554 other with *L. porteri* leaves. Then every 10-20 min for the subsequent 2-3 h, we recorded
555 whether ants were present (in both 2017 and 2018) and their identities (in 2018 only) on all arms
556 and baits of the two-choice test to test whether ants were more likely to select baits associated
557 with the leaf chemicals on which they had been trained.
558
559 **Fig. 2.** The effects of training (color) and bait scent (x-axis) on the proportion of baits occupied
560 by (a) *Formica podzolica* and (b) *Tapinoma sessile*, the two most common ant species observed
561 in baits in 2018. Numbers inside the bars indicate sample sizes. Overall, ants occupied a
562 significantly greater proportion of the baits associated with the same (vs. different) chemical cues
563 on which they had been trained (GLM: $\chi^2 = 5.31$, $P = 0.021$).
564
565 **Fig. 3.** The effects of training (color) and bait scent (x-axis) on the proportion of baits occupied
566 by all ant taxa combined in (a) 2017 and (b) 2018. Numbers inside the bars indicate sample sizes.
567 Overall, ants occupied a significantly greater proportion of the baits associated with the same (vs.
568 different) chemical cues on which they had been trained (GLM: $\chi^2 = 16.19$, $P < 0.001$). There
569 was also a significant main effect of year (GLM: $\chi^2 = 11.49$, $P < 0.001$), with ants occupying
570 more baits in 2017 than 2018. The bait scent x training x year interaction was marginally

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571 significant (GLM: $\chi^2 = 3.72$, $P = 0.054$), although no other main or interactive effects were
572 statistically significant.

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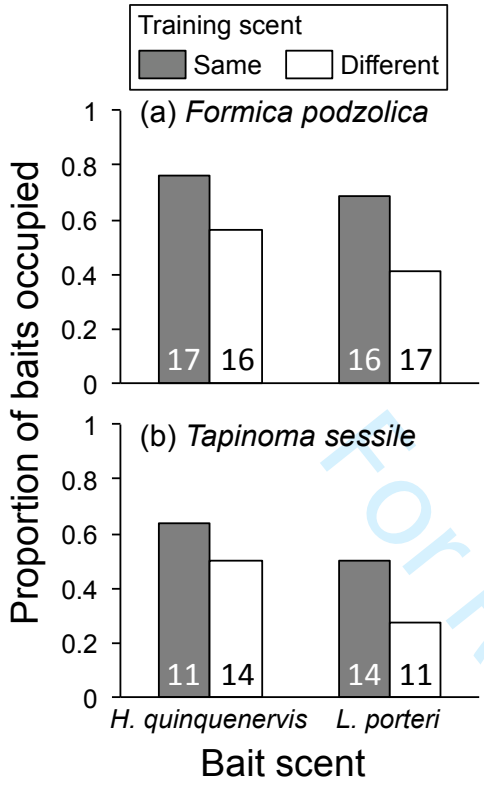
573 **Figure 1.**



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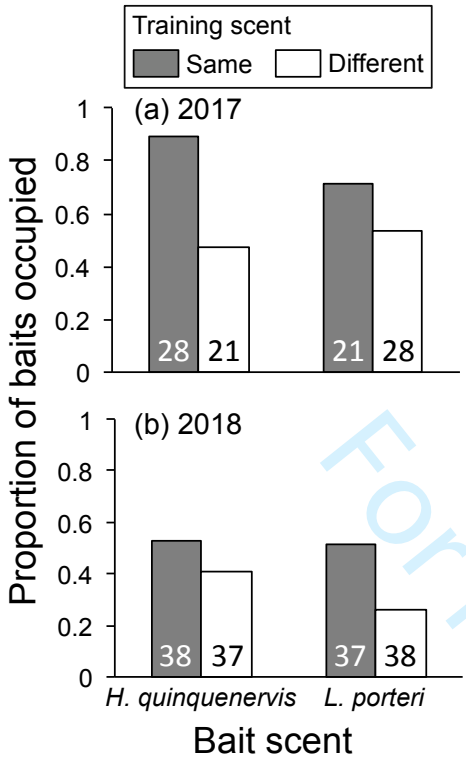
575 **Figure 2.**



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577 **Figure 3.**



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Appendix S1

Table S1.1 Study site locations.

Year	Site	Latitude	Longitude
2017	1	38.938861	-106.979028
2017	2	38.964500	-106.993361
2017	3	38.963972	-106.993667
2017	4	38.960306	-106.983389
2017	5	38.966250	-106.992806
2017	6	38.965194	-106.993389
2017	7	38.966028	-106.992944
2018	8	38.924697	-106.962622
2018	9	38.960594	-106.984317
2018	10	38.966331	-106.993453
2018	11	38.964514	-106.988944
2018	12	38.965503	-106.993858
2018	13	38.925719	-106.963186
2018	14	38.925803	-106.962400
2018	15	38.966472	-106.989578

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Title: Are ants botanists? Ant associative learning of plant chemicals mediates foraging for carbohydrates

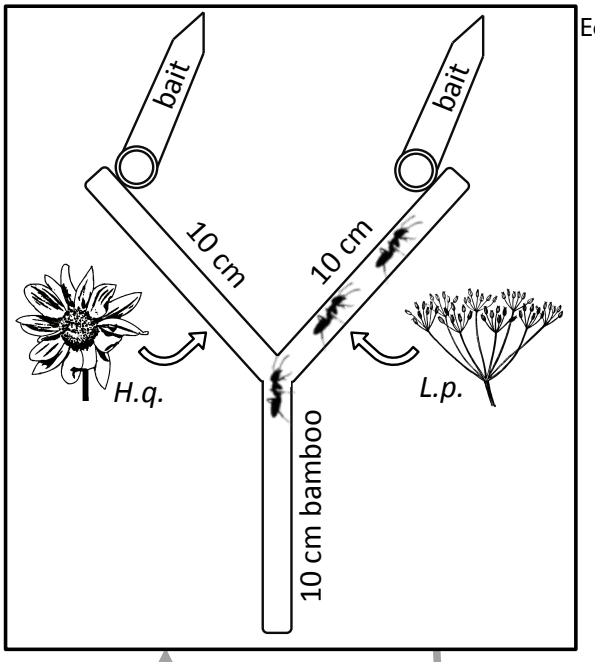
Authors: Nelson, Annika*; Zapata, Guillermo; Sentner, Keegan; Mooney, Kailen

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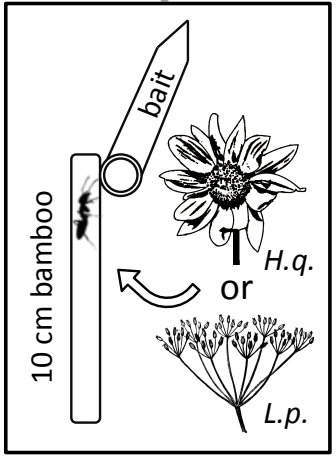
Highlights:

- Associative learning is widely documented in animals, but its relevance is unclear because learning is rarely studied in the field where training cues are juxtaposed against backgrounds of uninformative noise.
- Because ants rely on chemical cues when foraging and engage in many ecologically important interactions with plants, associative learning of plant chemicals could mediate ant selection of sugar-rich rewards.
- Here, we demonstrate associative learning of chemicals from two co-occurring plants by two ecologically and taxonomically distinct ant species across two years.

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choice



training

evidence for ant associative learning

