

Honey Bees Avoiding Ant Harassment at Flowers Using Scent Cues

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Abstract

Pollinators require resources throughout the year to maintain healthy populations. Along the urban–natural interface, floral resource availability may be limited especially when the system experiences extreme drought and fire threats. In such areas, succulents, such as *Aloe* spp., are commonly planted to serve as functional drought-tolerant, fire-protective landscaping, which can also support pollinator populations. However, access to this resource may be restricted by competition from other floral foragers, including invasive pests. We measured free-foraging honey bee (*Apis mellifera* L.) visitation rate and visitation duration to aloe flowers with and without Argentine ants (*Linepithema humile* (Mayr)) in a drought-stressed environment and found that bees actively avoided foraging on the ant-occupied flowers. To determine the mechanisms of avoidance, our subsequent experiments assessed visitation in the absence of ants and compared aloe flowers treated with ant pheromone to unmanipulated flowers lacking ant pheromone. Bees approached all flowers equally, but accepted flowers without ants at a higher rate than flowers with ants. Visitation duration also increased twofold on ant-excluded flowers, which suggests that Argentine ants may limit resource acquisition by bees. Honey bees similarly avoided flowers with Argentine ant pheromone and preferentially visited unmanipulated flowers at threefold higher rate. This study demonstrates that honey bees avoid foraging on floral resources with invasive Argentine ants and that bees use ant odors to avoid ant-occupied flowers. Resource limitation by this invasive pest ant may have serious implication for sustaining healthy pollinator populations at the urban–natural interface.

Key words: pollinator harassment, pheromone, invasive species, urban

Insects have evolved efficient foraging strategies that optimize reward intake and minimize opportunity costs (Heinrich 1975). Costs incurred when foragers encounter competitors at the resource (Corbet et al. 1995) may lead to subsequent shifts in foraging patterns and resource acquisition (Fontaine et al. 2008, Ishii 2013, Rogers et al. 2013, Tan et al. 2013). For species that provide vital ecosystem services, such as pollinators, any change in foraging behavior or strategy can have cascading effects throughout the ecosystem (Wardle et al. 2011).

Bees provide essential pollination services in natural and agricultural systems as well as in urban areas, such as parks or home gardens (Winfrey 2010). To maintain healthy populations, bees require consistent nectar and pollen resources from the environment, and are limited to flowers available within foraging distance from their nests (Lonsdorf et al. 2009). In some areas of the United States, such as southern California, meeting these nutritive needs may be especially challenging in times of drought (Minckley et al. 2013).

Floral resource availability (Mohan et al. 1984, Alqudah et al. 2011) and quality (Wyatt et al. 1992, Carroll et al. 2001) can be drastically reduced under drought conditions. Such drought-induced

changes may lead to shifts in plant–pollinator networks (Alarcón et al. 2008), with important implications for the stability of pollination services. Currently, much of the western United States is experiencing a multiyear drought, with California in extreme and exceptional drought conditions (Brown 2014). As such, water is strictly regulated and conservation measures are in place throughout urban areas. Adoption of water-wise and fire-safe landscaping has led to a change in the amount and type of floral resources available to sustain our urban pollinators. In particular, ornamental succulents are becoming increasingly popular in gardens and green roofs (Murray 2014) and, at some times of year, they can be the dominant plants in bloom. Thus, pollinators foraging in peri-urban areas may become increasingly reliant on ornamental plants to acquire resources when drought reduces the resource availability in natural areas.

Concurrently there has been increased interest by U.S. federal and state agencies, and the general public, in providing supplemental forage plants for pollinator management and conservation (Shepherd et al. 2003, Committee on the Status of Pollinators in North America 2007, Vaughan and Skinner 2009, Decourtye et al. 2010). Urban and peri-urban areas can be challenging systems to

manage owing to high anthropogenic activity and disturbance. However, the management of urban systems is of vital importance because they provide multiple ecosystem services and support biodiversity (Gardiner et al. 2013). The pollination service demands of urban areas dominated by ornamental plants typically are lower compared with those of natural or agricultural areas, where fruit and seed set is more important, but conservation in adjacent urban areas can help support pollinators along urban–natural and urban–agricultural interfaces (Colding 2007).

While urban environments may provide nutritional resources (Frankie et al. 2013), one of the challenges peri-urban pollinators face may be competition from urban pests that are attracted to these same resources. Argentine ants, *Linepithema humile* (Mayr), are a major nuisance pest in urban areas throughout the world, including South Africa, New Zealand, Australia, Europe, and the United States (Knight and Rust 1990, Wetterer et al. 2009). Argentine ants have been documented to reduce floral visitor diversity along the urban–natural interface (LeVan et al. 2014). Ants that displace visiting pollinators may reduce both resource acquisition by bees (Cembrowski et al. 2014) and reduce plant reproductive success (Hanna et al. 2015). Unlike other floral visitors—particularly bees that collect both nectar and pollen—Argentine ants collect only nectar (Lach 2005). As such, if exploitative competition between bees and ants is occurring, foragers collecting nectar would be most affected, whereas pollen foragers would be unaffected (Junker et al. 2010, Junker and Bluethgen 2010). However, if interference competition or any direct interaction between ants and pollinators is occurring, we would expect both nectar and pollen forager visitation to decline in the presence of ants.

To investigate these hypotheses, we examined European honey bee (*Apis mellifera* L.) resource acquisition from ornamental succulents in a drought-stricken urban area in southern California where Argentine ants are a major pest and ecological threat to native communities. We examined visitation to aloes (*Aloe* L.), which are increasingly popular plants in drought-stressed southern California because of their drought tolerance, beautiful floral displays, and high resistance to fire. In mild climates such as southern California, *Aloe* blooms in the winter and provides copious amounts of nectar to insect and bird pollinators (Koptur and Truong 1998, Symes et al. 2008, Symes and Nicolson 2008, Symes et al. 2009, Botes et al. 2009). Interestingly, aloe flowers are tubular, composed of elongated corollas (Fig. 1); as such, multiple ants may forage inside the flower consuming resources, but are not visually apparent to other floral foragers. Bee foragers may rely on other cues, such as ant odors or pheromone signals, to avoid ant competition.

Bee pollination is not required in this system, but aloe can provide vital floral resources to pollinators when few other flowering plants are in bloom. Further, water conservation and agencies recommend such xeriscaping with succulents for climates like southern California because they also highly resistant to fire and serve as defensible space (Shuler 1993, Costello and Jones 1994, Kent 2005, Knutson-Pederson 2005, Cobourn 2010, Hightower 2014); however, little is known about how these plantings impact the peri-urban pollinator community.

Here we investigated urban floral visitation to succulents in a drought-stressed environment and the mechanisms underlying interspecific interactions amongst floral visitors. This study represents an initial step in developing the foundation for supporting bees with drought-tolerant plants in urban settings. Using a combination of observational and manipulation experiments with the only bee and ant species present at the time of peak flower bloom, we addressed 1) how honey bee foraging behavior and floral resource utilization changes in the presence of Argentine ants, and 2) whether ant odor, in the absence of ants themselves, is sufficient to elicit shifts in honey bee foraging.



Fig. 1. *Aloe* L. hybrid cv. William Hertrich (*Aloe arborescens* x *Aloe succotrina*) visited by honey bee (*Apis mellifera* L.; located center-left). The flower structure and color are typical of *Aloe* spp. observed in this study. Photo by C.S. Sidhu.

Materials and Methods

We observed free-flying foragers of ornamental aloes on the campus of the University of California-Riverside (Riverside, CA). The campus is located at an urban–natural interface. This is a developed, high human-activity area adjacent to Box Springs Reserve, a natural area with low disturbance. All observations occurred from mid-January to late-February 2014 (average temp 18–24°C).

Native to South Africa, multiple aloe species are planted in southern California as ornamental plants, and are common in xeriscaping owing to drought tolerance (Cousins and Witkowski 2012). The aloe plants utilized in this study had bright red-orange colored flowers growing on stalks rising above the leaves of the plant. Each inflorescence consisted of multiple flowers at various stages (pre-bloom, in bloom, post-bloom), with a limited number of flowers available for resource acquisition by ants, bees, and birds (Fig. 1).

Bee Visitation Rate and Visitation Duration to *Aloe*

Bee pollinator visitation rate and duration were measured on plants of *Aloe ferox* in mid-January. Seven inflorescences on separate stems were treated with Tanglefoot (ConTech Inc., Victoria, BC) spread on 10 cm of flagging tape (L.E. Cooke Co., Visalia, CA) wrapped around the base of the stalk the day before observation, which excluded ants from the flowers. During each observational period, seven un-manipulated inflorescences with ant activity (ant-accessible) were selected, each paired with an ant-excluded inflorescence. We paired inflorescences based on similar inflorescence shape and number of blooming flowers.

Before observation, we assessed the ant activity on each inflorescence by counting the number of ants traveling up each stalk for 2 min. In addition, the total number of ants inside open flowers was counted immediately after each observation period. The counting destroyed the flowers, thus new flowers on inflorescences were observed each day. We observed these seven pairs for seven observational periods ($N = 49$ paired observations).

Visitation data were collected by two separate researchers observing one inflorescence in each pair simultaneously for 2 min, with observers randomly assigned to the ant-present or ant-excluded treatment. A flower was deemed “accepted” if the bee landed for >2 sec and manipulated the flower in any way. In contrast, a flower was considered “rejected” if the bee approached <1 cm directly in front of the corolla opening within antennal contact, but did not land or if the landing lasted <2 sec (Goulson et al, 2007). We measured visitation rate (number of bee acceptances per 2 min) and visitation duration (length of each visit in seconds). We also recorded if a bee fully entered the corolla.

Analysis

All statistical analyses were conducted in R v. 3.1.2 (R Core Team 2014). To analyze the effect of ants, we used GLMM with a Poisson error structure to compare acceptances relative to rejections at each flower across treatments; the ratio of acceptances to rejections for each flower during each observation trial was the y-response, the number of rejections was the weight, ant treatment was the fixed effect, while ant activity (number of ants walking on the stem), number of blooms per plant, date, and flower ID were random effects. Because observations occurred on separate days with only one exception, only date was included in the model. Within the GLMM construct, we assessed and removed one outlier from analysis (romr.fnc in package LMERConvenienceFunctions; Tremblay and Ransijn 2015) and reran the statistical analysis. To assess how visit duration was affected by ant presence, we used a GLMM, where ln(visit duration) was the y-response; treatment, ant rate, and total number of ants in flower were fixed effects; and number of blooms per plant, flower ID, and date were random effects. Again using romr.fnc, outliers were removed within the lmer object, resulting in two outliers being omitted from further analysis.

Visitation Avoidance: Bee Response to Ant Odor

The second part of this study was conducted at the University of California-Riverside Botanic Gardens (33.9714153, -117.3185336) on 10 *Aloe* species (Supp Table 1 [online only]) mid to late February 2014. During each observational period, —three to four plants were selected for observation. Three inflorescences with similar number of flowers in bloom, but lacking ants, were selected from each plant and treated with ant pheromone in hexane (“Pheromone” treatment), hexane only (“Hexane” treatment), or no treatment (“Control”). The pheromone (*Z*)-9-hexadecenal (Bedoukian, Danbury, CT) is an Argentine ant pheromone that is implicated in their aggregation and foraging behavior (Choe et al. 2012). This pure pheromone was mixed into hexane as a solvent that dissipates quickly upon application; however, a hexane-only treatment was included to control for any effects of the solvent itself. Similar to other Argentine ant studies (Westermann et al. 2014), we applied 0.1 ml of the appropriate liquid treatment to the edges of the corollas for each flower. The pheromone concentration was 1 ng/μl, which is low compared with other concentrations found in nature (Choe et al. 2014).

Each day, the visitation of honey bees to *Aloe* flowers was observed to each of the three treatments for 1 min each, consecutively. This was repeated five consecutive times for a total duration of 5 min per treatment per plant within a 15-min period. Visitation (acceptances and rejections of the flower by a bee) was recorded as bees interacted with the flowers. In total, 20 observation periods occurred over 7 days.

Analysis

To assess how honey bee foraging was affected by ant pheromone, we again used GLMM, where the ratio of acceptances to rejections was the y-response, number of rejections was the weight, treatment was the fixed effect, and *Aloe* species, observational period, time, and date were random effects. Again using romr.fnc, outliers were removed within the lmer object, resulting in eight outliers being omitted from further analysis. The mcposthoc.fnc (package: LMERConvenienceFunctions; Tremblay and Ransijn 2013) permitted post hoc testing from within the lmer object with Bonferroni corrections, and allowed for assessment of differences among the different treatments (pheromone, hexane, and control).

Latency of Hexane and Pheromone and Their Subsequent Effects on Bee Foraging

To assess the degree to which the effects of hexane diminished over time, we compared bee visitation rate of flowers with hexane with control flowers without hexane. We observed Hexane and Control flowers for two sets of three consecutive trials (total of six trials). Each trial was 20 min in duration, such that inflorescences were each observed for 2 h in total. For the first set of trials, we had the following groups: two Controls (no manipulation), and one Hexane (treated with hexane, as described earlier, before initiation of observations). This was followed by the second set of three consecutive trials, where the one Control remained unmanipulated, hexane was re-applied to the Hexane treatment, and the former second control group was treated with hexane to become a second Hexane treatment. The one Control and two Hexane treatments were all observed as before. The entire procedure was replicated seven times. To control for any intrinsic differences between flowers in the two treatments, one group was a Control in the first set and treated with Hexane in the second set of trials. Ultimately, the Control-turned-Hexane group did not differ from the Control treatment during its unmanipulated phase in the first trial set and nor did it differ from the Hexane treatment once hexane was applied in the second trial set; therefore, this treatment was pooled appropriately within the other treatments for analysis.

To assess the degree to which the negative effects of pheromone diminished over time, we observed visitation to flowers with pheromone applied or to control flowers as described in the *Visitation avoidance* section. For 20 flower pairs, we observed visitation to Control and Pheromone treatments twice, the second observation occurring 2 h after the initial pheromone application. We then compared visitation rates to both the first Control and Pheromone treatments.

Analysis

We analyzed visitation for both dissipation experiments using GLMMs as previously described; however, we included an additional fixed effect of time, which was crossed with treatment.

Results

Visitation Rate and Visitation Duration Increased in Absence of Ants

Honey bees initially approached all flowers equally (mean ± SE, ant-excluded: 2.7 ± 0.4 vs. ant-accessible: 2.29 ± 0.4 approaches per 2 min, GLMM: $F=0.16$; $df=1, 74$, $P=0.69$). However, ant exclusion had a significant effect on whether the bee landed to accept the flower. Honey bees accepted ant-excluded flowers at a threefold higher rate compared with flowers with ants (Fig. 2A:

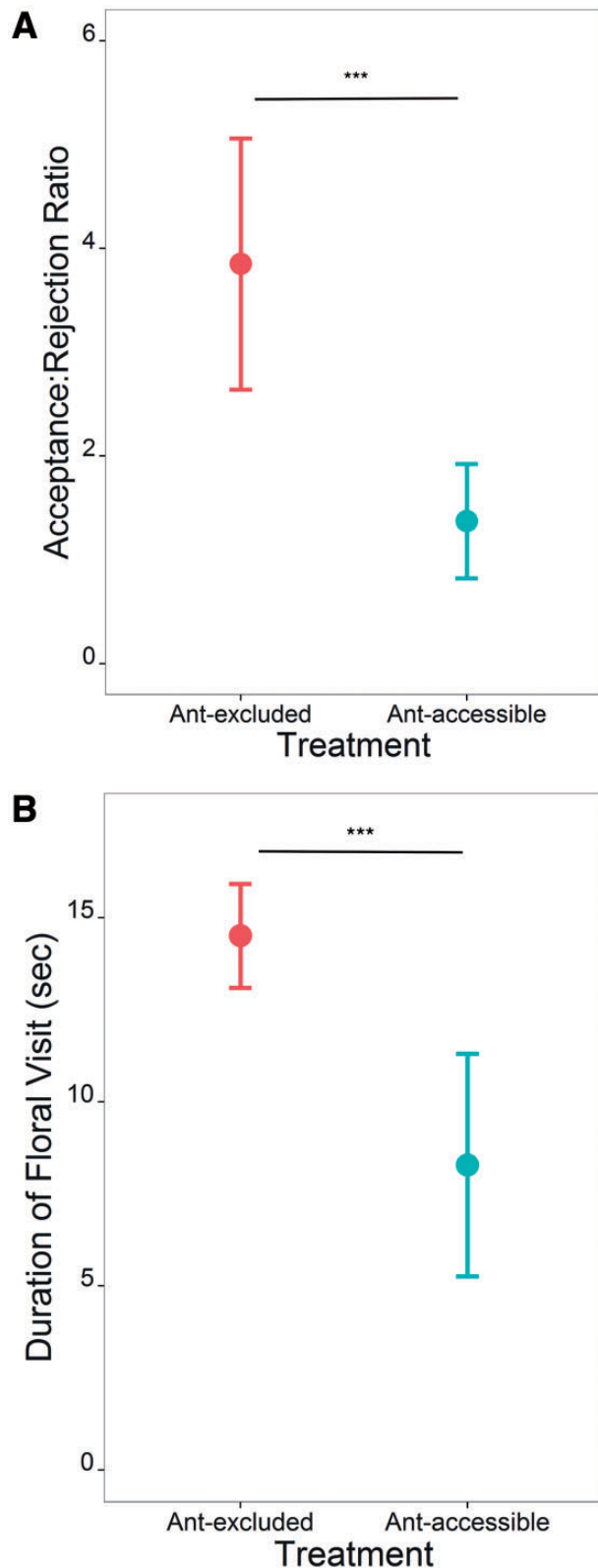


Fig. 2. Ant acceptance and visitation duration to ant-excluded and ant-accessible flowers. *** indicates $P < 0.001$. $N = 49$ paired observations (A) Ant-excluded flowers had a higher ratio of floral acceptance to floral rejection than did un-manipulated flowers accessible to ants (i.e., with ants present; GLMM: Treatment: $F = 28.665$; $df = 1, 90$; $P = 0.0007$). (B) Duration of floral visits (i.e., acceptances) differed with ant treatment. Bees spent 75% more time foraging on ant-excluded flowers than on un-manipulated ant-accessible flowers. (GLMM: Treatment: $F = 13.41$; $df = 1, 92$; $P = 0.0004$).

GLMM: Treatment: $F = 28.665$; $df = 1, 90$; $P = 0.0007$). Furthermore, once the flower was accepted, the duration of a honey bee visit was 75% longer on ant-excluded flowers than ant-present flowers (Fig. 2B: GLMM: Treatment: $F = 13.41$; $df = 1, 92$; $P = 0.0004$). Some bees fully entered the corolla when visiting the flower. Of the bees that did so, their visit was sixfold longer than bees that remained on but not in the flower (GLMM: $F = 51.09$; $df = 1, 89$; $P < 0.0001$; entered corolla, $N = 20$: 55.7 ± 17.5 sec; visited but did not enter, $N = 75$: 9.04 ± 0.95 sec). It was also noted that only 2 of 18 (11%) individuals fully entered the corolla of the ant-accessible flowers, while 18 of 77 (23%) individuals entered the corolla of the ant-excluded flowers.

Bees Avoided Flowers With Ant Cues

When honey bees visited flowers without ants but had the choice among unmanipulated control flowers, flowers with hexane applied, and flowers with ant pheromone component applied, chemical treatment had a strong effect on floral acceptance relative to rejection (Fig. 3: GLMM: Treatment: $F = 65.7$; $df = 2, 265$; $P < 0.0001$). As compared with control flowers, honey bees visited pheromone flowers only 11% as often (post hoc test: $t = 6.76$; $P < 0.0001$), and hexane flowers 38% as often (post hoc test: $t = 4.47$; $P < 0.0001$). Notably, foragers visited hexane-treated flowers threefold more often than they visited pheromone-treated flowers (post hoc test:

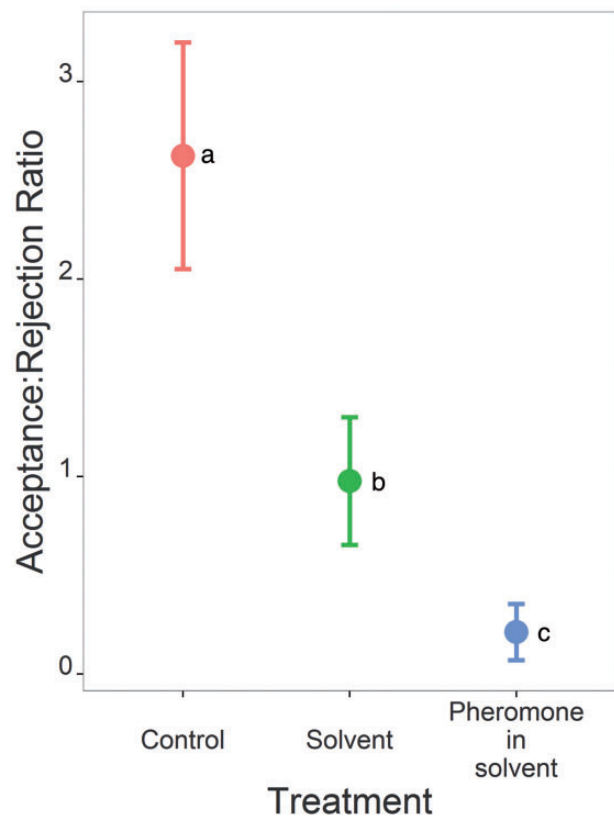


Fig. 3. Treatment had a strong effect on subsequent acceptance or rejection by honey bees (GLMM: Treatment: $F = 65.7$; $df = 2, 265$; $P < 0.0001$). Using post hoc tests within the GLMM, we found that Control treatments had higher acceptance relative to rejection than Hexane (post hoc test: $t = 5.06$; $P < 0.00001$) and Pheromone (post hoc test: $t = 7.376$; $P < 0.00001$) treatments. Additionally, Hexane treatments had significantly higher acceptance relative to rejection than Pheromone treatments (post hoc test: $t = 2.34$; $P = 0.0196$). Different letters indicate significant difference; $P < 0.05$. $N = 20$ observations per treatment.

$t = 2.33$; $P = 0.0205$). Similar to the ant-exclusion experiment, the total number of initial approaches did not differ among treatment (pheromone: 3.23 ± 0.40 vs. hexane: 3.19 ± 0.39 vs. control: 2.72 ± 0.35 approaches).

Hexane Application Decreases Visitation Over the Short-term

We detected a significant negative effect of the solvent, hexane, only in the first trial (0–20 min). In immediately subsequent trials, the hexane application did not impact visitation by Trial 2 (21–40 min) and Trial 3 (41–60 min; GLMM: Treatment: $F = 15.89$; $df = 1, 55$; $P < 0.0001$; Time: $F = 1.76$; $df = 2, 55$; $P = 0.18$; Time \times Treatment: $F = 6.23$; $df = 2, 55$; $P = 0.0036$). Post hoc tests within the GLMM indicate that Hexane is only significantly different from Control in the first 20-min period (Trial 1) immediately following application, (post hoc: $t = 2.61$; $P = 0.01$), and not in any other period (Trial 2: $t = 0.30$; $P = 0.77$, and Trial 3: $t = 1.03$; $P = 0.31$). Thus, recovery in visitation rate to foraging levels observed before hexane application occurred within 20 min.

Pheromone Effectively Decreases Visitation for Hours After Application

Two hours after initial treatment, we still detected a significant effect of treatment (GLMM: Treatment: $F = 38.8$; $df = 1, 333$; $P < 0.0001$; Time: $F = 2.10$; $df = 1, 37$; $P = 0.16$; Time \times Treatment: $F = 13.91$; $df = 1, 333$; $P = 0.0002$). Even 2 h after treatment with pheromone, visitation was 50% lower in comparison with control flowers (0.26 ± 0.06 vs. 0.52 ± 0.08 acceptances, respectively; post hoc $t = 3.73$; $P = 0.0002$). We did see marginal increases in acceptance to pheromone-treated flowers after 2 h as compared with after application (0.26 ± 0.06 vs. 0.06 ± 0.03 acceptances, respectively; post hoc $t = 3.22$; $P = 0.0014$)—a much slower recovery response than observed for hexane.

Discussion

Our study demonstrates that honey bees actively avoid foraging on flowers that have invasive Argentine ants and spend significantly less time on ant-occupied flowers. As time spent actively foraging on a flower is known to be positively correlated to the amount of resource collected (Cembrowski et al. 2014), bees likely collect fewer resources from flowers when ants are present. Moreover, honey bees fully entered the corolla only half as often when the flower was occupied by ants as compared with when entering ant-excluded flowers. This avoidance behavior corresponds with other studies that document similar reduction in pollinator visitation rate in the presence of Argentine ants (Lach 2008, LeVan et al. 2014, Hanna et al. 2015).

This study identifies ant pheromone as one mechanism honey bees use to avoid ants at flowers. Our findings, which were conducted in a realistic free-foraging urban environment, are consistent with a recent laboratory study that showed bumble bees avoid artificial flowers recently visited by ants (Cembrowski et al. 2014), and a field study that showed Giant Asian honey bees avoiding live weaver ants at the same rate they avoid weaver ant pheromone (Li et al. 2014). The shape of the *Aloe* flower with its elongated, tubular corolla likely limits the use of visual cues because foraging ants regularly stay hidden within the corolla at the nectar source (C.S.S., personal observation). This is supported by equal numbers of approaches in both experiments to flowers with and without ants or their odors. Only upon proximity did bees then use alternative cues,

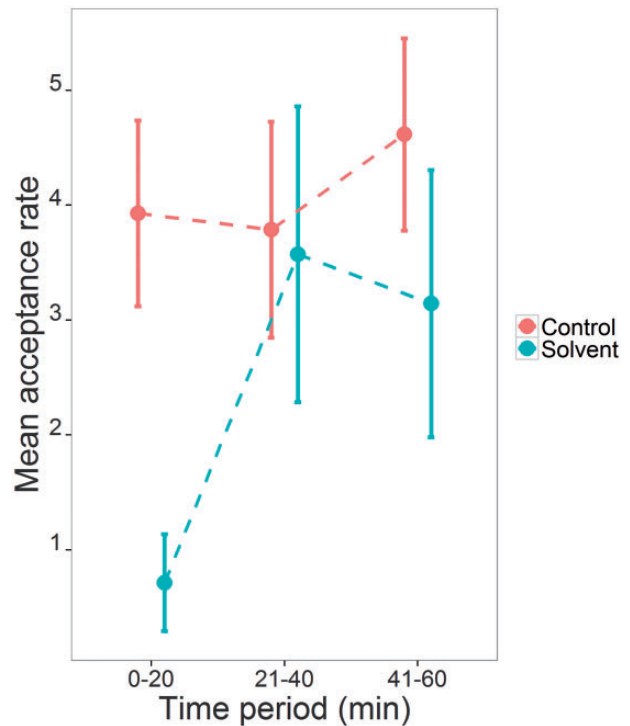


Fig. 4. Application of solvent led to decreased pollinator acceptance of a flower only in the first 20-min observation period (0–20 min). There was no evidence of decreased visitation at subsequent time points (21–40 min and 41–60 min). $N = 21$ paired observations.

such as pheromone signals, to assess ant presence and subsequently chose to avoid occupied flowers.

Despite Argentine ants' aggressive reputation, we did not observe direct agonistic interactions between bees and these invasive ants. Honey bees exhibited a strong avoidance of flowers with ants, as both experiments detected a threefold difference in floral utilization between flowers with and without ants or their odor. Our results are consistent with evidence that pollinators often assess risk to avoid hazards (Corbet et al. 1995, Bray and Nieh 2014) and will use multiple cues to detect dangerous situations (Dawson and Chittka 2014). The bees did not reject all flowers occupied by ants (20% of all visits were to flowers with ants or their pheromone signals); future studies should quantify an ant-presence threshold that foraging bees are willing to tolerate. Indeed, the threat of risk is known to reduce visitation to floral resources by bees (Goncalves-Souza et al. 2008, Llandres et al. 2012) such that bees prioritize predator avoidance at the expense of maximizing floral reward (Wang et al. 2013). Honey bees also tend to avoid interference when foraging (Rogers et al. 2013); for example, avoiding recently visited flowers (where resources are presumably already taken) by rejecting flowers with conspecific scent (Giurfa and Nunez 1992). Here, harassment may be a proximate cause of the observed threat avoidance behavior. However, because our study did not specifically capture harassment behavior, additional research using naïve bees could provide elucidation as to what—if any—agonistic interactions are sufficient to elicit the ant avoidance.

We acknowledge that the solvent used for pheromone application reduced visitation rate of honey bees to ant-free flowers; however, visitation to pheromone flowers was significantly reduced relative to both hexane and control flowers. We found that the effects of hexane had dissipated after 20 min (Fig. 4). Thus, we likely

observed the negative solvent effect because observations of the primary ant scent experiment were conducted within 15 min of initial chemical application. Unlike volatile hexane alone, we found that the negative effect of pheromone on bee visitation was still detectable up to 2 h after application: the control flowers received nearly *fourfold more visitors* than pheromone-treated flowers 2 h after application. These results are completely consistent with the observed differences between pheromone-treated and control flowers from the visitation avoidance experiment, and those between ant-occupied and ant-excluded flower experiment. Therefore, we demonstrate that the pheromone itself elicits a stronger and longer-lasting avoidance behavior in bees. Future studies using hexane as a solvent for pheromone application should account for hexane dissipation or consider an alternative solvent.

In this study, we examined pollinator foraging on an ornamental succulent at the urban–natural interface. At certain times of the year, in semi-arid or drought-prone climates, ornamental plants can provide supplementary resources to honey bees and other pollinators along the urban–natural boundary (Hernandez et al. 2009, Frankie et al. 2013). Here, we showed that honey bees regularly visit flowering succulents in drought-stressed peri-urban environments. The presence of Argentine ants (or even their odors) is sufficient to negatively impact bee foraging behavior despite limited resources. Decreased visitation and resource collection activities have serious implications for sustaining healthy urban pollinator populations, especially under drought conditions. As a result, ants are a serious pest to consider in such landscapes when developing strategies to manage pollinators and promote their pollination services, while minimizing the negative impact of invasive urban pests on pollinators.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

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Contribution of authors: C.S.S. and E.W.R. designed the experiment, C.S.S. conducted data collection, E.W.R. conducted statistical analyses, and C.S.S. and E.W.R. wrote the manuscript.

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