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NATURAL HISTORY NOTE

Ants and Ant Scent Reduce Bumblebee Pollination of Artificial Flowers

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ABSTRACT: Ants on flowers can disrupt pollination by consuming rewards or harassing pollinators, but it is difficult to disentangle the effects of these exploitative and interference forms of competition on pollinator behavior. Using highly rewarding and quickly replenishing artificial flowers that simulate male or female function, we allowed bumblebees (*Bombus impatiens*) to forage (1) on flowers with or without ants (*Myrmica rubra*) and (2) on flowers with or without ant scent cues. Bumblebees transferred significantly more pollen analogue both to and from ant-free flowers, demonstrating that interference competition with ants is sufficient to modify pollinator foraging behavior. Bees also removed significantly less pollen analogue from ant-scented flowers than from controls, making this the first study to show that bees can use ant scent to avoid harassment at flowers. Ant effects on pollinator behavior, possibly in addition to their effects on pollen viability, may contribute to the evolution of floral traits minimizing ant visitation.

Keywords: ant-pollinator conflict, pollination, competition, *Bombus impatiens*, *Myrmica rubra*.

Introduction

Trait-mediated indirect interactions arise when a focal species causes phenotypic changes, including behavioral modifications, in a second species and these effects cascade to still other species (Werner and Peacor 2003). Although trait-mediated indirect interactions are often studied in food webs (e.g., Werner and Peacor 2003; Preisser et al. 2005), they are not limited to trophic interactions. For example, the threat of predation can change the behavior of a mutualist, thus affecting its partners (Suttle 2003). In animal-pollinated plants, predators can disrupt pollination directly through density-mediated indirect interactions (Dukas 2005) or via trait-mediated indirect interactions by changing pollinator behavior. When predators are present, pollinators may switch to visiting less rewarding flowers, or they may avoid flowers altogether, potentially reducing the amount of pollen donated or received by a flower and thus decreasing plant fitness (Gonçalves-Souza 2008; Ings and Chittka 2009). Similarly, competition for floral rewards with other flower visitors may cause behavioral changes in pollinators (Maloof and Inouye 2000; Ohashi et al. 2008). Previous research has shown that bees may spend less time visiting flowers depleted of rewards (Thomson 1986) and may avoid flowers bearing scent marks that indicate recent visits by other individuals of the same or different bee species, as these flowers are likely to be depleted (Stout and Goulson 2002).

Whereas competition between pollinators may not be particularly costly for the plant because both competitors are likely to provide pollination services, competition between pollinators and organisms that do not usually provide a pollination service, such as ants, has a greater potential to reduce plant fitness. Ants are common floral visitors; they are attracted to flowers for nectar (Lach 2007) and, in some cases, pollen (Byk and Del Claro 2010) and will often defend these resources against other flower visitors (Altshuler 1999). However, ants rarely contribute much useful pollination; antibiotic secretions present on their cuticles kill pollen grains (Beattie et al. 1985; Dutton and Frederickson 2012), and when foraging in flowers, ants sometimes impede female function by damaging stigmas (Galen and Cuba 2001). We will henceforth consider ants to be nonpollinators and will contrast them to animals like bees that are pollinators. Ants are capable of competing with pollinators in two ways: (1) by consuming floral rewards and reducing their availability to pollinators (i.e., exploitative competition) and (2) by directly antagonizing and excluding pollinators from flowers (i.e., interference competition).

Many plants benefit from the presence of ants; numerous plant species recruit ants using extrafloral nectar, food bodies, or domatia because ants provide protection against folivores (Heil and McKey 2003). Similarly, some plants

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have extrafloral nectaries on or near reproductive tissues that recruit ants that deter florivores (e.g., Inouye and Taylor 1979). However, plants may incur reproductive costs as a result of their association with ants. Some ant species that nest in myrmecophytes sterilize flowers to shunt plant resources from reproduction to vegetative growth, allowing for greater ant colony growth (Frederickson 2009). Also, ants visiting extrafloral nectaries may be attracted to floral nectaries, where they can harass pollinators (Ness 2006). There is growing evidence that many angiosperms have evolved floral traits that prevent ants from accessing flowers during anthesis (Willmer and Stone 1997; Ballantyne and Willmer 2012). The effects of flower-visiting ants can be substantial. Ants can decrease the frequency, duration, or species diversity of pollinator visits to flowers (Lach 2008; Hansen and Müller 2009; Junker et al. 2010; Gonzálvez et al. 2012), all of which potentially impact pollen donation and receipt. In some studies, changes to pollinator behavior induced by ants have also been linked to seed set.

It is difficult, however, to disentangle the intertwined effects of exploitative and interference competition in nature. If ants disrupt pollination, then plants may often evolve traits to deter ants from flowers (Willmer et al. 2009). From a practical standpoint, this would then limit our ability to study the effects of ants on pollinator visitation, because ants would not visit flowers. Here we used artificial flowers to explore ant-bee interactions in the absence of floral defenses against ants. We used highly rewarding, quickly replenishing artificial flowers to examine how direct harassment (i.e., interference competition expressed through behavior) changes bee foraging behavior and how this affects donation and receipt of a pollen analogue (powdered food dye) while minimizing the effects of exploitative competition. We predicted that flowers visited by ants would both donate and receive less pollen analogue than flowers without ants because bees would avoid flowers with ants or leave them sooner. Because scent plays a large role in bumblebee communication and flower choice (Stout and Goulson 2002), we also tested whether the presence or absence of ant scent on artificial flowers would affect pollen analogue donation because of changes in the foraging behavior of bumblebees.

Methods

Subjects

Myrmica rubra is an invasive ant in eastern North America with a range and habitat preferences overlapping those of *Bombus impatiens*, a common bumblebee. Because *M. rubra* visits flowers (A. Cembrowski, personal observation), the two species likely interact in nature. We collected 12 *M. rubra* colonies in the fall of 2011 and 2012 from Toronto, Ontario, and the surrounding area and maintained them in environmental chambers on an artificial diet (Dussutour and Simpson 2009) and a 16L : 8D schedule (light 6:00–22:00). We used these colonies as sources of *M. rubra* workers for experiments.

Workers from commercially supplied colonies of *B. impatiens* (Biobest Canada, Leamington, Ontario) foraged on artificial flowers in flight cages (either 2.4 × 2.4 × 2.1 m or 7.9 × 3.4 × 2.0 m) at the University of Toronto. We tested a total of five bee colonies: four colonies were used in the ant presence trials, and two of these and one additional colony were used in the ant scent trials. Flight cages had overhead fluorescent lights attached to timers. In contrast to most previous studies in which bees have been trained and tested individually, the entire worker force of a bee colony was free to forage at will in our experiments. Colonies were trained to forage on artificial flowers for at least 4 days before being used in trials. After being used for a trial, the colony was not used for at least 2 days to reduce dye carryover between trials. Between trials, bumblebees were fed pollen and given sugar water.

Artificial Flowers

The flowers (fig. 1; Thomson et al. 2012; see also Makino 2008) consisted of glass jars filled with 30% w/v sucrose solution. Sugar water traveled by capillary action up a sewing-thread wick to a hole in a blue-painted lid, accumulating in a knot that acts as a nectary. Flowers depleted by visitors were quickly replenished via capillary

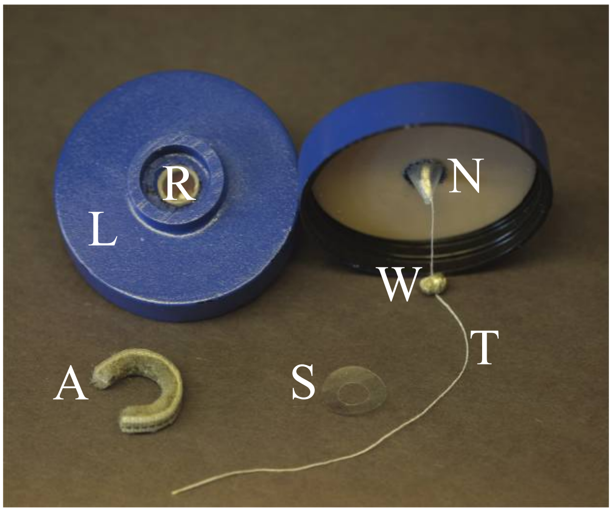

Figure 1: Artificial flower lids. A = anther, L = lid, N = nectary, R = region where anther or stigma is placed, S = stigma, T = thread, W = weight.

action and were nonrewarding only very briefly after visits, taking less than a minute to accumulate 0.5 μL; note that bumblebee visits to a single flower are often separated by several minutes or more (A. Cembrowski, unpublished data).

Unlike most previous artificial flower designs, these flowers allow for estimation of male and female fitness, because we can measure both the amount and type of dye received by female flowers (see "Dye Quantification," below). In order to access nectar on a "male" flower, a bee must crawl through a circular "anther" of brushlike weather-stripping material dusted in a consistent manner with our pollen analogue, powdered food dye (FD&C 5 or FD&C 6), which is transferred to the bee in the process. On a "female" flower, a bee crawls through a sticky plastic reinforcement that functions as a stigma, receiving dye from the bee's body. Male flowers dispensed dye particles over multiple bee visits and could still dispense dye at the end of trials. They resemble many real flowers or flower heads in that pollen is dispensed gradually over time, but less dye is available for transfer with each subsequent bee visit (Harder and Thomson 1989).

Flight Cage Trials

We conducted 6 ant scent trials between March 22 and June 4, 2012, and the remaining trials (16 ant presence trials and 9 ant scent trials) between November 9, 2012, and January 6, 2013. Ant presence trials lasted for 8 h, and ant scent trials lasted for 4 h. Artificial flowers were prepared and placed individually in small plastic containers treated with Fluon (Insect-a-Slip, BioQuip, Rancho Dominguez, CA) to prevent ants from escaping. In ant presence trials, we used 32 flowers (16 male flowers and 16 female flowers), arranged in an 8 × 4 array, with flowers spaced 45 cm apart between rows and 30 cm within rows. Ant scent trials used 20 flowers (10 male flowers and 10 female flowers) in a 4 × 5 array, with flowers spaced 30 cm apart between and within rows. In all of the ant presence trials and nine of the ant scent trials, we counted the number of bees actively foraging after 1 h to get a measure of colony activity.

Ant Presence Trials

We examined the effects of ants on the amount of dye donated by male flowers and received by female flowers in 16 trials, testing four bee colonies four times each. The containers of 8 randomly chosen male flowers and 8 randomly chosen female flowers received 15 *M. rubra* workers each; the other 16 flowers remained free of ants. Isolated from their colonies, *M. rubra* workers have nowhere to deposit sugar water they collect and, therefore, may become sated; nonetheless, a force of 15 ant workers was enough to maintain visitation to the nectaries where bees foraged while still rarely having more than one or two ants visit the nectary at any time. As ants attacked bees, bees would occasionally carry or throw attacking ants off flowers, but despite this, some ants maintained their presence at the nectary throughout the trials. Because ants the size of *M. rubra* consume liquids slowly (∼0.17–0.24 μL/min; Davidson et al. 2004), flowers replenished nectar more quickly than ants consumed it. We used two colors of dye (FD&C 5 and FD&C 6) to differentiate male flowers with and without ants. In two trials for each bee colony, anthers of male flowers with ants were coated with FD&C 5 dye, while brushes of male flowers lacking ants were coated with FD&C 6 dye. In the other two trials, we reversed dye colors to control for effects of dye type and color. Dye color was assigned in a random order. Artificial flowers were placed in randomly assigned positions in the array before we opened the colony and allowed the bees to begin foraging.

Scent Trials

We explored the effect of ant scent on dye donation in 15 trials, testing three bee colonies in 6, 5, and 4 trials each. We first exposed bees to ants by allowing the bees to forage for 8 h on 20 flowers (10 male and 10 female), of which 5 male flowers had 15 ants while all others had none. No dye was used during this exposure day. We then collected all but the 5 ant-free male flowers in the flight cage, leaving these flowers to keep bees foraging. Next, we individually stored five new male lids in Fluon-treated containers with 10 *M. rubra* workers. Five control male lids were put in identical containers lacking ants. The following morning, we removed the remaining flowers and set out 10 new male and female flowers in a random spatial arrangement, using the lids having or lacking ant scent. Thus, the ant-scented flowers were not in the same positions as the ant-visited flowers on which the bees were trained. Only 5 male flowers had ant scent, and the other 15 flowers (5 male and 10 female) did not. We used the same two dye colors as in the ant presence trials to differentiate male flowers with and without ant scent and randomized which color was used for ant-scented flowers between trials. We collected and replaced stigmas from female flowers after 1 h and collected the stigmas again after 4 h. In the first trial performed, we also collected stigmas after 2 h, but due to the small amount of dye transferred, this was not repeated.

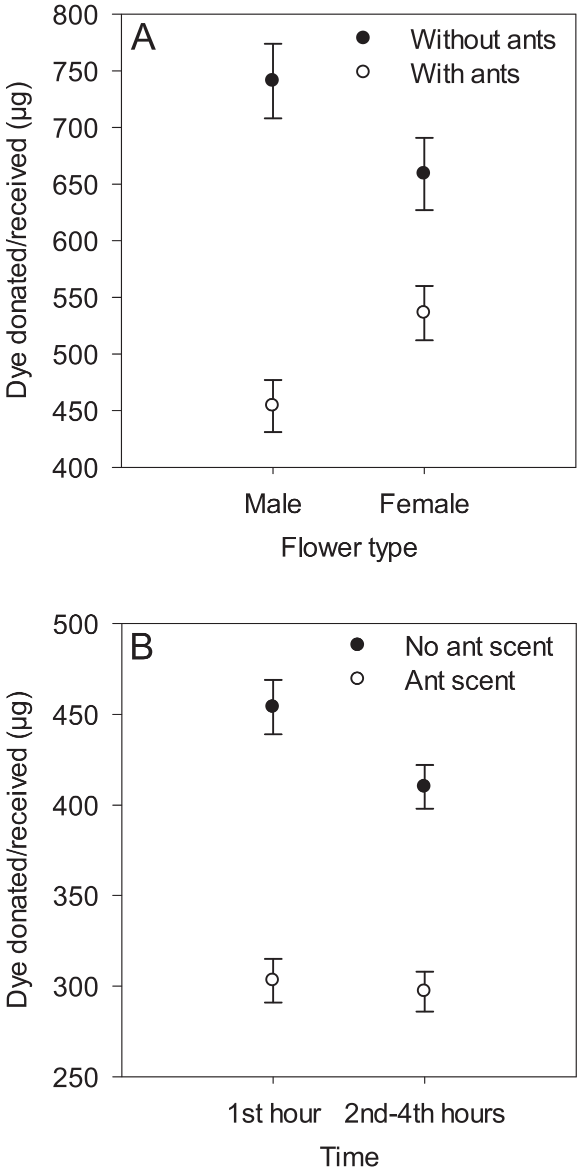

Figure 2: Dye transferred (mean ± 1 SE) per trial by *Bombus impatiens* workers from artificial male and to artificial female flowers in the presence (open circles) and absence (filled circles) of *Myrmica rubra* workers (*A*) and from artificial male flowers with (open circles) or without (filled circles) *M. rubra* scent to ant-free female flowers in the first or the second to fourth hours of the trials (*B*).

Dye Quantification

After each trial, we quantified the amount of dye transferred to female flowers using a spectrophotometer. We removed the stigmas from female flowers, placed them in test tubes, added 5.1 mL of distilled water to each tube, and vortexed each tube thoroughly to ensure the dye was evenly diluted. These were diluted further, as needed, if the absorbance exceeded the sensitivity range of the spectrophotometer. In the first six scent trials, each stigma was analyzed separately, and the dye amounts were summed to obtain a total amount of each dye color transferred to female flowers in each trial. In all the ant presence trials and the other nine scent trials, we opted to treat the experiment as the unit of replication. Therefore, we combined stigmas from each treatment type (ant-visited or ant-free) in a test tube and measured the total amount of each dye color transferred in each treatment in each trial.

Because we put different dye colors on male flowers with and without ants, we could use the amount of each dye color donated to all female flowers to measure the reproductive success of ant-visited and ant-free male flowers. The total amount of dye (of both colors) received by female flowers with and without ants was our measure of female reproductive success. We calculated the amount of each dye color in the sample by measuring absorbance at 428 or 486 nm and converting absorbance to micrograms following computational methods for overlapping spectra (Blanco et al. 1989).

Statistical Analyses

In two trials (one ant presence and one ant scent), most female flowers received no dye because of low bee activity, so we excluded these trials from analyses. Because dye reception and donation values were non-normally distributed, we square-root transformed the data before examining the effects of ant presence or ant scent on dye transfer in ANCOVAs. For ant presence trials, we included ant presence on male and female flowers and their interaction as main effects and the total amount of dye transferred in each trial as a covariate to account for the large variation in overall dye transfer among trials. For ant scent trials, we included ant scent as the main effect, time (1 h or 4 h) as a repeated measure, the interaction between scent and time, and the total amount of dye transferred as a covariate. Covariate by treatment (ant presence or ant scent) interactions were never significant and so were excluded in final analyses.

Results

Bees usually started foraging within minutes of the beginning of the trial and continued until flowers were collected from the flight cage or the lights were extinguished. An average of 3.4 ± 0.12 and 4.0 ± 0.15 (mean ± SE) bees were foraging after an hour in the ant presence trials and ant scent trials, respectively. Male flowers with ants donated significantly less dye than male flowers lacking ants (fig. 2*A*; $F_{1,55} = 40.19$, $P < .0001$). Similarly, female flowers with ants received significantly less dye than female flowers lacking ants (fig. 2*A*; $F_{1,55} = 4.61$, $P = .036$). There was no significant interaction between ant presence on male flowers and ant presence on female flowers ($F_{1,55} = 1.18$, $P = .28$). Flowers with ant scent donated significantly less dye than flowers without ant scent (fig. 2*B*; $F_{1,25} = 112.16$, $P < .0001$). There was no significant effect of time ($F_{1,25} = 1.21$, $P = .28$) or interaction between time and scent ($F_{1,25} = 1.11$, $P = .30$) in the model. Data underlying figure 2 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3v7k3 (Cembrowski et al. 2013).

Discussion

In this study, ants altered bumblebee pollination behavior and exhibited trait-mediated indirect interactions with (artificial) flowers. Through interference competition, *Myrmica rubra* workers significantly affected the pattern of dye transfer by *Bombus impatiens*, causing a preferential flow of dye from male flowers lacking ants to female flowers lacking ants. If manifested in nature, then such effects would reduce the reproductive success of plants visited by ants through both male and female function.

Ants could have changed the attractiveness of artificial flowers in at least two ways. First, as ants interrupted or altogether prevented bumblebees from foraging at nectaries, bumblebees may have learned to avoid flowers with ants due to the relative inefficiency of foraging at these flowers, something bumblebees take into account (Heinrich 2004). Second, bees attempt to minimize their risk of being attacked during foraging bouts. Ants often attacked or harassed visiting bees by biting, grasping, and appearing to sting them, thus preventing the bees from accessing the nectary or reducing their time on flowers (see video 1, available online), and bees sometimes avoided ant-tended flowers entirely. This harassment was sometimes physically traumatic (video 1), and bees often appeared to have trouble flying after being attacked by ants. Previous research has demonstrated that bumblebees leave or avoid flowers where they have been harassed (Jones and Dornhaus 2011) and avoid foraging where there is visual or olfactory evidence of a predator or predation event (Abbott 2006; Goodale and Nieh 2012). Though it is unclear whether bumblebees viewed ants as competitors or predators, they responded similarly to flowers having ants as they do to flowers housing predators (Gonçalves-Souza et al. 2008).

To avoid artificial flowers with ants, bees likely used a combination of visual and olfactory cues. Previous research has shown that bees respond to conspicuous predators or predator "dummies" on flowers (Suttle 2003; Gonçalves-Souza et al. 2008), decreasing the frequency and duration of their visits to these flowers. Thus, bees may have been able to avoid flowers harboring ants by sight alone. However, even in the absence of ants, bees still preferentially visited flowers lacking ant scents (fig. 2*B*), suggesting that they had learned to associate ant scent with harassment. Bees are adept at associative learning (Wright and Schiestl 2009) and can learn to recognize unique scents left behind by both conspecific and heterospecific flower visitors (Stout et al. 1998). Bees can use these various scents, often arising from tarsal gland deposits (Stout et al. 1998), to recognize recently visited flowers that are less likely to be profitable (Stout and Goulson 2002). Recently, Ballantyne and Willmer (2012) demonstrated that bees learn to associate ant scents with unrewarding artificial flowers and decrease their visitation to these flowers. Our results complement their findings by showing that bees can associate ant scent with harassment at otherwise rewarding flowers.

Video 1: Still from a video (video 1, available online). Interaction between a *Bombus impatiens* bumblebee and a *Myrmica rubra* ant, with the bumblebee trying to dislodge the attacking ant.

In our study, ant scent caused bees to adjust their foraging strategy and decreased the amount of pollen analogue that was donated by ant-scented flowers. Thus, the effects of interference competition with ants on flowers can extend beyond immediate interactions and may have fitness consequences for plants, even when ants are absent. Like other olfactory cues, these effects are likely transitory (Stout et al. 1998). Although more dye was still donated by male flowers lacking ant scent than those with ant scent, the ratio of dye donated was, on average, closer to equality in the second to fourth hour than in the first hour (fig. 2*B*). This effect may be partially driven by dye depletion of male flowers without ant scent, but the lack of a strong corresponding decrease in flowers with ant scent suggests that visitation patterns became more similar. We did not test whether *B. impatiens*'s avoidance of ant scent was an innate or a learned behavior, but previous work has shown that *Bombus terrestris* does not innately avoid flowers with ant scent (Ballantyne and Willmer 2012).

Ants may be necessary for plant survival and growth but can be costly for plant reproduction. The evolution of ant attractants such as extrafloral nectaries in some plant lineages suggests that the costs of ants can be outweighed by their protective abilities. However, in this study, flowers visited by ants received and donated significantly less dye, although they did retain some sexual function. The net benefit of having ants depends on whether ants increase plant fitness by reducing herbivory more than they decrease plant fitness by disrupting pollination. Alternatively, plants may actually benefit from the costs of ants to plant reproduction; ants that castrate flowers may be better defenders, increasing plant survival or vegetative growth when plants are young, allowing for increased reproduction later in life when the plant is colonized by less aggressive, noncastrating ants (Frederickson 2009; Palmer et al. 2010). In some plant species, pollinator harassment by ants may even be beneficial. Altshuler (1999) reported that *Ectatomma* ants greatly increased fruit-set of *Psychotria limonensis*, despite reductions in pollinator visitation rates, presumably due to increases in the rate of pollen outcrossing. Similarly, Gonzálvez et al. (2012) found that the presence of *Oecophylla smaragdina* ants on *Melastoma malabathricum* flowers reduced visitation by less effective pollinators and increased visitation by more effective *Xylocopa* bees, increasing plant fitness.

Cases of ants being beneficial to flowers appear to be the minority, and many plant species have traits that limit ant access to flowers. Several studies have detailed floral volatiles that are thought to mimic ant alarm pheromones and thus repel ants (Junker and Blüthgen 2008; Willmer et al. 2009). Other plants use structural modifications, such as narrow corollas or slippery stems, to limit ant access to flowers (reviewed in Willmer et al. 2009). Exploitative competition between ants and pollinators (Lach 2005; Ballantyne and Willmer 2012), as well as the lethal effects of ant antibiotic secretions on pollen grains (Beattie et al. 1985; Dutton and Frederickson 2012), may have resulted in selection on plants to reduce ant visits to flowers. Our results suggest that trait-mediated indirect interactions resulting from interference competition between ants and bees may favor plants that defend their flowers and their pollinators against ants.

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Literature Cited

Abbott, K. R. 2006. Bumblebees avoid flowers containing evidence of past predation events. Canadian Journal of Zoology 84:1240–1247.

Altshuler, D. L. 1999. Novel interactions of non-pollinating ants with pollinators and fruit consumers in a tropical forest. Oecologia (Berlin) 119:600–606.

Ballantyne, G., and P. Willmer. 2012. Floral visitors and ant scent marks: noticed but not used? Ecological Entomology 37:402–409.

Beattie, A. J., C. Turnbull, T. Hough, S. Jobson, and R. B. Knox. 1985. The vulnerability of pollen and fungal spores to ant secretions: evidence and some evolutionary implication. American Journal of Botany 72:606–614.

Blanco, M., H. Runiaga, S. Maspoch, and P. Tarin. 1989. A simple method for spectrophotometric determination of two-components with overlapped spectra. Journal of Chemical Education 66:178–180.

Byk, J., and K. Del Claro. 2010. Nectar- and pollen-gathering *Cephalotes* ants provide no protection against herbivory: a new manipulative experiment to test ant protective capabilities. Acta Ethologica 13:33–38.

Cembrowski, A. R., M. G. Tan, J. D. Thomson, and M. E. Frederickson. 2013. Data from: Ants and ant scent reduce bumblebee pollination of artificial flowers. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.3v7k3.

Davidson, D. W., S. C. Cook, and R. R. Snelling. 2004. Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. Oecologia (Berlin) 139:255–266.

Dukas, R. 2005. Bumble bee predators reduce pollinator density and plant fitness. Ecology 86:1401–1406.

Dussutour, A., and S. J. Simpson. 2009. Communal nutrition in ants. Current Biology 19:740–744.

Dutton, E. M., and M. E. Frederickson. 2012. Why ant pollination is rare: new evidence and implications of the antibiotic hypothesis. Arthropod-Plant Interactions 6:561–569.

Frederickson, M. E. 2009. Conflict over reproduction in an ant-plant symbiosis: why *Allomerus octoarticulatus* ants sterilize *Cordia nodosa* trees. American Naturalist 173:675–681.

Galen, C., and J. Cuba. 2001 Down the tube: pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. Evolution 55:1963–1971.

Gonçalves-Souza, T., P. M. Omena, J. C. Souza, and G. Q. Romero. 2008. Trait-mediated effects on flowers: artificial spiders deceive pollinators and decrease plant fitness. Ecology 89:2407–2413.

Gonzálvez, F. G., L. Santamaría, R. T. Corlett, and M. A. Rodríguez-Gironés. 2012. Flowers attract weaver ants that deter less effective pollinators. Journal of Ecology 101:78–85.

Goodale, E., and J. C. Nieh. 2012. Public use of olfactory information associated with predation in two species of social bees. Animal Behaviour 84:919–924.

Hansen, D. M., and C. B. Müller. 2009. Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. Biotropica 41:202–208.

Harder, L. D., and J. D. Thomson. 1989. Options for maximizing pollen dispersal of animal-pollinated plants. American Naturalist 133:323–344.

Heil, M., and D. McKey. 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. Annual Review of Ecology, Evolution, and Systematics 34:425–453.

Heinrich, B. 2004. Bumblebee economics. 2nd ed. Harvard University Press, Cambridge, MA.

Ings, T. C., and L. Chittka. 2009. Predator crypsis enhances behaviourally mediated indirect effects on plants by altering bumblebee foraging preferences. Proceedings of the Royal Society B: Biological Sciences 276:2031–2036.

Inouye, D. W., and O. R. Taylor Jr. 1979. A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. Ecology 60:1–7.

Jones, E. I., and A. Dornhaus. 2011. Predation risk makes bees reject rewarding flowers and reduce foraging activity. Behavioral Ecology and Sociobiology 65:1505–1511.

Junker, R. R., R. Bleil, C. C. Daehler, and N. Blüthgen. 2010. Intra-floral resource partitioning between endemic and invasive flower visitors: consequences for pollinator effectiveness. Ecological Entomology 35:760–767.

Junker, R. R., and N. Blüthgen. 2008. Floral scents repel potentially nectar-thieving ants. Evolutionary Ecology Research 10:295–308.

Lach, L. 2005. Interference and exploitative competition of three nectar-thieving invasive ant species. Insect Sociaux 52:257–262.

———. 2007. A mutualism with a native membracid facilitates pollinator displacement by Argentine ants. Ecology 88:1994–2004.

———. 2008. Argentine ants displace floral arthropods in a biodiversity hotspot. Diversity and Distributions 14:281–290.

Makino, T. T. 2008. Bumble bee preference for flowers arranged on a horizontal plane versus inclined planes. Functional Ecology 22: 1027–1032.

Maloof, J. E., and D. W. Inouye. 2000. Are nectar robbers cheaters or mutualists? Ecology 81:2651–2661.

Ness, J. H. 2006. A mutualism's indirect costs: the most aggressive plant bodyguards also deter pollinators. Oikos 113:506–514.

Ohashi, K., A. Leslie, and J. D. Thomson. 2008. Trapline foraging by bumble bees. V. Effects of experience and priority on competitive performance. Behavioral Ecology 19:936–948.

Palmer, T. M., D. F. Doak, M. L. Stanton, J. L. Bronstein, E. T. Kiers, T. P. Young, J. R. Goheen, and R. M. Pringle. 2010. Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. Proceedings of the National Academy of Sciences of the USA 107:17234–17239.

Preisser, E. L., D. I. Bolnick, and M. E. Benard. 2005. Scared to death? the effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509.

Stout, J. C., and D. Goulson. 2002. The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers. Behavioral Ecology and Sociobiology 52:239–246.

Stout, J. C., D. Goulson, and J. A. Allen. 1998. Repellent scent-marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). Behavioral Ecology and Sociobiology 43:317–326.

Suttle, K. B. 2003. Pollinators as mediators of top-down effects on plants. Ecology Letters 6:688–694.

Thomson, J. D. 1986. Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. Journal of Ecology 74:329–341.

Thomson, J. D., J. E. Ogilvie, T. T. Makino, A. Arisz, S. Raju, V. Rojas-Luengas, and M. Tan. 2012. Estimating pollination success with novel artificial flowers: effects of nectar concentration. Journal of Pollination Ecology 9:108–114.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.

Willmer, P. G., C. V. Nuttman, N. E. Raine, G. N. Stone, J. G. Pattrick, K. Henson, P. Stillman, L. McIlroy, S. G. Potts, and J. T. Knudsen. 2009. Floral volatiles controlling ant behaviour. Functional Ecology 23:888–900.

Willmer, P. G., and G. N. Stone. 1997. How aggressive ant-guards assist seed-set in Acadia flowers. Nature 388:165–167.

Wright, G. A., and F. P. Schiestl. 2009. The evolution of floral scent: the influence of olfactory learning by insect pollinators on the honest signaling of floral rewards. Functional Ecology 23:841–851.

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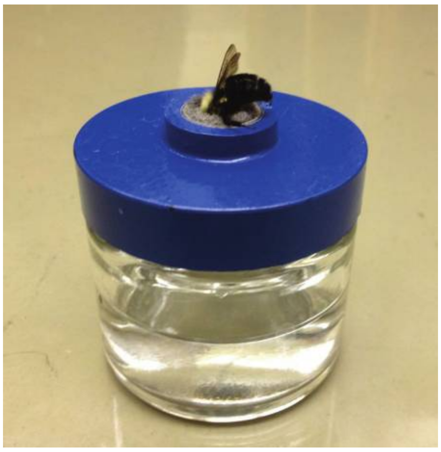

Bombus impatiens bumblebee visiting an artificial flower. Photograph by M. G. Tan.