Bees without Flowers: Before Peak Bloom, Diverse Native Bees Find Insect-Produced Honeydew Sugars

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ABSTRACT: Bee foragers respond to complex visual, olfactory, and extrasensory cues to optimize searches for floral rewards. Their abilities to detect and distinguish floral colors, shapes, volatiles, and ultraviolet signals and even gauge nectar availability from changes in floral humidity or electric fields are well studied. Bee foraging behaviors in the absence of floral cues, however, are rarely considered. We observed 42 species of wild bees visiting inconspicuous, nonflowering shrubs during early spring in a protected Mediterranean habitat. We determined experimentally that these bees were accessing sugary honeydew secretions from scale insects without the aid of standard cues. While honeydew use is known among some social Hymenoptera, its use across a diverse community of solitary bees is a novel observation. The widespread ability of native bees to locate and use unadvertised, nonfloral sugars suggests unappreciated sensory mechanisms and/or the existence of an interspecific foraging network among solitary bees that may influence how native bees cope with scarcity of floral resources and increasing environmental change.

Keywords: native bees, nonfloral cues, honeydew sugars, optimal foraging behaviors, interspecific foraging mechanism, bee communities.

Introduction

Bees and flowers are inextricably linked. Their mutualistic relationship has been a timeless focus for poets, artists, and naturalists as well as field ecologists, behavioral scientists, and evolutionary biologists. The obsession is not without merit. Bee visits to flowers for nectar and pollen are so crucial to angiosperm reproduction that bee preferences for floral colors, shapes, and scents have been credited with driving floral trait evolution, a radiation in angiosperm species diversity during the Late Cretaceous, and current plant community composition (Regal 1977; Ohashi and Yahara 2001; Wright and Schiestl 2009; de Jager et al. 2011; Ollerston et al. 2011; Bukovac et al. 2017). Because of this influential mutualism, research on bee foraging has focused on how bees detect and respond to floral visual and olfactory cues, petal thermal signatures, humidity signals from nectar reserves, and even floral electric fields (Herrera 1995; Chittka et al. 1999; Dyer et al. 2006; Whitney et al. 2008; Wright and Schiestl 2009; de Jager et al. 2011; Clarke et al. 2013; Frisch 2014; Orbán and PLoewright 2014). Very little, however, is known about bee foraging behaviors in the absence of floral cues, particularly among wild, solitary bee species.

Bees require sugar, usually as floral nectar, and protein, typically from pollen, for energy and reproduction (Michener 2007). While specialist bee species are particular about their pollen sources, bee visits to flowers for nectar sugars are usually indiscriminate (Linsley 1958). Honeydew is a nectar-like carbohydrate-rich excretion produced as a feeding by-product by phytophagous Hemipterans, such as scale insects (Hemiptera: Coccoidea) and aphids (Hemiptera: Aphididae), that can sometimes be more nutrient-rich than floral nectar (Batra 1993; but see Konrad et al. 2009). As a supplementary sugar source, it has been shown to promote increased fitness and longevity of some forest insects and was observed to be attractive to a variety of nonbee pollinators in New Zealand, even to the point of disrupting floral visitation patterns (Zoebelein 1957; Jacob and Evans 1998; Wäckers et al. 2008; Koch et al. 2011; Gardner-Gee et al. 2014). Some insects, most notably ants, cultivate mutualistic relationships with honeydew producers to ensure its continued flow, while others benefit from harvesting associated resources, such as the sooty mold fungus that grows...
on honeydew-laden branches or the waxy coating on scale insect cuticles (Morales et al. 1988; Bach 1991).

Despite similar potential benefits to our most important and imperiled pollinators, honeydew use by bees has been only sparsely documented, usually as isolated occurrences and almost exclusively among social, colonial species. Honey bees (Apis mellifera) and tropical, colonial stingless bees (Apidae: Meliponini) are known to incorporate honeydew into honey production, sometimes competing with ants or wasps for access to it, and to collect wax from scale insects, or even the insects themselves, for use in nest construction (Santas 1983; Crane and Walker 1985; Markwell et al. 1993; Camargo and Pedro 2002; Dimou and Thrasyvoulou 2007; Koch et al. 2011). A pair of articles from the 1990s document rare observations of bumble bees (Bombus spp.) “licking crystallizing droplets of honeydew from balsam twigs” in nectar-poor alpine tundra environments (Batra 1993; Bishop 1994). But while honeydew has been proven digestively plausible in the laboratory for at least one solitary bee species (Konrad et al. 2009), its use across a bee community has not been evaluated despite its potential role as an emergency resource for wild, solitary bee species during periods of temporary nectar limitation caused by habitat degradation, urbanization, or climate-induced temporal mismatches between pollinators and their host flowers (Potts et al. 2010; Bartomeus et al. 2011; Robbirt et al. 2014; but see Forrest 2015).

Widespread use of honeydew by diverse solitary bee species would have interesting implications for bee ecology, behavior, and conservation for two important reasons: (1) it represents a departure from the classic paradigm of the bee-flower mutualism as a tightly coupled relationship and (2) it suggests an as-yet unstudied source of resilience, both behavioral and physiological, among bees foraging to survive in a changing world. Honeydew as a sugar compound is nonvolatile and colorless, does not fluoresce or absorb UV light, and occurs independently of flowering resources (Thorpe et al. 1975; Friel et al. 2000; Frisch 2014). Prior to blooming of the host plant, therefore, it is a resource without apparent visual, olfactory, or floral advertisement. As such, the availability of honeydew before floral nectars provides a unique opportunity to evaluate natural, wild bee sensory abilities isolated from the floral attributes with which they may often be confounded. Ecologically, an ability of bees to expand conventional search images and diet breadth to include resources such as honeydew could be an important adaptation in habitats, like Mediterranean biomes, where the flora is predicted to be especially sensitive to global change (Klausmeyer and Shaw 2009). Faced with increasingly unpredictable foraging scenarios, honeydew could be an emergency resource for bees that can find it, helping them persist through nectar droughts and await the floral resources necessary to reproduce.

The Mediterranean chaparral habitats of Pinnacles National Park in the Inner South Coast Range of California are known for their dynamic, punctuated bloom cycles and rich, solitary bee fauna (Messinger and Griswold 2003; Meiners et al. 2015; Meiners 2016). Working in this area, one of us (J. M. Meiners) observed a diverse array of native, mostly solitary bee species visiting large, woody, prebloom Adenostoma fasciculatum shrubs (Rosaceae) during the early spring, when floral resources were still very limited (fig. 1). Some of these shrubs were covered in a dark “sooty mold” known to grow on the honeydew excretions of scale insects (Homoptera: Coccoidea; Santas 1983; Crane and Walker 1985; Wäckers et al. 2008). It was difficult to see exactly what the bees were doing on these plants, so we began noting the mold and bloom condition of each A. fasciculatum shrub on which we collected a bee during sampling for a broader biodiversity survey to quantify this perplexing attraction to moldy plants. Surprisingly, we recorded four times as many bees visiting moldy, prebloom A. fasciculatum shrubs as visiting mold-free varieties or either mold condition after flowering, confirming the association of bees with mold but raising new questions about the appeal and mechanism (fig. 2). These results prompted us to design an experiment for the following early spring to evaluate three central questions. First, what are bees getting from these prebloom plants (honeydew sugars, nutrients from the mold, something else)? Second, what are the potential visual, olfactory, thermal, or insect-insect cues alerting bees to this resource? And third, how widespread is this behavior across the bee community?

Material and Methods

Experimental Design

We designed seven experimental treatments to differentiate the possible mechanisms and causes of bee attraction to sooty mold and randomly assigned them to Adenostoma fasciculatum shrubs at three distinct 1-ha experimental sites in natural areas within Pinnacles National Park in San Benito County, California. Each selected site was a homogeneous chaparral habitat type dominated by the large, hardy, allelopathic A. fasciculatum shrubs and included an interspersed mixture of shrubs of similar stature that we could designate as either mold-free (absent of all sooty mold and scale insects) or naturally moldy (visibly covered on at least 50% of branches by sooty mold). Shrubs that were covered with sooty mold on fewer than 50% of branches (and thus fell in between our criteria for designation as either moldy or mold-free) were not included in the experiment. We applied each treatment (outlined below and in table A1, available online) to three woody shrubs of prebloom A. fasciculatum at each of the three sites, for a total of nine shrub replicates for each of seven treatments.
To control for any potential attraction, reflectance, or humidity signal to bees of differing quantities of moisture between plants, all seven treatments consisted of 5 oz of fluid sprayed on the assigned shrub (enough to coat the shrub in a thin layer of moisture) as described below.

Naturally moldy plants were sprayed with either (i) water to assess baseline bee visitation to moldy plants or (ii) a natural, short-residual insecticide (Orange Guard water-based indoor/outdoor home pest control; active ingredient, d-limonene, 5.8%) to evaluate the influence of live scale insects on bee visitation by halting their activity while leaving sugars and mold intact. The effectiveness of this d-limonene, which was selected to meet National Park Service restrictions against toxic substances, was tested and verified in the field by the inclusion of an insecticide control treatment (see item [ii] below).

Mold-free plants were sprayed with (i) water to quantify stochastic bee visitation; (ii) insecticide to test for an effect of this chemical on bee activity; (iii) nontoxic black paint to test for an attraction to either the dark visual cue of mold or potentially higher branch surface temperatures, which recent research has found to be attractive to bees (Dyer et al. 2006); (iv) a colorless, odorless 20% solution of sucrose and fructose (1:1) mixed from chemical-grade sugars to mimic the composition of insect honeydew (Wäckers et al. 2008); or (v) a combination of both the black paint and the sugar mixture to simulate the attraction of natural mold and examine interaction effects (treatments are summarized in table A1).

**Sampling Protocol**

Because the pilot study indicated that bee visits to honeydew were restricted to the early season (fig. 2), we concentrated our experiment in the period before peak bloom. We visited each site three times between late February...
and late April, when native bee activity has begun at Pinnacles National Park but prior to peak bloom of the plant community (Meiners et al. 2015). Sampling was conducted at one of the three sites per week on calm, sunny days above 15°C to ensure adequate bee activity. At 9 a.m. on each sampling day, we began by refreshing all plants with 5 oz of their assigned treatment spray, which remained the same throughout the experiment. After waiting an hour for the effect of the short-residual insecticide to take place and subside and for bee activity to commence for the day, a randomly ordered shrub list was divided between two collectors, who spent 5 min sequentially netting all bees visiting each respective plant. Temperature, wind speed, humidity, barometric pressure, and an estimate of cloud cover were recorded every 30 min during sampling. We sampled all 21 plants at a site once in the morning, beginning around 10 a.m., and once in the afternoon, around 1 p.m., to capture bees across the spectrum of diurnal activity. On sampling days, we recorded all flowering species in bloom within the site, approximately a hectare in size, to provide an estimate of floral richness and seasonal bloom progression. We also used an infrared thermometer to record surface temperatures of three different external branches of each plant at noon on sampling days to test for the possibility that darkened branches, by either natural mold or our sprayed paint treatment, offered increased perch warmth to foraging bees.

**Specimen Processing**

All bees were labeled and pinned into field boxes each evening, frozen for 48 h to protect from insect infestations, and transported to Utah, where they were identified to described species or unique morphospecies by experts at the USDA-ARS Pollinating Insects Research Unit (“Logan Bee Lab”). Bee specimens were examined under Leica dissecting microscopes and identified using the appropriate taxonomic keys and an extensive bee reference collection of approximately 1.5 million specimens. Bees were assigned unique matrix code numbers that were included with stan-
dard insect label data printed on labels affixed to each specimen pin and were curated into the Logan Bee Lab Museum collection.

Scale insect specimens were collected by breaking off moldy branches of *A. fasciculatum* plants not included in the study on which their carapaces were evident. These plant samples were sealed and securely mailed to Gainesville, Florida, where they were identified and retained by scale taxonomist experts at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry.

**Statistical Analyses**

We employed a generalized linear mixed-effects model with a negative binomial distribution to assess differences in bee visitation counts per 5-min sample period (the statistical model selection procedure is detailed in the supplemental material). Each experimental manipulation was included as a fixed effect, along with a linear time-of-day effect and a fixed effect for each site (there were not enough sites to estimate a site-level random effect). Two random effects were included: one to model variation in average bee visitation among the 63 plants, and the other to model fluctuations in bee abundance or activity across the nine sampling dates. We also evaluated the performance of smaller models that omitted some of the predictors to help determine variable importance using the Akaike information criterion (AIC; supplemental material, sec. 4). Finally, we compared these negative binomial models with simplified counterparts that assumed Poisson-distributed errors (i.e., that there was no overdispersion). If the negative binomial models outperformed the Poisson models (according to the AIC or likelihood ratio tests), this would provide evidence that bees were clustering on individual plants at a given point to an extent that cannot be explained by the fixed or random effects alone (Coxe et al. 2009).

Because we intentionally collected on warm, sunny, calm days, the variation in environmental variables was minimal; their inclusion in the statistical model did not improve the fit or change treatment significance (supplemental material, sec. 8). They were therefore omitted from the final model for simplification.

Differences among treatments were estimated by comparing the number of bees that would be expected to visit a given plant in a given 5-min observation window under different conditions according to the negative binomial model (e.g., if an experimental manipulation had a coefficient of 2 on the log link scale, then applying that manipulation would be expected to increase the number of bee visits by a factor of e², which is about 7.4). Ninety-five percent confidence intervals (CIs) for the effect of each treatment versus the control were calculated using the model's variance-covariance matrix (Lawless 1987). To compare the branch temperatures between blackened and not-blackened branches, we built a linear mixed-effects model with branch color (blackened or not), day of year, and site as fixed effects and plant as a random effect (fig. A1; figs. A1, A2 are available online).

All analyses were performed in the R programming language using the lme4 package (Bates et al. 2015; R Core Team 2015). Data have been deposited in the Dryad Digital Repository: http://dx.doi:10.5061/dryad.00t8g (Meiners et al. 2017). Code has been included in the supplemental material and has been deposited in Zenodo (Meiners and Harris 2017).¹

**Results**

**Insect Collection**

Despite a lack of floral cues and the early spring setting, our 378 plant samples yielded 308 bees from 42 different species across nine genera and five of the six North American bee families (table 1). Approximately three-quarters of total bee abundance and species richness came from the two sprayed sugar treatments (sugar treatment, sugar + paint treatment; table 1). Shrubs with naturally occurring mold (natural mold treatment)—and, hence, honeydew sugars—atracted more bees and species than any of the three treatments not anticipated to be attractive to bees (control, insecticide, and natural mold + insecticide treatments; table 1) or the treatment designed as a visual mimic of the dark color of mold (paint treatment; table 1).

Our data distribution was zero inflated, like most biological count data, with a mean of 0.81 bees per 5-min plant sample and a standard deviation of 2.0 (fig. A2). Unlike typically Poisson-distributed count data, we also recorded several very high values (up to 22 bees per 5-min plant sample). Indeed, the results of our likelihood ratio test of overdispersed error distribution suggest that our data fit a negative binomial model that includes clustering on individual plants in specific 5-min periods much better than the Poisson model that assumes independent arrivals (χ² = 30, df = 1, P < .0001; supplemental material, sec. 4; Coxe et al. 2009).

The scale insects present in this system were identified from first instars as belonging to *Parthenolecanium*, possibly *P. corni* (Hemiptera: Coccidae), which are known to infest *Adenostoma fasciculatum* and secrete honeydew in this region of California (Jordan et al. 1921; fig. 1c).

**Seasonal and Spatial Context**

Floral richness increased linearly across the season at all three experimental sites, as expected, from zero to 13 species recorded in bloom during sampling, confirming that sampling

¹. Code that appears in The American Naturalist is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.
### Table 1: Faunal list and count of bees collected on each of seven experimental treatments

| Family            | Genus       | (Subgenus) | Species                  | Sugar present on plant | Sugar not present on plant (controls) | No. bees collected for each of seven treatments |
|-------------------|-------------|------------|--------------------------|------------------------|---------------------------------------|-----------------------------------------------|
|                   |             |            |                          | Sugar                  | Natural mold + insecticide             | Natural mold + insecticide | Insecticide | Paint | Control (water) |
| Andrenidae        | Andrena    | (Derandrena) | californiensis            | 2                      | 2                                     | 3                              | 1                        |
|                   |             |            | n. sp.                   | 20                     | 13                                    | 10                             | 4                        | 6     | 4               | 8               |
|                   |             |            | chlorura                 | 4                      | 6                                     | 2                              | 1                        |
|                   |             |            | cerasifoli               | 8                      | 4                                     | 1                              | 1                        |
|                   |             |            | sola                     | 1                      |                                        |                                |                          |
|                   |             |            | chlorogaster             | 4                      | 5                                     | 4                              | 1                        | 1     | 1               | 1               |
|                   |             |            | atypica                  | 1                      |                                        |                                |                          |
|                   |             |            | hypoleuca                | 5                      |                                        |                                |                          |
|                   |             |            | w-scripta sp.            | 2                      |                                        |                                |                          |
|                   |             |            | sp. 17                   | 1                      |                                        |                                |                          |
|                   |             |            | sp. 18                   | 1                      |                                        |                                |                          |
| Panurginus        |             |            | gracilis                 | 1                      |                                        |                                |                          |
|                   |             |            | melanocephalus           | 2                      |                                        |                                |                          |
| Apidae            | Apis        | (Nomada)    | mellifera                | 1                      | 1                                     | 1                              | 1                        |
|                   |             |            | sp. F                    | 1                      |                                        |                                |                          |
|                   |             |            | sp. U                    | 3                      | 7                                     | 1                              |                          |
|                   |             |            | sp. W                    | 1                      | 1                                     |                                |                          |
| Colletidae        | Hylaeus     | (Hylaeus)    | granulatus               | 1                      |                                        |                                |                          |
|                   |             |            | verticalis              | 1                      |                                        |                                |                          |
|                   |             |            | calvus                   | 2                      | 8                                     |                                |                          |
|                   |             |            | nevadensis               | 8                      | 1                                     | 2                              |                          |
|                   |             |            | aff. episcopalis         | 2                      |                                        |                                |                          |
| Halictidae        | Halictus    | (Nealictus)   | farinosus                | 1                      | 1                                     |                                |                          |
|                   |             |            | tripartitus              | 3                      | 3                                     | 1                              | 1                        |
| Lasioglossum      | Dialictus   | (Seladonia)   | nevadense                | 9                      | 7                                     | 4                              | 2                        |
|                   |             |            | punctatoventre           | 11                     | 3                                     | 3                              | 1                        | 1     | 1               | 1               |
|                   |             |            | argemonis                | 2                      | 3                                     | 1                              |                          |
|                   |             |            | robustum                | 1                      |                                        |                                |                          |
|                   |             |            | sp. A                    | 1                      |                                        |                                |                          |
|                   |             |            | kincaidii               | 1                      |                                        |                                |                          |
|                   |             |            | rufscorner              | 1                      | 1                                     |                                |                          |
|                   |             |            | egregium                 | 6                      | 2                                     |                                |                          |
|                   |             |            | sisymbrii                | 11                     | 5                                     | 1                              |                          |
|                   |             |            | avalenense              | 9                      | 3                                     | 1                              | 1                        |
|                   |             |            | nigrescens              | 7                      | 8                                     | 5                              | 1                        |
| Sphexodes         |             |            | arvensiformis            | 1                      |                                        |                                |                          |
|                   |             |            | sp. B                    | 1                      |                                        |                                |                          |
| Megachilidae      | Protosmia   | (Chelostomopsis) | rubrifloris              | 1                      | 2                                     |                                |                          |

Total specimens (overall = 308) 119 101 41 12 17 7 11
Total species (overall = 42) 26 30 15 8 11 4 4
Statistical difference in bee count from control:

*a* See table 2.

* *P* < .05.

*** *P* < .001.
captured bee activity during the relatively nectar-depauperate period leading up to peak bloom, which occurs in May at Pinnacles and results in higher floral richness and abundance than was observed during the time frame (February to April) of this study (Meiners et al. 2015). Total bee specimens collected also increased over the 9-week duration of the study at all three sites, although including this trend in the model did not improve model fit. Similarly, the environmental variables recorded (e.g., cloud cover, ambient temperature, wind speed, humidity) did not improve model fit and did not affect the significance of treatment results (supplemental material, sec. 8). Bee abundance did not differ significantly between sites (supplemental material, sec. 5).

**Experimental Manipulations**

Sugar-treated plants averaged more than 12 total bee visits across the three sampling periods, while naturally moldy plants without insecticide averaged 4.5 visits and plants without sprayed or natural honeydew sugars averaged only 1.3 bee visits over the course of the experiment (fig. 3a). Our generalized linear mixed model allows us to assess the statistical significance of these differences while controlling for site, plant ID, and random day-to-day fluctuation in bee activity (table 2; supplemental material).

Model results confirmed our original observation that native bee visitation to prebloom *A. fasciculatum* is signifi-
Our unadvertised honeydew-mimic sugar solution induced significantly elevated levels on plants with natural mold, despite this resource lacking any floral cue (sample mean = 3.6 [95% CI: 1.2–8.4], P = .02; table 2). We found no base effect of the insecticide treatment on bee visitation compared with the control treatment (P = .39), indicating that its application to plants neither deterred nor attracted bees to treated plants 1 h after application. A significant interaction between the mold and insecticide treatments (reducing the expected bee count threefold; P = .039; fig. 3b; table 2), on the other hand, confirms both that the insecticide was effective in halting scale insect activity and that the active production of honeydew by scale insects is a greater attraction to bees than residual sugars on branches or any visual olfactory cue from scale insect carapaces.

Our unadvertised honeydew-mimic sugar solution increased bee visitation by an estimated factor of 12.5 compared with the control treatment (95% CI: 4.4–28.3, P < .001; table 2) and by a factor of 3.8 compared with naturally moldy plants without insecticide (95% CI: 1.6–7.8, P = .002; table 2), identifying simple sugars as the resource of interest in these nectar-poor landscapes. Omitting the sugar treatment from the model led to dramatically worse model performance (χ² = 39.2, df = 2, P < 1 × 10⁻⁴; supplemental material, sec. 4). According to the AIC, none of the other experimental manipulations were nearly as important in accounting for bee visitation as the presence of sugar on experimental plants (supplemental material, sec. 4).

We found no evidence that bees used the dark color of mold as a cue to locate honeydew, as indicated by the lack of significant bee visitation to the paint treatment (P = .443) or any interaction between the sugar and paint treatments (P = .907; fig. 3c; table 2). Since branch infrared thermometer readings did not differ between treatments (P = .53; fig. A1), observed bee behaviors can also not be explained by a response to thermal cues. In summary of the results from this experiment, we determined that a highly
diverse array of native, mostly nonsocial bees are visiting prebloom *A. fasciculatum* shrubs for sugars gleaned from honeydew and are able to do so using foraging strategies outside the current framework centered around floral displays.

**Discussion**

Our study documents the use of honeydew as a sugar resource across a diverse community of native bees and strongly suggests widespread sugar foraging behaviors seemingly divorced from floral cues. Honeydew is nutritionally valuable for a variety of insects, including diverse nonbee pollinators and some social bee species (Zoebelein 1957; Santas 1983; Crane and Walker 1985; Koch et al. 2011; Gardner–Gee et al. 2014); however, its use by solitary bees or across an entire native bee community had not been considered, nor had its mechanism of detection in the absence of associated cues. Overall, we recorded 42 bee species in nine genera and five of the six North American bee families exhibiting foraging patterns largely outside the general understanding that bee search images are behaviorally and evolutionarily tied to elaborate floral displays. Thirty-eight species of these native, mostly solitary bees were accessing our honeydew-mimic sugars sprayed on inconspicuous, nonflowering shrubs that offered no other reward; 15 species of bees visited prebloom plants for natural honeydew absent any floral signal; and 18 bee species displayed non-floral-centric foraging behaviors on other plant treatments (table 1).

These results raise the question: how are so many species of bees rapidly locating sugar sprayed on a stick? Current understanding of the sensory and learning capabilities of bees does not explain this phenomenon. Our treatment results show no indication that bees are responding to the color of the mold associated with honeydew, the scent or appearance of the scale insect honeydew producers, or even the application of insecticide as a control (fig. 3). Yet they are locating nonvolatile, colorless sugar 1 h after its application to our sugar-treatment plants and are doing so in numbers far exceeding those predicted by the model of independent arrivals one might expect for solitary bees (Lawless 1987). While biological clustering can be explained in many ways and it remains possible that bees are independently finding these plants via some unknown sensory cue from the sugar, we propose that this pattern might be the result of an unstudied strategy by which solitary bees locate nontraditional sugars using visual cues from other bee foragers, in combination with routine exploration of resources outside the floral realm.

Many animals respond to cues from other foragers in their habitats to optimize search efficiency, especially when resources are variable across space and time (Deygout et al. 2010). Information about quality resources can be exchanged between cooperative foragers, as with the honeybee waggle dance (intraspecific cues), or can be detected by unintended recipients via "eavesdropping," such as occurs between primary predators and scavengers (interspecific cues; Stahler et al. 2002; Frisch 2014). Evidence of olfactory eavesdropping has been found in some social stingless bees (Hymenoptera: Apidae: Meliponini), in which pheromone trails intended to guide nest mates to a food source are also detected and followed by competing species (Nieuw et al. 2004; Lichtenberg et al. 2011). Interspecific foraging dynamics involving solitary bees, however, are not understood. That previous research has overlooked this potential component of bee foraging behaviors may be due to the difficulty of distinguishing the source of foraging cues, whether from the flowers themselves or from the activity of other bee foragers near those flowers, in systems with ample bloom where bee foraging is typically studied. Taking advantage of the natural separation of bee foraging activities from floral cues present in the honeydew-foraging scenario, we used an experimental approach to determine that nonfloral, interspecific cues may play a role in solitary bee optimal foraging strategies. For solitary bees that must provision a nest for offspring in habitats lacking sufficient bloom and without the help of nest mates, cueing off the activity of heterospecifics in their community to opportunistically harvest unusual sugar resources not only could extend their longevity to await additional bloom but may help fuel energetically expensive foraging flights necessary to locate distant pollens. Clearly, more research into these patterns and the ability of bees to locate nonfloral sugars is required.

Regardless of the mechanism by which bees find honeydew secretions, this behavior displayed by so many different wild bee species may have important implications for how bees will respond to a changing world with increasingly unpredictable conditions. Mediterranean habitats, where bees are most diverse (Michener 2007), have been identified as being particularly vulnerable to climate change, exotic species invasions, and urbanization (Klausmeyer and Shaw 2009). Warming temperatures threaten to cause shifts in the emergence time of solitary bees in relation to their preferred host plants, resulting in a temporal decoupling of plants from their pollinators (Inouye 2008; Bartomeus et al. 2011; Forrest and Thomson 2011; Robbirt et al. 2014; but see Forrest 2015). Ongoing habitat loss, fragmentation, and degradation are also threats to wild bee species (Fahrig 2003; Cane et al. 2006), many of which are active for only one month out of the year and rely on their preferred pollens being available during that time (Linsley 1958). For bees that emerge during the early season into a habitat of unusually poor floral resources, the ability to subsist on alternate sugar sources that would extend longevity until nectar and pollens can be located could be critical to survival and production of offspring. Future research comparing the taxonomic and functional diversity of the species using (and not using) honeydew will provide important
insights into when and how honeydew use may influence bee community responses to periods of poor floral resources.

In conclusion, the occurrence of more than 40 different species of native bees on an unadvertised, nonfloral sugar resource suggests widespread, previously undocumented plasticity in bee foraging behaviors and diet breadth that may become increasingly relevant to the conservation of this globally important pollinator with continued disruptions in floral bloom. This discovery not only represents a novel behavioral phenomenon and notable departure from the historical focus on bee use of visual, olfactory, and floral cues but may also have implications related to both the resilience of bee communities to temporary habitat perturbations and the interspecific complexity of their foraging dynamics. Our finding that diverse, solitary bees use nontraditional resources and foraging strategies during times of low bloom suggests that bee use of honeydew may be only one example of adaptive bee foraging strategies that have yet to be described. Future research on native bee foraging behaviors may benefit from considering the effect of interspecific foraging behaviors, nontraditional sensory cues, and the use of nonfloral, unadvertised resources.

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