

1 **Title:**

2 **Bees Without Flowers:**

3 **Before Peak Bloom, Diverse Native Bees Visit Insect-produced Honeydew Sugars**

4

5 **Authors:** Joan M. Meiners^{1,2*}, Terry L. Griswold², David J. Harris³, S.K. Morgan Ernest³

6

7 **Author Affiliations:**

8 ¹School of Natural Resources and Environment, University of Florida, Gainesville, FL 32611.

9 ²USDA-ARS Pollinating Insects Research Unit, Utah State University, Logan, UT 84321.

10 ³Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611.

11 *Correspondence to: jmmeiners@ufl.edu

12

13 **Keywords:** native bees, non-floral foraging, honeydew sugars, foraging behaviors, social cues,
14 bee communities.

15

16 **List of manuscript elements in expanded online edition (Appendix A):**

17 - **Table A1:** Summary of plant types and treatment sprays used in seven experimental treatments.

18 - **Figure A1:** Surface temperatures (C°) for "blackened" and "not blackened" branches of

19 treatment plants, measured at noon with an infrared thermometer on each of six sampling days.

20 - **Figure A2:** Negative binomial distribution of bee count response variable.

21 **Abstract:**

22 Bee foragers respond to complex visual, olfactory, and extrasensory cues to optimize
23 searches for floral rewards. Their abilities to detect and distinguish floral colors, shapes,
24 volatiles, and ultraviolet signals, and even gauge nectar availability from changes in floral
25 humidity or electric fields are well studied. Bee foraging behaviors in the absence of floral cues,
26 however, are rarely considered. We observed forty-four species of wild bees visiting
27 inconspicuous, non-flowering shrubs during early spring in a protected, Mediterranean habitat.
28 We determined experimentally that these bees were accessing sugary honeydew secretions from
29 scale insects without the aid of standard cues. While honeydew use is known among some social
30 Hymenoptera, its use across a diverse community of mostly solitary bees is a novel observation.
31 The widespread ability of native bees to locate and use unadvertised, non-floral sugars suggests
32 unappreciated sensory mechanisms and/or the existence of a social foraging network among
33 solitary bees that may influence how native bee communities cope with increasing environmental
34 change.

35

Introduction

36 Bees and flowers are inextricably linked. Their mutualistic relationship has been a
37 timeless focus for poets, artists and naturalists, as well as field ecologists, behavioral scientists,
38 and evolutionary biologists. The obsession is not without merit. Bee visits to flowers for nectar
39 and pollen are so crucial to angiosperm reproduction that bee preferences for floral colors,
40 shapes, and scents have been credited with driving floral trait evolution, a radiation in
41 angiosperm species diversity during the Late Cretaceous, and current plant community
42 composition (Regal 1977; Ohashi and Yahara 2001; Wright and Schiestl 2009; de Jager et al.
43 2011; Ollerton et al. 2011; Bukovac et al. 2016). Because of this influential mutualism, research
44 on bee foraging has focused on how bees detect and respond to floral visual and olfactory cues,
45 petal thermal signatures, humidity signals from nectar reserves, and even floral electric fields
46 (Herrera 1995; Chittka et al. 1999; Dyer et al. 2006; Whitney et al. 2008; Wright and Schiestl
47 2009; de Jager et al. 2011; Clarke et al. 2013; Frisch 2014; Orbán and Plowright 2014). Very
48 little, however, is known about bee foraging behaviors in the absence of floral cues, particularly
49 among wild, solitary bee species.

50 Bees require sugar, usually as floral nectar, and protein, typically from pollen, for energy
51 and reproduction (Michener 2007). While specialist bee species are particular about their pollen
52 sources, bee visits to flowers for nectar sugars are usually indiscriminate (Linsley 1958).
53 Honeydew is a nectar-like carbohydrate-rich excretion produced as a feeding by-product by
54 phytophagous Hemipterans, such as scale insects (Hemiptera: Coccoidea) and aphids
55 (Hemiptera: Aphididae), that can sometimes be more nutrient-rich than floral nectar (Batra
56 1993). Some insects, most notably ants, attain increased fitness and longevity by using honeydew
57 as an additional sugar source (Zoebelein 1957; Wäckers et al. 2008; Koch et al. 2011).

58 Honeydew use among bees, while digestively plausible and potentially broadly advantageous
59 given global concern about bee declines and their temporal isolation from host flowers (Potts et
60 al. 2010; Bartomeus et al. 2011), has been only sparsely documented, usually as isolated
61 occurrences, and almost exclusively among social, colonial species (Santas 1983; Crane and
62 Walker 1985; Batra 1993; Bishop 1994; Konrad et al. 2009; Koch et al. 2011).

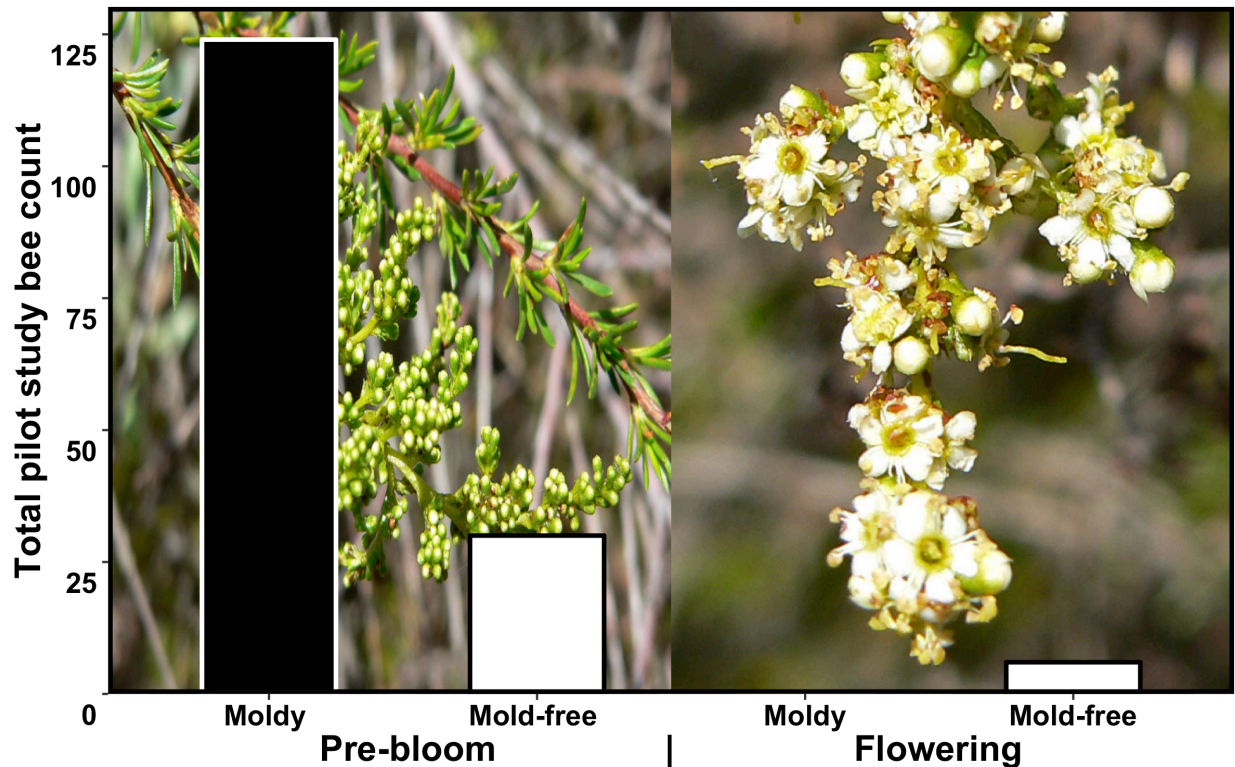
63 Widespread use of honeydew by diverse solitary bee species would have interesting
64 implications for bee ecology, behavior, and conservation for two important reasons: 1) it
65 represents a departure from the classic paradigm of the bee-flower mutualism as a tightly
66 coupled relationship, and 2) it suggests an as-yet unstudied source of resilience, behavioral and
67 physiological, among bees foraging to survive in a changing climate. Honeydew as a sugar
68 compound is non-volatile, colorless, does not fluoresce or absorb UV, and occurs independently
69 of flowering resources (Thorp et al. 1975; Friel et al. 2000; Frisch 2014). Prior to blooming of
70 the host plant, therefore, it is a resource without apparent visual, olfactory, or floral
71 advertisement. An ability of bees to expand conventional search images and diet breadth to
72 include resources such as honeydew could be an important adaptation in habitats, like
73 Mediterranean biomes, where the flora is predicted to be especially sensitive to global change
74 (Klausmeyer and Shaw 2009). Faced with increasingly unpredictable foraging scenarios,
75 honeydew could be an invaluable emergency resource for bees who are able to find it.

76 Working in the Mediterranean, chaparral habitats of Pinnacles National Park in the Inner
77 South Coast Range of California, one of us (J. Meiners) observed a diverse array of native,
78 mostly solitary bee species visiting large, woody, pre-bloom *Adenostoma fasciculatum* shrubs
79 (Rosaceae) during the early spring when floral resources were still very limited (Fig. 1). Some of
80 these shrubs were covered in a dark ‘sooty mold,’ known to grow on the honeydew excretions of

81 scale insects (Hemiptera:Coccoidea) (Santas 1983; Crane and Walker 1985; Wäckers et al.
82 2008). To evaluate this perplexing attraction to moldy plants, we began noting the mold and
83 bloom condition of each *A. fasciculatum* shrub every time we collected a bee from these plants
84 during sampling for a broader biodiversity survey. Surprisingly, we recorded nearly four times as
85 many bees visiting moldy, pre-bloom *A. fasciculatum* individuals as visited mold-free varieties,
86 or either mold condition after flowering, confirming the association of bees with mold but raising
87 new questions about the appeal and mechanism (Fig. 2). These results prompted us to design an
88 experiment for the following early spring to evaluate three central questions: 1) Why are bees
89 visiting these pre-bloom plants?; 2) What are the potential visual, olfactory, thermal, or insect-
90 insect cues alerting bees to this resource?; and 3) How widespread is this behavior across the bee
91 community?



94 **Figure 1:** Images of organisms involved in the described system. (a) Native bee (*Andrena* sp.)
95 foraging on a moldy, non-flowering *Adenostoma fasciculatum* shrub (left, Photo Credit Paul
96 Johnson, NPS), (b) a typical *A. fasciculatum* shrub in a pre-bloom Pinnacles landscape (top right,
97 J. Meiners), and (c) an image of lac scales (*Tachardiella* sp.) on an *A. fasciculatum* branch
98 (bottom right, Creative Commons United States National Collection of Scale Insects
99 Photographs, USDA Agricultural Research Service, Bugwood.org).



100

101 **Figure 2:** Number of bees collected on different *Adenostoma fasciculatum* plant conditions: pre-
102 bloom (left panel), flowering (right panel), moldy (black bars) and mold-free (white bars).

103 Between February and June during the pilot year of study, we collected a total of 160 native bees
104 visiting *A. fasciculatum* shrubs, 124 of which were on non-flowering, moldy plants, and 30 of
105 which were visiting plants without mold or flowers. After flowering commenced, we did not
106 collect a single bee visiting plants with mold and flowers, and only six bees on non-moldy shrubs
107 in bloom, perhaps because other floral resources are preferred at that time. Based on these
108 results, we conducted our study during the period prior to *A. fasciculatum* flowering. Photos by
109 Stan Shebs, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=2407692>.

110 **Materials and Methods**

111 *Experimental Design*

112 We designed seven experimental treatments to differentiate the possible mechanisms and
113 causes of bee attraction to sooty mold, and randomly assigned them to 'naturally moldy' and
114 'mold-free' *Adenostoma fasciculatum* shrubs at three distinct 1-hectare experimental sites in
115 natural areas within Pinnacles National Park in San Benito County, California. Each selected site
116 was dominated by the large, hardy, allelopathic *A. fasciculatum* shrubs and included a mixture of
117 shrubs of similar stature that we could designate as either 'mold-free' (absent of sooty mold and
118 scale insects) or 'naturally moldy' (visibly covered on more than 50% of branches by sooty
119 mold). We applied each treatment (outlined below and in Table A1) to three woody shrubs of
120 pre-bloom *A. fasciculatum* at each of the three sites, for a total of nine shrub replicates for each
121 of seven treatments.

122 To control for any attraction, reflectance, or humidity signal of moisture, all seven
123 treatments consisted of 5 ounces of fluid sprayed on the assigned shrub, as follows:

124 Naturally-moldy plants were sprayed with either (i) water to assess baseline bee visitation
125 to moldy plants, or (ii) a natural, short-residual insecticide (*Orange Guard*® Water Based
126 Indoor/Outdoor Home Pest Control, active ingredient d-Limonene, 5.8%) to evaluate the
127 influence of live scale insects on bee visitation by halting their activity, while leaving sugars and
128 mold intact.

129 Mold-free plants were sprayed with either (i) water to quantify random bee visitation, (ii)
130 insecticide to test for an effect of this chemical on bee activity, (iii) non-toxic black paint to test
131 for an attraction to either the dark visual cue of mold or to potentially higher branch surface
132 temperatures, which recent research has found to be attractive to bees (Dyer et al. 2006), (iv) a

133 colorless, odorless 20% 1:1 Sucrose:Fructose solution mixed from chemical-grade sugars to
134 mimic the composition of insect honeydew (Wäckers et al. 2008), or (v) a combination of both
135 the black paint and the sugar mixture to simulate the attraction of natural mold and examine
136 interaction effects (treatments summarized in Table A1).

137 *Sampling Protocol*

138 Because the pilot study indicated that bee visits to honeydew were restricted to the early
139 season (Fig. 2), we concentrated our experiment in the period before peak bloom. We visited
140 each site three times between late February and late April, when native bee activity has begun at
141 Pinnacles National Park but prior to peak bloom of the plant community. Sampling was
142 conducted at one of the three sites per week on calm, sunny days over 15°C to ensure adequate
143 bee activity. At 9am on each sampling day, we began by refreshing all plants with 5oz of their
144 assigned treatment spray, which remained the same throughout the experiment. After waiting an
145 hour for the effect of the short-residual insecticide to take place and subside, and for bee activity
146 to approach peak levels for the day, a randomly ordered shrub list was divided between two
147 collectors, who spent five minutes sequentially netting all bees visiting each respective plant.
148 Temperature, wind speed, humidity, barometric pressure, and an estimate of cloud cover were
149 recorded every thirty minutes during sampling. We sampled all twenty-one plants at a site once
150 in the morning, beginning around 10am, and once in the afternoon, around 1pm, to capture bees
151 across the spectrum of diurnal activity. On sampling days, we recorded all flowering species in
152 bloom within the site, approximately a hectare in size, to provide an estimate of floral richness
153 and seasonal bloom progression. We also used an infrared thermometer to record surface
154 temperatures of three different external branches of each plant at noon on sampling days to test
155 for effects of potentially warmer, darker plants.

156 *Specimens Processing & Data Management*

157 All bees were labeled and pinned into field boxes each evening, then frozen for 48 hours
158 to protect from insect infestations, and transported to Utah where they were identified to
159 described species or unique morphospecies by experts at the USDA-ARS Pollinating Insect
160 Research Unit (“Logan Bee Lab”). Bee identifications were completed using high quality
161 ‘Leica’ dissecting microscopes, the appropriate taxonomic keys where available, and confirmed
162 by comparison with the Logan Bee Lab’s extensive reference collection of approximately 1.5
163 million specimens. Bees were assigned unique matrix code numbers that were included with
164 standard insect label data printed on labels affixed to each specimen pin. The unique identifier
165 and specimen field data were captured in a MySQL relational database, which was then managed
166 and queried for statistical analyses using Microsoft Access front end software.

167 *Statistical Analyses*

168 We employed a generalized linear mixed effects model with a negative binomial
169 distribution to assess differences in bee visitation rates among the different plant treatments,
170 which were modeled as fixed effects. We also used fixed effects to control for linear changes in
171 visitation rates over the course of the day and differences in average visitation rates among the
172 three sites. Variation in average visitation rates among the 63 plants and among the 9 sampling
173 dates were each accounted for as a random effect. Because we intentionally collected on warm,
174 sunny, calm days, the variation in environmental variables was minimal and their inclusion in the
175 statistical model did not change treatment significance. They were therefore omitted from the
176 final model for clarity.

177 Differences among treatments were estimated by comparing the number of bees that
178 would be expected to visit a given plant in a given five-minute observation window under

179 different conditions according to the negative binomial model. Ninety-five percent confidence
180 intervals for the effect of each treatment versus the control were calculated using the model's
181 variance-covariance matrix (Lawless 1987). To assess the possible tendency for bees to cluster
182 on individual plants at a given point in time beyond what would be expected by treatment
183 effects, we used a likelihood ratio test to compare one version of this model with an
184 overdispersed error distribution (the negative binomial) to a version without overdispersion (the
185 Poisson) (Coxe et al. 2009).

186 To compare the branch temperatures between blackened and not blackened branches, we
187 built a linear mixed effects model with branch color (blackened or not) and day of year as fixed
188 effects, and the plant within the site as a random effect (Fig. A1). All analyses were performed in
189 the R programming language using the *lme4* package (Bates et al. 2015, p. 4; R Core Team
190 2015). All data and code used are freely available by contacting the corresponding author.

191

192

Results

193

Bee Collection

194 Despite a lack of floral cues, our 378 plant samples yielded 308 bees from forty-four
195 different species across nine genera and five of the six North American bee families (Table 1).
196 Approximately three-quarters of this bee abundance and diversity came from the two sprayed
197 sugar treatments (N=220, Species=38). Shrubs with naturally-occurring mold, and hence
198 honeydew sugars, attracted more bees and species (N=41, Spp.=15), than any of the three
199 treatments not anticipated to be attractive to bees (*Control* N=11, Spp.=4; *Insecticide* N=17,
200 Spp.=11; *Natural Mold + Insecticide* N=12, Spp.=8), or the treatment designed as a visual mimic
201 of the dark color of mold (*Paint* N=7; Spp.=4).

202 **Table 1:** Faunal list and count of bees collected on treated non-flowering *A. fasciculatum*.

	Family	Genus	Subgenus	Species	# Bees on Mold (1 trt)	# Bees on Sugar (2 trts)	# Bees on Other (4 trts)	
1	Andrenidae	Andrena	(Derandrena)	<i>californiensis</i>	3	4	1	
2				<i>n. sp.</i>	10	33	21	
3			(Euandrena)	<i>chlorura</i>	2	10	1	
4			(Melandrena)	<i>aff. cerasifolii</i>	1	12	2	
5				<i>sola</i>		1		
6			(Micrandrena)	<i>chlorogaster</i>	4	9	3	
7			(Pelicandrena)	<i>atypica</i>		1		
8			(Simandrena)	<i>hypoleuca</i>		5		
9			(Thysandrena)	<i>aff. candida</i>		2	1	
10				<i>candida</i>	1			
11				<i>w-scripta</i>				1
12				<i>sp. 17</i>				2
13				<i>sp. 18</i>			1	
14				<i>sp. 19</i>	1		3	
15				<i>sp. 22</i>			1	
16			<i>sp. 25</i>			1		
17			Panurginus		<i>gracilis</i>	2	1	
18	<i>morrisoni</i>	1						
19	Apidae	<i>Apis</i>		<i>mellifera</i>		1	2	
20		Nomada	(Nomada)	<i>sp. F</i>			1	
21				<i>sp. U</i>	1	10		
22	<i>sp. W</i>				2			
23	Colletidae	Hylaeus	(Hylaeus)	<i>granulatus</i>		1		
24				<i>verticalis</i>		1		
25			(Paraprosopis)	<i>calvus</i>		10		
26				<i>nevadensis</i>	2	9		
27				(Prosopis)	<i>episcopalis</i>		2	
28	Halictidae	Halictus	(Nealictus)	<i>farinosus</i>		2		
29			(Protohalictus)	<i>rubicundus</i>		1		
30			(Seladonia)	<i>tripartitus</i>		5	1	
31			(Dialictus)	<i>nevadense</i>	4	16	2	
32		<i>punctatoventre</i>		3	14	2		
33		(Evylaeus)		<i>argemonis</i>		5	1	
34				<i>robustum</i>		1		
35				<i>sp. 1</i>		1		
36				<i>sp. 9</i>		12	2	
37		<i>sp. A</i>		1				
38	(Hemihalictus)	<i>pulveris</i>	1	1				
39	(Lasioglossum)	<i>egregium</i>		8				
40		<i>sisymbrii</i>		16	1			
41	(Sphecodogastra)	<i>nigrescens</i>	5	15	1			
42	Sphecodes		<i>sp. A</i>		1			
43			<i>sp. B</i>		1			
44	Megachilidae	Protosmia	(Chelostomopsis)	<i>rubifloris</i>			2	
Total specimens:					41	220	47	
Total species:					15	38	18	

203 Note: Bee counts are grouped into treatment ("trt") categories based on availability of natural
 204 sugars from honeydew (*Natural Mold*), sprayed honeydew-mimic sugars (*Sugar*, *Sugar + Paint*),
 205 or no known sugars accessible (*Control*, *Insecticide*, *Mold + Insecticide*, *Paint*).

206

Seasonal and Spatial Context

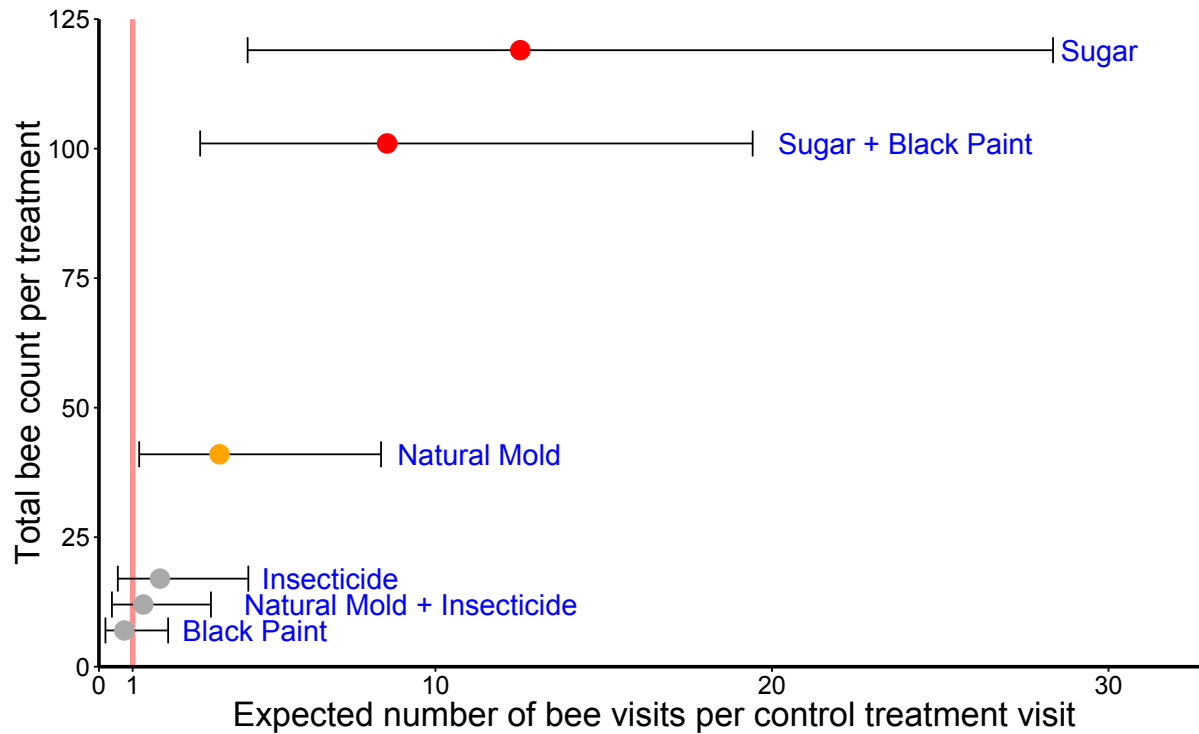
207 Floral richness increased linearly across the season and across 1-hectare experimental
208 sites as expected, from zero to thirteen species recorded in bloom during sampling, confirming
209 that sampling captured bee activity during the relatively nectar-depauperate period leading up to
210 peak bloom (which typically occurs at much higher richness and abundance at Pinnacles than
211 was observed during the study). Likewise, total bee specimens collected increased over the nine-
212 week duration of the study at all three sites, from the first sampling round (N=85) to approach
213 peak bee activity during the third and final sampling round (N=146). Bee abundance differed
214 somewhat between sites, with bee activity at sites C (N=125) and B (N=115) consistently higher
215 than bee activity at site A (N=68). None of these temporal or site variables, however, nor any of
216 the environmental variables recorded (e.g. cloud cover, ambient temperature, wind speed,
217 humidity) influenced the modeled significance of treatment results.

218

Treatment Significance

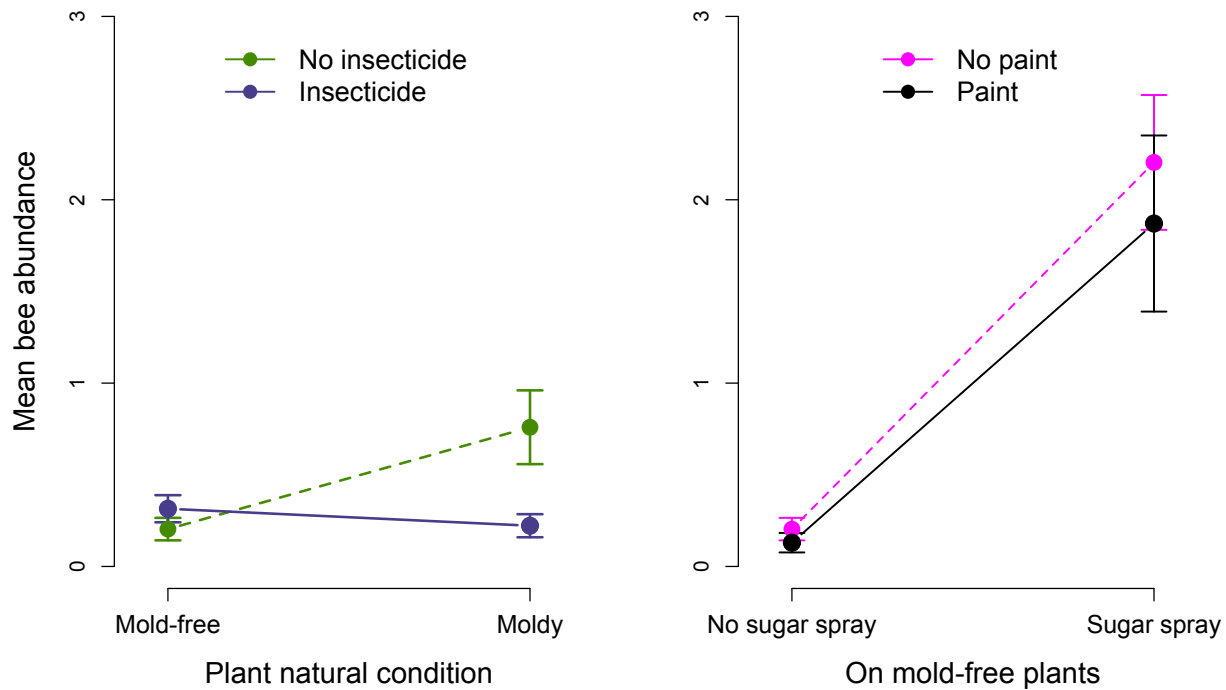
219 Our model results confirmed our original observation that native bee visitation to pre-
220 bloom *Adenostoma fasciculatum* is significantly elevated on plants with sooty mold, despite this
221 resource lacking any floral cue ($p=0.02$). Model results also revealed our unadvertised
222 honeydew-mimic solution to be significantly more attractive to bees than mold ($p<0.001$; Fig. 3),
223 identifying simple sugars as the resource of interest in these nectar-poor landscapes.
224 Furthermore, though there was no base effect of the *Insecticide* treatment on bee visitation rate
225 compared to the *Control* ($p=0.38$, Fig. 4), a significant interaction between the *Mold* and
226 *Insecticide* treatments reflects lower bee counts on moldy plants on which insecticide was
227 applied to stop the production of honeydew ($p=0.04$; Fig. 4), indicating that active sugar
228 production by live scale insects was a greater attraction to bees than residual sugars on branches

229 or any visual or olfactory cue from scale insect carapaces. Bees were also not using the dark
230 color of mold as a cue to locate honeydew, as evidenced by the lack of significant bee visitation
231 effects of the *Paint* treatment ($p=0.44$; Fig. 3) or any interaction between the *Sugar* and *Paint*
232 treatments ($p=0.91$; Fig. 4). Finally, since branch infrared thermometer readings did not differ
233 between treatments ($p=0.55$; Fig. A1), observed bee behaviors can also not be explained by a
234 response to thermal cues. From this experiment, we conclude that a highly diverse array of
235 native, mostly non-social bees are visiting pre-bloom *Adenostoma fasciculatum* shrubs for sugars
236 gleaned from honeydew, and are able to do so using foraging strategies outside the current
237 framework centered around floral displays.



238

239 **Figure 3:** Effect sizes of bee visitation with 95% confidence intervals (x-axis) and total bee
240 counts (y-axis) for each of six experimental plant treatments (labeled in blue) compared to the
241 control treatment value (red vertical line). According to our generalized linear mixed effects
242 model, the presence of *Natural Mold* increased the expected bee visitation rate by an estimated
243 factor of 4 over the *Control* ($p = 0.02$, orange dot). Bee visitation to both sprayed *Sugar*
244 treatments, even in the absence of any obvious cues, was significantly higher than that to *Natural*
245 *Mold* ($p < 0.001$), and higher by an estimated factor of 13 over the *Control* ($p < 0.0001$, red
246 dots). The three treatments without natural or sprayed sugars did not differ in bee visitation from
247 the *Control* ($p > 0.05$, grey dots, 95% CIs overlapping the red line representing the *Control*
248 treatment value). Observed counts on the y-axis are based on 54 observations of each treatment,
249 divided evenly among the three sites.



250

251 **Figure 4:** Two-way interactions of mean sample bee abundance between key treatments. A
252 negative-binomial generalized linear mixed effects model with random intercepts for individual
253 plants and for individual sampling dates found a significant interaction between the *Natural*
254 *Mold* and *Insecticide* treatments (left, $p=0.04$), but not between the *Sugar* and *Black Paint*
255 treatments (right, $p=0.91$). Error bars represent +/- one s.e.m. Number of samples and total bee
256 counts per treatment are as reported in Figure 3.

257

258

Discussion

259

260

261

262

Our study is the first to document the use of honeydew as a sugar resource across a diverse community of native bees as well as the first to bring to light widespread sugar foraging behaviors seemingly divorced from floral cues. Overall, we recorded forty-four bee species in nine genera and five of the six North American bee families exhibiting foraging patterns largely

263 outside the general understanding that bee search images are behaviorally and evolutionarily tied
264 to elaborate floral displays. Thirty-eight species of these native, mostly solitary bees were
265 accessing our honeydew-mimic sugars sprayed on inconspicuous, non-flowering shrubs that
266 offered no other reward, fifteen species of bees visited pre-bloom plants for natural honeydew
267 absent any floral signal, and eighteen bee species displayed non-floral-centric foraging behaviors
268 on other plant treatments (Table 1).

269 These results raise the question: how are so many species of bees rapidly locating sugar
270 sprayed on a stick? Our current understanding of sensory abilities in wild bees does not explain
271 this phenomenon. While it remains possible that bees are independently finding these plants via
272 some unknown sensory cue from the sugar, our data distribution (Fig. 2A) includes several very
273 high values on *Sugar* treatment plants (up to 22 bees in five minutes) that are more compatible
274 with non-independent arrivals (Lawless 1987). Indeed, our data fit a negative binomial model
275 that includes clustering on individual plants in specific 5-minute periods much better than the
276 Poisson model that assumes independent arrivals ($\chi^2=30$, $df=1$, $p<0.0001$) (Coxe et al. 2009).
277 One way to explain this non-independence might be a strategy by which solitary bees are
278 locating nontraditional sugars using social cues from other bee foragers, in combination with
279 stochastic exploration of resources outside the floral realm. Social foraging mechanisms, such as
280 the honeybee waggle dance (intraspecific) or the relationship between scavengers and primary
281 predators (interspecific), are well-known for many animals, especially when resources are
282 variable across space and time (Stahler et al. 2002; Deygout et al. 2010; Frisch 2014).
283 Interspecific foraging dynamics among bees, however, are not understood. For solitary bees that
284 must provision a nest for offspring without the help of nest mates, cueing off the activity of
285 heterospecifics in their community to opportunistically harvest unusual sugar resources could

286 help optimize energetically-expensive foraging flights, especially in early-season or degraded
287 habitats lacking sufficient bloom. Clearly, more research into these patterns and the ability of
288 bees to locate non-floral sugars is required.

289 Regardless of the mechanism by which bees are able to find honeydew secretions, this
290 behavior displayed by so many different wild bee species may have important implications for
291 how bees will respond to a changing world with increasingly unpredictable conditions.
292 Mediterranean habitats, where bees are most diverse, have been identified as particularly
293 vulnerable to climate change, exotic species invasions, and urbanization (Michener 2007;
294 Klausmeyer and Shaw 2009). Warming temperatures have been found to cause shifts in the
295 emergence time of solitary bees in relation to their preferred host plants, resulting in a temporal
296 decoupling of plants from their pollinators (Inouye 2008; Bartomeus et al. 2011; Forrest and
297 Thomson 2011; Robbirt et al. 2014). Ongoing habitat loss, fragmentation, and degradation are
298 also threats to wild bee species (Steffan-Dewenter et al. 2002; Fahrig 2003; Cane et al. 2006),
299 many of which are only active for one month out of the year and rely on their preferred pollens
300 being available during that time (Linsley 1958). For bees that emerge during the early season
301 into a habitat of unexpectedly poor floral resources, the ability to subsist on alternate sugar
302 sources that would extend longevity until nectar and pollens can be located could be critical to
303 survival and production of offspring.

304 In conclusion, the occurrence of over forty different species of native bees on an
305 unadvertised, non-floral sugar resource suggests widespread, previously undocumented plasticity
306 in bee foraging behaviors and diet breadth that may become increasingly relevant to bee
307 conservation with continued disruptions in floral bloom. This discovery represents not only a
308 novel behavioral phenomenon and notable departure from the historical focus on bee use of

309 visual, olfactory, and floral cues, but may also have implications related to both the resilience of
310 bee communities to temporary habitat perturbations and the social complexity of their foraging
311 dynamics. Our finding that diverse solitary bees use nontraditional resources and foraging
312 strategies during times of low bloom suggests that bee use of honeydew may be only one
313 example of adaptive bee foraging strategies that have yet to be described. Future research on
314 native bee foraging behaviors may benefit from considering the effect of stochastic and socially-
315 mediated foraging behaviors, and investigating the use of non-floral, unadvertised resources.

316

317

Literature Cited

- 318 Bartomeus, I., J. S. Ascher, D. Wagner, B. N. Danforth, S. Colla, S. Kornbluth, and R. Winfree.
319 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants.
320 *Proceedings of the National Academy of Sciences* 108:20645–20649.
- 321 Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models
322 Using lme4. *Journal of Statistical Software* 67:1–48.
- 323 Batra, S. W. T. 1993. Opportunistic Bumble Bees Congregate to Feed at Rare, Distant Alpine
324 Honeydew Bonanzas. *Journal of the Kansas Entomological Society* 66:125–127.
- 325 Bishop, J. A. 1994. Bumble Bees (*Bombus hypnorum*) Collect Aphid Honeydew on Stone Pine
326 (*Pinus pumila*) in the Russian Far East. *Journal of the Kansas Entomological Society* 67:220–
327 222.
- 328 Bukovac, Z., A. Dorin, V. Finke, M. Shrestha, J. Garcia, A. Avarguès-Weber, M. Burd, et al.
329 2016. Assessing the ecological significance of bee visual detection and colour discrimination
330 on the evolution of flower colours. *Evolutionary Ecology* 1–20.
- 331 Cane, J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, and N. M. Williams. 2006. Complex
332 Responses Within A Desert Bee Guild (Hymenoptera: Apiformes) To Urban Habitat
333 Fragmentation. *Ecological Applications* 16:632–644.
- 334 Chittka, L., N. M. Williams, H. Rasmussen, and J. D. Thomson. 1999. Navigation without
335 vision: bumblebee orientation in complete darkness. *Proceedings of the Royal Society of
336 London. Series B: Biological Sciences* 266:45–50.
- 337 Clarke, D., H. Whitney, G. Sutton, and D. Robert. 2013. Detection and Learning of Floral
338 Electric Fields by Bumblebees. *Science* 340:66–69.
- 339 Cox, S., S. G. West, and L. S. Aiken. 2009. The Analysis of Count Data: A Gentle Introduction
340 to Poisson Regression and Its Alternatives. *Journal of Personality Assessment* 91:121–136.
- 341 Crane, E., and P. Walker. 1985. Important Honeydew Sources and their Honeys. *Bee World*
342 66:105–112.
- 343 de Jager, M. L., L. L. Dreyer, and A. G. Ellis. 2011. Do pollinators influence the assembly of
344 flower colours within plant communities? *OECOLOGIA* 166:543–553.

- 345 Deygout, C., A. Gault, O. Duriez, F. Sarrazin, and C. Bessa-Gomes. 2010. Impact of food
346 predictability on social facilitation by foraging scavengers. *Behavioral Ecology* 21:1131–1139.
- 347 Dyer, A. G., H. M. Whitney, S. E. J. Arnold, B. J. Glover, and L. Chittka. 2006. Bees associate
348 warmth with floral colour. *Nature* 442:525–525.
- 349 Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology,*
350 *Evolution, and Systematics* 34:487–515.
- 351 Forrest, J. R. K., and J. D. Thomson. 2011. An examination of synchrony between insect
352 emergence and flowering in Rocky Mountain meadows. *Ecological Monographs* 81:469–491.
- 353 Friel, E. N., R. S. T. Linforth, and A. J. Taylor. 2000. An empirical model to predict the
354 headspace concentration of volatile compounds above solutions containing sucrose. *Food*
355 *Chemistry* 71:309–317.
- 356 Frisch, K. von. 2014. *Bees: Their Vision, Chemical Senses, and Language*. Cornell University
357 Press.
- 358 Herrera, C. M. 1995. Floral Biology, Microclimate, and Pollination by Ectothermic Bees in an
359 Early-Blooming Herb. *Ecology* 76:218–228.
- 360 Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance
361 of montane wildflowers. *Ecology* 89:353–362.
- 362 Klausmeyer, K. R., and M. R. Shaw. 2009. Climate Change, Habitat Loss, Protected Areas and
363 the Climate Adaptation Potential of Species in Mediterranean Ecosystems Worldwide. *PLoS*
364 *ONE* 4:e6392.
- 365 Koch, H., C. Corcoran, and M. Jonker. 2011. Honeydew Collecting in Malagasy Stingless Bees
366 (Hymenoptera: Apidae: Meliponini) and Observations on Competition with Invasive Ants.
367 *African Entomology* 19:36–41.
- 368 Konrad, R., F. L. Wäckers, J. Romeis, and D. Babendreier. 2009. Honeydew feeding in the
369 solitary bee *Osmia bicornis* as affected by aphid species and nectar availability. *Journal of*
370 *insect physiology* 55:1158–1166.
- 371 Lawless, J. F. 1987. Negative binomial and mixed Poisson regression. *Canadian Journal of*
372 *Statistics* 15:209–225.
- 373 Linsley, E. G. 1958. The Ecology of Solitary Bees. *Hilgardia* 27:543–599.
- 374 Michener, C. D. 2007. *The Bees of the World*. Johns Hopkins University Press, Baltimore.
- 375 Ohashi, K., and T. Yahara. 2001. Behavioural responses of pollinators to variation in floral
376 display size and their influences on the evolution of floral traits. Pages 274–296 *in* *Cognitive*
377 *Ecology of Pollination*. Cambridge University Press.
- 378 Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by
379 animals? *Oikos* 120:321–326.
- 380 Orbán, L. L., and C. M. S. Plowright. 2014. Getting to the start line: how bumblebees and
381 honeybees are visually guided towards their first floral contact. *Insectes Sociaux* 61:325–336.
- 382 Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010.
383 Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*
384 25:345–353.
- 385 R Core Team. 2015. R: A language and environment for statistical computing. [https://www.R-](https://www.R-project.org)
386 [project.org](https://www.R-project.org). Vienna, Austria.
- 387 Regal, P. J. 1977. Ecology and Evolution of Flowering Plant Dominance. *Science* 196:622–629.
- 388 Robbirt, K. M., D. L. Roberts, M. J. Hutchings, and A. J. Davy. 2014. Potential Disruption of
389 Pollination in a Sexually Deceptive Orchid by Climatic Change. *Current Biology* 24:2845–
390 2849.

- 391 Santas, L. 1983. Insects producing honeydew exploited by bees in Greece. *Apidologie* 14.2:93–
392 103.
- 393 Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially
394 associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour*
395 64:283–290.
- 396 Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tschardt. 2002. Scale-
397 Dependent Effects of Landscape Context on Three Pollinator Guilds. *Ecology* 83:1421–1432.
- 398 Thorp, R. W., D. L. Briggs, J. R. Estes, and E. H. Erickson. 1975. Nectar Fluorescence under
399 Ultraviolet Irradiation. *Science* 189:476–478.
- 400 Wäckers, F. L., P. C. J. van Rijn, and G. E. Heimpel. 2008. Honeydew as a food source for
401 natural enemies: Making the best of a bad meal? *Biological Control, Conservation Biological*
402 *Control* 45:176–184.
- 403 Whitney, H. M., A. Dyer, L. Chittka, S. A. Rands, and B. J. Glover. 2008. The interaction of
404 temperature and sucrose concentration on foraging preferences in bumblebees.
405 *Naturwissenschaften* 95:845–850.
- 406 Wright, G. A., and F. P. Schiestl. 2009. The evolution of floral scent: the influence of olfactory
407 learning by insect pollinators on the honest signalling of floral rewards. *Functional Ecology*
408 23:841–851.
- 409 Zobelein, G. 1957. Die Rolle des Waldhonigtaus im Nahrungshaushalt forstlich nützlicher
410 Insekten. *Forstwissenschaftliches Centralblatt* 76:24–34.
- 411

412

Acknowledgments

413 The authors are grateful to Pinnacles National Park for funding this project through the
414 Great Basin Cooperative Ecosystem Studies Unit (Task Agreement number P10AC00577). JMM
415 is currently supported by a University of Florida Biodiversity Institute Graduate Fellowship, and
416 previously by the Utah State University Ecology Center. DJH is supported by Gordon and Betty
417 Moore Foundation's Data-Driven Discovery Initiative Grant GBMF4563 to E.P. White. We owe
418 thanks to Paul Johnson for on-site guidance, photography, and field errands, Edward W. Evans
419 for honeydew discussions and feedback on early drafts, J. Therese Lamperty for diligent
420 fieldwork, H. Ikerd and S. Burrows for meticulous lab work, G. Yenni, A. Kleinhesselink and S.
421 Durham for statistical advice, and the Weecology lab group for manuscript feedback. JMM
422 would also like to thank Dr. Yael Mandelik for hosting her for a related field project at the
423 Hebrew University of Jerusalem in Rehovot, Israel, which was funded by a 'Rahamimoff Travel
424 Grant for Young Scientists' from the US-Israel Binational Science Foundation.

425

Author Contributions

426 JMM initiated and designed the project, executed the field work and analyses, and wrote the
427 paper. TLG oversaw bee identifications and advised on protocol. DJH improved the statistical
428 analyses and assessed statistical significance. SKME guided analyses, concept, and writing. All
429 authors discussed results and commented on the manuscript.

430

Additional Information

431 Upon article publication, data for this project will be available at www.datadryad.org. Code and
432 data are currently available online at [https://github.com/beecycles/Bees-without-flowers-](https://github.com/beecycles/Bees-without-flowers-project2016)
433 [project2016](https://github.com/beecycles/Bees-without-flowers-project2016) and are citable using doi.org/10.5281/zenodo.162054. Correspondence and requests
434 for materials should be addressed to JMM (jmmeiners@ufl.edu).

435

Expanded Online Materials

436

Online Appendix A: Additional Methodological and Data Details

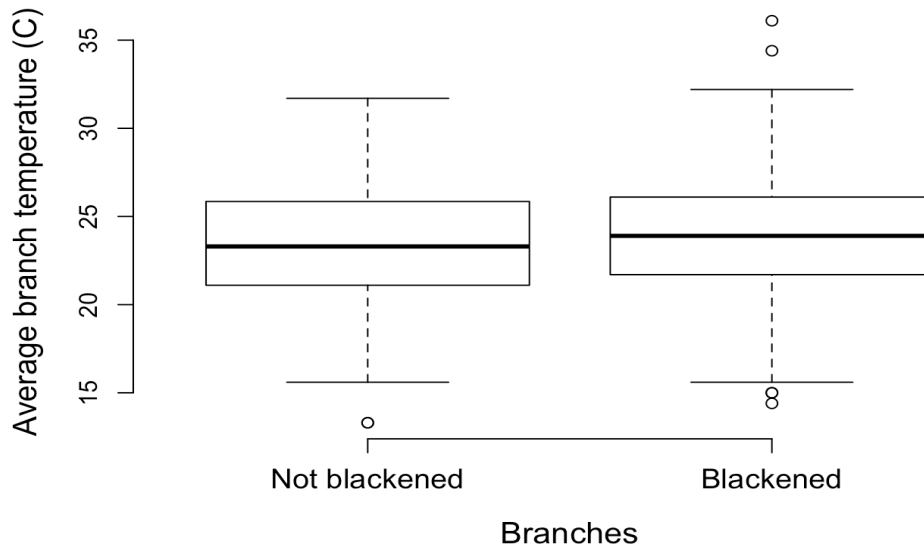
437 **Table A1:** Summary of plant types and treatment sprays used in seven experimental treatments.

Natural Plant Condition	Treatment Number	Treatment Description	Treatment Spray applied to each plant
Moldy	Moldy (i)	Natural Mold	5ml distilled water
	Moldy (ii)	Natural Mold + Insecticide	5ml Orange Guard® short-residual insecticide
Mold-free	Mold-free (i)	Control	5ml distilled water
	Mold-free (ii)	Insecticide	5ml Orange Guard® short-residual insecticide
	Mold-free (iii)	Black Paint	5ml non-toxic black paint
	Mold-free (iv)	Sugar	5ml 20% chemical-grade Fructose:Sucrose
	Mold-free (v)	Sugar + Black Paint	5ml 20% chemical-grade Fructose:Sucrose + 5ml non-toxic black paint

438 Note: Each treatment was replicated with three plants at three different sites, for a total of nine

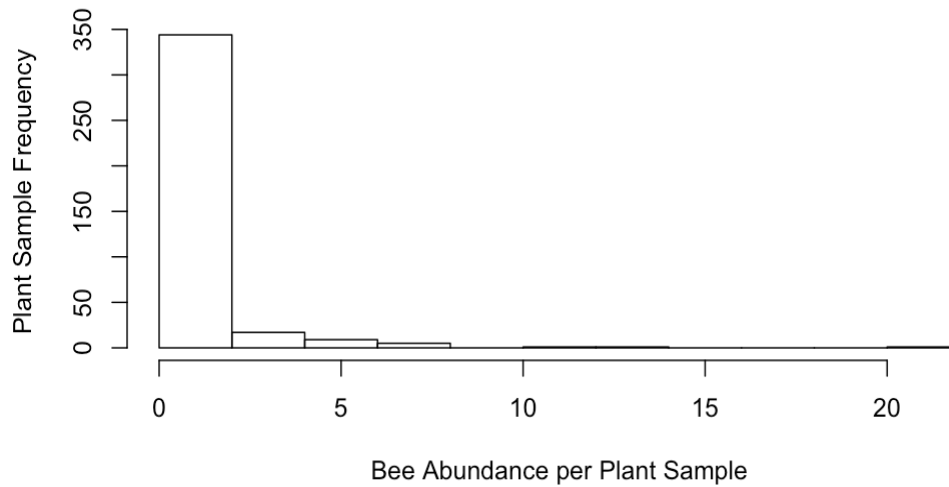
439 plants per treatment and sixty-three plants total. Each site was sampled in the morning and

440 afternoon on three separate occasions.



441

442 **Figure A1:** Surface temperatures (C°) for "blackened" and "not blackened" branches of
443 treatment plants, measured at noon with an infrared thermometer on each of six sampling days.
444 A linear mixed effects model that controlled for day of year as a fixed effect and plant within site
445 as a random effect found no difference in surface temperatures between blackened (N=324) and
446 not blackened (N=243) branches ($p=0.55$).



447

448 **Figure A2:** Negative binomial distribution of bee count response variable (N=308, from 378
449 samples at treatment plant). Bee visitors to experimental plants were collected with an aerial net
450 during randomly-ordered five-minute sampling periods at each plant. Many periods of zero bees
451 collected and a few events where up to 22 bees were collected on an experimental plant produce
452 this data distribution, which limited statistical analyses to the tests described in methods. Since
453 biological count data are typically Poisson-distributed and do not include the high values we see
454 on the right side of this histogram from bees visiting *Sugar* treatment plants (N = 22, 14, 11, 8, 8,
455 8), we point to these select high values as possible evidence of feedback from a social foraging
456 mechanism, and encourage further research in this area (Lawless 1987).