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FORAGING STRATEGY PREDICTS FORAGING ECONOMY IN A FACULTATIVE
SECONDARY NECTAR ROBBER

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25 **Abstract**

26 In mutualistic interactions, the decision whether to cooperate or cheat depends on the
27 relative costs and benefits of each strategy. In pollination mutualisms, secondary nectar robbing is a
28 facultative behavior employed by a diverse array of nectar-feeding organisms, and is thought to be a
29 form of cheating. Primary robbers create holes in floral tissue through which they feed on nectar,
30 whereas secondary robbers, which often lack chewing mouthparts, feed on nectar through existing
31 holes. Because primary robbers make nectar more readily available to secondary robbers, primary
32 robbers facilitate the behaviors of secondary robbers. However, the net effect of facilitation on
33 secondary robber fitness has not been empirically tested: it is unknown whether the benefit
34 secondary robbers receive is strong enough to overcome the cost of competing with primary robbers
35 for a shared resource. We conducted foraging experiments using the bumble bee *Bombus bifarius*,
36 which can alternatively forage “legitimately” (from the floral opening) or secondary-rob. We
37 measured the relative foraging efficiencies (handling time per flower, flowers visited per minute,
38 proportion of foraging bout spent consuming nectar) of these alternative behaviors, and tested
39 whether the frequency of primary robbing and nectar standing crop in primary-robbed flowers of
40 *Linaria vulgaris* (Plantaginaceae) affected foraging efficiency. Surprisingly, there was no effect of
41 primary robbing frequency on the foraging efficiency of secondary-robbing *B. bifarius*. Instead,
42 foraging strategy was a major predictor of foraging efficiency, with legitimate foraging being
43 significantly more efficient than secondary robbing. Legitimate foraging was the more common
44 strategy used by *B. bifarius* in our study; however, it is rarely used by *B. bifarius* foraging on *L.*
45 *vulgaris* in nature, despite indications that it is more efficient. Our results suggest the need for
46 deeper investigations into why bees adopt secondary robbing as a foraging strategy, specifically, the
47 environmental contexts that promote the behavior.

48

49 **Introduction**

50 Nectar robbers disrupt many pollination mutualisms by usurping floral rewards intended for
51 pollinators (Inouye 1980, Irwin et al. 2010). Two distinct nectar robbing strategies can be identified.
52 Primary nectar robbers feed on floral nectar through holes they chew or pierce into the side or at the
53 base of flowers with long, tubular corollas or otherwise recessed nectaries, whereas secondary
54 robbers feed on nectar through holes created by primary robbers (Inouye 1980). Nectar robbers,
55 unlike visitors that feed through the floral opening (henceforth termed “legitimate” foragers),
56 usually bypass floral reproductive structures and thus typically do not act as pollen vectors (Irwin et
57 al. 2010; however, see, e.g., Higashi et al. 1988 and Navarro 2000 for exceptions). Primary robbing
58 requires specific morphology, usually sharp or toothed mouthparts, to puncture the floral tissue.
59 Secondary robbing, however, does not (Irwin et al. 2010). For this reason, secondary robbing is an
60 additional behavior, available to any nectar feeder, that can only be conducted in the presence of
61 primary robbers (Irwin et al. 2010). Often, legitimate foragers will switch to secondary robbing on
62 the same plant species once robbing holes have accumulated in flowers (Rust 1979, Dedej and
63 Delaplane 2004, Kjonaas and Rengifo 2006).

64 Why bees shift away from foraging legitimately is unknown. Nor are the environmental
65 conditions that promote secondary robbing clear (Irwin et al. 2010). It is commonly thought that
66 secondary robbing is a more efficient strategy relative to legitimate foraging (Dedej and Delaplane
67 2005). Specifically, because secondary robbing allows nectar robbers to circumvent a
68 morphological mismatch with a flower that would otherwise make access to nectar difficult, it can
69 reduce flower handling times and lead to increased nectar removal (Olesen 1996, Newman and
70 Thomson 2005, Dedej and Delaplane 2005). If adopting a secondary robbing over a legitimate
71 foraging strategy is more energetically efficient, it should alleviate some of the fitness costs
72 associated with foraging, including energetic costs, predation risk and missed opportunity costs,

73 such as those incurred when missing a mating opportunity (Brown et al. 1988). However, few
74 studies have tested this conventional wisdom (but see Thomson 2004).

75 Floral visitors that secondary-rob, but cannot primary-rob, are dependent upon the activities
76 of primary robbers. As robbing holes accumulate in a floral patch, progressively more opportunities
77 are made available for visitors that can potentially secondary rob to adopt that strategy. However, as
78 the number of flowers with robbing holes in a patch approaches 100%, primary robbers will re-visit
79 flowers through the robbing holes they have previously created. These “secondary” visits further
80 reduce overall nectar standing crop. Competition between primary and secondary robbers may be
81 fierce, as robbed flowers tend to have less available nectar than unrobbed flowers (Stout et al. 2000,
82 Temeles and Pan 2002, Newman and Thomson 2005). Therefore, in order to understand the net
83 effect of primary robbers’ facilitation of secondary robbers, we must compare the presumed benefit
84 of increased foraging efficiency associated with the switch to secondary robbing, with the potential
85 cost of competition for nectar. Determining whether primary robbers indirectly increase secondary
86 robbers’ foraging efficiency will provide ecological insight into the costs and benefits of secondary
87 nectar robbing, as well as how interactions between nectar robbers (i.e., exploiters of mutualism)
88 potentially affect the functioning of plant-pollinator mutualisms.

89 By observing the foraging behavior of facultative secondary robbing bumble bees within
90 floral arrays manipulated to mimic different effects of primary robbing (primary robbing rate and
91 extent of nectar drainage from robbed flowers due to primary robbing), we tested the hypothesis
92 that shifting to secondary robbing from legitimate foraging leads to higher individual foraging
93 efficiency. From this initial hypothesis, three predictions follow. (1) If secondary robbing is a more
94 efficient foraging strategy, we predict that secondary robbers will achieve higher foraging efficiency
95 in patches with higher rates of primary robbing, as long as nectar standing crop in primary-robbed
96 flowers is high, due to limited “secondary” visits from primary robbers. In this case, we would

97 expect that the benefits of primary robbers' feeding activities (i.e., creating robbing holes) would
98 outweigh the cost of competing with them for nectar, leading to facilitation (Fig. 1A). (2) If nectar
99 standing crop in primary-robbed flowers is instead low, due to a high number of "secondary" visits
100 from primary robbers, we predict that secondary robbers will experience reduced foraging
101 efficiency in the presence of primary robbers, as a result of having to spend more time finding
102 rewarding flowers. In this case, the cost of competing with primary robbers should outweigh the
103 benefit of access to robbing holes (Fig. 1A). (3) If legitimate foraging is a more efficient strategy
104 than secondary robbing regardless of primary robbing rate or nectar drainage in flowers, foragers
105 should be more likely to adopt this strategy. In this case, we predict that there will not be a
106 facilitative benefit due to primary robbing, as legitimate foragers do not utilize robbing holes.
107 Rather, we expect that legitimate foragers will only pay a competitive cost from interacting with
108 primary robbers (Fig. 1B).

109

110 **Materials and Methods**

111 *Study site and system*

112 Experiments were performed in a 2.5 m x 3 m x 2.1 m flight cage at the Rocky Mountain
113 Biological Laboratory (RMBL, elevation 2895 m), Gothic, CO USA. The flight cage was outdoors,
114 and was made of a metal frame covered with white canvas (WeatherPort Shelter Systems, Delta,
115 CO). Mesh windows on all sides allow for ambient light and temperature inside. We observed
116 individual foraging bouts of the facultative secondary robbing bumble bee *Bombus bifarius* on
117 arrays of the host plant *Linaria vulgaris* (Plantaginaceae, henceforth *Linaria*). *Linaria* is a long-
118 lived, rhizomatous perennial that produces racemes of 15-30 zygomorphic flowers (Arnold 1982).
119 Flowers are yellow with an orange palate and a nectar spur 15-20 mm in length (Stout et al. 2000).
120 Nectar is continually produced, with flowers producing up to 2.8 μ L in 48 hr (Nepi et al. 2003).

121 *Linaria* was introduced by European settlers into North America and is now widespread (Arnold
122 1982). In its North American range, *Linaria* has been incorporated into the foraging diet of a variety
123 of pollinators, including bumble bees (Burkle et al. 2007). In addition, *Linaria* experiences primary
124 nectar robbing by the bumble bee *Bombus occidentalis*, which uses its toothed mandibles to create
125 holes in the nectar spurs. *Bombus bifarius* cannot primary rob but can secondary rob flowers
126 primary-robbed by *B. occidentalis*. Both species exhibit flexibility in foraging behavior: *B.*
127 *occidentalis* often switches from primary robbing to secondary robbing as the rate of primary
128 robbing holes in flowers increases, whereas *B. bifarius* can also legitimately forage from *Linaria*
129 flowers for nectar and pollen (Newman and Thomson 2005). However, there is preliminary
130 evidence that secondary robbing is a more efficient strategy for *B. bifarius* in field conditions
131 (Newman and Thomson 2005). Workers possess short probosces, making access to nectar through
132 legitimate foraging difficult; furthermore, workers can consume more nectar per unit time by
133 foraging from robbing holes (Newman and Thomson 2005).

134

135 *Collection of individuals for foraging observations*

136 We conducted foraging observations 5 d/wk from 25 July 2014 to 26 August 2014. Each
137 morning and afternoon, we collected 10-15 individual *B. bifarius* workers as they foraged from
138 natural *Linaria* populations within the vicinity of the RMBL. Bees were collected in vials and
139 immediately placed into a cooler before being transferred to a 10°C refrigerator for 1 hr. Upon
140 capture, we recorded the foraging strategy being employed (legitimate foraging or secondary
141 robbing). All bees used the foraging strategy recorded at capture during the experimental trials (see
142 Results).

143

144

145 *Experimental treatments*

146 We collected stalks 15-20 cm in length from *Linaria* populations within the vicinity of the
147 RMBL. The stalks had been enclosed in mesh cages for 24 hr to allow flowers to refill with nectar.
148 After collecting, we inserted stalks into florist picks filled with water. Picks were placed into 10 cm
149 pots, filled with soil to keep the picks stable. When necessary, we removed flowers from stalks so
150 that each stalk displayed 20 flowers, none of which had pre-existing robbing holes. We then
151 performed manipulations to reflect the pattern of floral damage stalks would typically encounter
152 after a bout of primary robbing by *B. occidentalis*. We used five experimental treatments. The first
153 four treatments were a 2x2 cross of primary robbing frequency (low vs. high) by nectar availability
154 (rewarding vs. unrewarding). In the low primary robbing treatment, we made robbing holes in 20%
155 (low primary robbing treatment) or 80% (high primary robbing treatment) of flowers. Nectar was
156 either removed from the artificially robbed flowers (unrewarding treatment) or was left in them
157 (rewarding treatment). Finally, in a Control treatment, no flowers received robber holes and all
158 flowers were rewarding. Low and high robbing rates were chosen based on observations of natural
159 variation in primary robbing rates in the field (S. Richman, personal observation). We chose to
160 remove all available nectar from flowers with robbing holes, as field studies indicate that robbed
161 *Linaria* are more likely to be empty than flowers without robbing holes (Newman and Thomson
162 2005). In all treatments, no nectar was removed from intact (unrobbed) flowers. All treatments were
163 applied at the stalk level; that is, each stalk used in the array received the same treatment. For
164 example, in a low primary robbing treatment, where 20% of flowers had robbing holes, we made
165 holes in 20% of the flowers on each stalk.

166 We created primary robbing holes by piercing the nectar spur with a pair of fine-tipped
167 forceps, creating the characteristic “u”-shaped perforation made by *B. occidentalis* (S. Richman,
168 personal observation). When necessary for the experimental treatment, we removed all available

169 nectar from flowers using a 10 uL microcapillary tube (Microcap, Drummond Scientific, Broomall,
170 PA) inserted into the robbing hole. This method removes nectar using capillary action and does not
171 damage the floral tissue or reproductive structures (Irwin and Brody 1998, Irwin et al. 2015).

172

173 *Foraging bout observations*

174 After treatments were applied, we assembled arrays of 30 flowering *Linaria* stalks in a 1 m x
175 1 m grid, each stalk having received the same treatment. For each foraging bout, we set out a new
176 array of stalks, numbering each stalk from 1-30. We placed one control stalk in the center of the
177 array. Bees were introduced from the refrigerator onto this control stalk before visiting the array to
178 ensure they had time to warm up and would readily forage from the treatment stalks.

179 We observed foraging bouts of individual *B. bifarius* on *Linaria* arrays, n = 10
180 bees/treatment, each bee given one array. Treatments were randomized by day of the week and time
181 of day (morning or afternoon). Once a bee began foraging from the treatment stalks, we recorded its
182 behavior using both a video recorder (Sony HDR SR-11) and a hand-held digital voice recorder
183 (Olympus VN-702PC). For each floral visit, we recorded the stalk number, how many flowers were
184 visited per stalk, the time spent nectar-feeding from each flower, and the foraging strategy
185 employed at each flower (legitimate foraging or secondary robbing). When possible, we recorded
186 the reward collected at each visit (pollen or nectar). After a bee finished its foraging bout, signified
187 by leaving the array and flying to the side or ceiling of the flight cage, we captured it and removed it
188 from the arena. It has been shown in another system that across species, body size can predict
189 bumble bees' decisions to legitimately forage or secondary rob, with smaller bees more likely to
190 secondary rob (Ishii 2013). Consequently, we measured radial cell length (mm) of the right
191 forewing using digital calipers (to the nearest 0.01 mm) as an estimate of bee size (Harder 1982).
192 Before releasing a bee back to the field at its point of collection, we marked it with a unique

193 numbered tag (The Bee Works, Oro-Medonte, ON, Canada) glued to its thorax using non-toxic
194 glue. This method ensured that we did not re-use bees for foraging observations.

195

196 *Statistical analyses and interaction strength calculations*

197 To test whether treatment predicted foraging strategy, we generated a contingency table
198 containing the number of bouts observed per foraging strategy, broken down by treatment. We
199 performed a Chi-squared Test of Independence based on this contingency table. To test the
200 hypothesis that foraging efficiency differed by foraging strategy, and that primary robbing
201 frequency and nectar availability (whether primary robbed flowers were rewarding or unrewarding)
202 affected foraging efficiency (predictions 1, 2), we calculated the following response variables: (1)
203 Feeding time per flower (s), calculated as (total time spent nectar feeding at flower (s))/total #
204 flowers visited; this time does not include time spent searching or probing for a robbing hole. (2)
205 Flowers visited per minute, calculated as (total # flowers visited/total bout time (min)). (3)
206 Proportion of bout spent nectar feeding, calculated as (total time spent nectar feeding at flower
207 (s))/total bout time (s)). For feeding time per flower and flowers visited per minute, we compared
208 primary robbing frequency (low/high) and nectar availability (rewarding/unrewarding) using a
209 linear model with foraging strategy, primary robbing frequency, nectar availability, and the
210 interaction of primary robbing frequency and nectar availability as fixed effects and bee size (radial
211 cell length) as a covariate. We excluded the two-way interaction of strategy with either primary
212 robbing frequency or nectar availability, as well as the three-way interaction between all three
213 variables, because initial analyses yielded all interactions as non-significant, and AIC comparison
214 indicated the simpler models as the best fit. For proportion of bout spent nectar-feeding, we
215 compared primary robbing frequency and nectar availability using GLM (binomial family) with the
216 same fixed effects and interactions as in the linear model analyses. We excluded two bouts from the

217 analyses that were < 1 min in length; it was unclear in these cases whether bees had completed a
 218 foraging bout or had probed flowers only briefly before deciding to leave the array. Of the 38
 219 treatment bouts, 25 bees foraged legitimately, 10 secondary robbed and 3 were inconstant, i.e., they
 220 employed each of the two strategies at least once. We assigned the inconstant bouts to either
 221 legitimate or secondary robbing foraging strategies as follows. In the first inconstant bout, assigned
 222 to legitimate foraging, 91% (19 of 22) of the visits were legitimate; in the second, assigned to
 223 secondary robbing, 96% (27 of 28) of the visits were secondary robbing. In the third bout, the bee
 224 switched strategies multiple times, although it secondary robbed the majority of the time (91%, 31
 225 of 34 visits); it was thus assigned secondary robbing as its overall foraging strategy. Excluding the
 226 inconstant bouts from the analysis yielded the same results (data not shown). Bouts from the control
 227 treatment were excluded from the linear model analyses, but were used to calculate interaction
 228 strength (see next). Effects of individual model terms were calculated using Type II ANCOVA for
 229 feeding time per flower and number of flowers visited per minute, and using a likelihood ratio test
 230 for proportion of bout spent nectar feeding. All analyses were performed using R version 3.2.3 (R
 231 Core Team 2016).

232 We used Relative Interaction Intensity (R_{II}) (Armas et al. 2004) to compare the costs and
 233 benefits of primary robbing on *B. bifarius* foraging efficiency, and to determine whether the
 234 cost/benefit ratio led to primary robbers facilitating secondary robbers (Prediction 3). R_{II} is typically
 235 used to calculate the effect of interspecific interactions, where the R_{II} value indicates the effect of
 236 species A on species B (Armas et al. 2004). We consider R_{II} to be valuable for this study, as we can
 237 use R_{II} values to extend our results and further quantify the strength of the interaction. We compared
 238 all experimental treatment conditions relative to the control for all three response variables,
 239 calculated as:

$$R_{II_{\text{Response}}} = (\bar{x}_{\text{Treatment}} - \bar{x}_{\text{Control}}) / (\bar{x}_{\text{Treatment}} + \bar{x}_{\text{Control}}).$$

240 R_{II} ranges from -1 to 1, where the effect of primary robbing on *B. bifarius* is more costly (i.e., the
 241 competitive effect of primary robbing on *B. bifarius* outweighs its facilitative effect) as the value
 242 approaches -1, and more beneficial (i.e., facilitative) as the value approaches 1. R_{II} values that do
 243 not differ from zero are considered to be neutral in effect. After calculating R_{II} for each treatment
 244 condition relative to the control, we performed a randomization test to generate 95% confidence
 245 intervals around each value in order to determine whether values significantly differed from zero.
 246 We interpret R_{II} values that are significantly different from zero (positive or negative) to point to a
 247 significant effect of primary robbing (i.e., the simulated effect of *B. occidentalis*) on *B. bifarius*
 248 foraging efficiency.

249

250 **Results**

251 *Foraging efficiency of secondary nectar robbing vs. legitimate foraging*

252 We observed a total of 48 bouts of *B. bifarius* foraging on 1,009 flowers across the 5
 253 treatments, 38 of which were from the four manipulative treatments. Average bout time was $6.37 \pm$
 254 0.72 min. Opposite to our initial prediction, we found that legitimate foraging was a more efficient
 255 foraging strategy than secondary robbing. Bees that legitimately foraged visited an average of 0.75
 256 more flowers/min than did those that secondary robbed ($F_{1,28} = 5.89$, $P = 0.02$; Fig. 2B). There was
 257 a significant, positive effect of body size on the number of flowers visited/min (adjusted $R^2 = 0.14$,
 258 $P = 0.02$). Legitimately foraging bees spent an average of 34.6% more time per bout nectar-feeding
 259 (as opposed to searching for flowers, searching for robbing holes, or grooming) than did secondary
 260 robbers ($\chi^2_1 = 10.47$, $P = 0.001$, Fig. 2C), with no significant effect of body size on time spent
 261 nectar-feeding ($P = 0.08$). There was no effect of treatment on foraging strategy ($\chi^2_3 = 2.68$, $P =$
 262 0.44).

263 *Effect of primary robbing on foraging efficiency*

264 Primary robbing frequency and nectar availability within the array did not significantly
265 affect the length of time that bees spent nectar-feeding at flowers, the number of flowers they
266 visited per minute (Tables 1 and 2), nor the proportion of each bout they spent nectar-feeding
267 (primary robbing frequency $\chi^2_1 = 1.23$, $P = 0.26$; nectar availability $\chi^2_1 = 0.10$, $P = 0.75$). Nor was
268 the interaction between primary robbing rate and nectar availability statistically significant for any
269 of the three response variables (Table 1 for average time/flower, number of flowers visited/minute;
270 proportion bout spent nectar feeding $\chi^2_1 = 1.18$, $P = 0.28$). Overall, neither foraging strategy nor
271 body size significantly affected feeding time (Fig. 2A for foraging strategy).

272

273 *Relative interaction intensity (R_{II})*

274 There was an overall weak negative effect of primary robbing on R_{II} associated with average
275 feeding time per flower (s), indicating that competitive effects of primary robbing on *B. bifarius*
276 outweighed its facilitative effects (Table 3, Fig. 3A). There was a weak positive effect of primary
277 robbing on R_{II} associated with number of flowers visited/min, although R_{II} was not significantly
278 different from zero in the Low robbing, Rewarding treatment (Fig. 3B). There was no effect on R_{II}
279 associated with the proportion of the bout spent nectar feeding, except in the Low robbing,
280 Unrewarding treatment, where there was a weak negative effect (Fig. 3B).

281

282 **Discussion**

283 We tested the prediction, emerging from limited field studies (Dedaj and Delaplane 2005,
284 Newman and Thomson 2005), that the advantage of secondary robbing is that it allows a bee to
285 make more frequent floral visits and consume more nectar per unit time than would foraging
286 legitimately, resulting in increased foraging efficiency. Higher foraging efficiency, in turn, should
287 decrease the costs and increase the benefits of secondary robbing, indicating that primary robbers

288 facilitate secondary robbers (Fig. 1A). Interestingly, after testing this prediction under controlled
289 conditions, we found the opposite. For the facultative secondary-robber *Bombus bifarius* foraging
290 on *Linaria vulgaris*, secondary-robbing individuals visited significantly *fewer* flowers per minute
291 and spent a *lower* proportion of their foraging bout consuming nectar than did legitimate foragers of
292 the same species. Furthermore, 71% of bees tested chose legitimate foraging over secondary
293 robbing. Consistent with our prediction for a scenario in which legitimate foraging is more efficient
294 (Fig. 1B), we did not find a benefit for *B. bifarius* of increased foraging efficiency in response to
295 primary robbing. In this scenario, the lack of benefits provided by primary robbers should produce
296 an outcome of no facilitation of secondary robbers (Fig. 1B). Indeed, our findings indicate that
297 primary robbers' feeding activities do not facilitate the success of species that can secondary rob.
298 Negative R_{II} values for average feeding time per flower and the proportion of the foraging bout
299 spent nectar-feeding indicate the potential for high competition with primary robbers for *B. bifarius*.
300 While positive R_{II} values for the number of flowers visited per minute indicate that primary robbing
301 can benefit *B. bifarius*' foraging efficiency, the interpretation of the results is confounded by the
302 fact that bees that visited more flowers per minute also spent less time per flower nectar-feeding.
303 This finding, that legitimate foraging is more efficient than secondary robbing, spurs interesting
304 questions about the ecology of secondary robbing, particularly given that *B. bifarius* secondary robs
305 *Linaria* commonly in nature.

306

307 *Why be a secondary nectar robber?*

308 If secondary robbing does not always maximize foraging efficiency, it becomes essential to
309 consider other factors that could contribute to adoption of the behavior. One hypothesis is that, due
310 to cognitive constraints (Gegear and Lavery 2001), secondary robbing is ultimately more efficient,
311 even though individuals can increase short-term efficiency if they foraged legitimately. For

312 instance, robbing holes may serve as a search image for secondary robbers. Use of a search image
313 can improve foraging efficiency by creating a “run” effect, allowing foragers to find the same
314 resource repeatedly (Tinbergen 1960, Bond and Riley 1991, Gegear and Lavery 2001), although no
315 empirical evidence of this phenomenon exists for nectar robbers. Additionally, robbing holes may
316 provide a visual stimulus that encourages learning of secondary robbing as a foraging strategy.
317 *Bombus terrestris* legitimate foragers can learn to secondary rob through social transmission after
318 foraging among flowers with robbing holes in a laboratory setting, and subsequently visit the
319 nectary (rather than the floral opening) faster than bees that do not learn to rob (Leadbeater and
320 Chittka 2008). Secondary robbers in our experiment often flew directly to the spur, sometimes
321 making the mistake of probing an intact spur, indicating that they have at least made an association
322 between the nectar spur and access to floral rewards. Similar behavior has been observed in other
323 *Bombus* species foraging on the long-spurred plant *Corydalis caseana* in the field (S. K. Richman,
324 pers. obs.).

325 Another explanation for why bees secondary-rob although it is less efficient than legitimate
326 foraging is that asymmetric inter- or intraspecific competition forces individuals to choose
327 secondary robbing, although they would prefer to forage legitimately. Body size, which was a
328 significant factor affecting foraging efficiency in our study, as well as proboscis length have been
329 shown to be important factors in structuring competitive hierarchies in *Bombus* spp., with longer-
330 tongued species often competitively dominant (Inouye 1978, Ishii et al. 2008). Moreover, there is
331 evidence that nectar-robbing *Bombus* individuals tend to have shorter tongues than legitimate
332 foraging individuals (Ishii 2013). It is also plausible that individuals adopt secondary robbing as a
333 foraging strategy in response to simultaneously interacting with a high density of foragers in a patch
334 or on a stalk, and utilizing robbing holes rather than floral openings is a resource partitioning
335 strategy that does not require the cognitive effort involved in switching to a new plant species.

336 There is evidence for partitioning of this kind in the field: Newman and Thomson (2005) report that
337 *Bombus* spp. individuals spatially segregate on floral stalks by foraging strategy (legitimate foraging
338 and secondary robbing). Our experimental design prohibited us from being able to detect any effect
339 of conspecific or heterospecific forager presence on *B. bifarius* foraging strategy because bees
340 foraged alone. If *B. bifarius* experiences higher foraging efficiency by foraging legitimately, we
341 would expect to see a high proportion of individuals using this strategy in the absence of other
342 foragers. Our results are consistent with this expectation. Approximately 80% of bees used in the
343 experiment foraged legitimately, a much higher proportion than is found in nature (Newman and
344 Thomson 2005). However, it is unknown whether the difference in proportion of legitimate foragers
345 in the flight cage versus in nature is indeed in response to other foragers being absent, or due to
346 another factor, such as one connected with foraging in an artificial setting. We have no reason to
347 expect that bees would forage differently in the flight cage than in nature, but it would be valuable to
348 conduct a similar study in a field setting and compare foraging behaviors. Finally, in order to fully
349 understand the dynamics of competition between forager types, it would be necessary to understand
350 the behavior of facultative secondary nectar robbers in response to overall competitor density as
351 well as the relative densities of con- and heterospecifics.

352

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430 Table 1. Effect of primary robbing frequency (low or high) and nectar availability (whether or not
 431 primary robbed flowers are rewarding) on metrics of *B. bifarius* foraging efficiency. Primary
 432 robbing frequency and nectar availability were used as fixed effects in a linear model followed by
 433 an F-test. Table reports F-values and *P*-values for each fixed effect as well as their interaction,
 434 degrees of freedom = 1 (model), 28 (residual) for all rows.

Response Variable	Model Variable	SS	F	<i>P</i>
Visit time/flower (s)	Primary rob rate	0.13	0.03	0.86
	Nectar available	13.76	3.17	0.09
	Interaction	1.62	0.37	0.55
Flowers visited/minute	Primary rob rate	2.11	0.82	0.37
	Nectar available	6.57	2.57	0.12
	Interaction	1.14	0.44	0.51

SS = Type II Sum of Squares

435 Table 2. Mean \pm SE values for primary robbing frequency and nectar availability for all *B. bifarius*
 436 foraging efficiency response variables. Both independent variables have two levels: high and low
 437 primary robbing frequency; nectar in robbed flowers present (available) or absent (unavailable). For
 438 all response variables, n = 48 bouts. Results shown combine both foraging strategies, as primary
 439 robbing and nectar availability treatments had no significant effect on strategy.

Independent variable	Visit time/flower (s)	Flowers visited/minute	Proportion bout nectar feeding
	Mean \pm SE	Mean \pm SE	Mean \pm SE
Primary rob frequency - High	6.47 \pm 0.98	3.72 \pm 0.54	0.33 \pm 0.03
Primary rob frequency - Low	6.15 \pm 0.47	2.97 \pm 0.29	0.29 \pm 0.03
Nectar available - No	5.21 \pm 0.45	3.70 \pm 0.49	0.29 \pm 0.03
Nectar available - Yes	7.30 \pm 0.89	3.03 \pm 0.38	0.23 \pm 0.03

440 Table 3. Mean \pm SE values of *B. bifarius* foraging efficiency for all experimental treatment
 441 conditions. Treatments indicate the combinations of crossed factors: primary robbing frequency
 442 (low or high), nectar availability (whether primary robbed flowers are rewarding; yes or no). Mean
 443 \pm SE values for the control condition are 9.68 ± 1.37 , 3.35 ± 0.44 and 0.35 ± 0.04 for feeding
 444 time/flower (s), flowers visited/minute and proportion bout nectar feeding, respectively. R_{II}
 445 (Relative Interaction Intensity) is a measure of interaction strength ranging from -1 to 1. Positive
 446 values represent a net positive effect (facilitation); negative values represent a net negative effect
 447 (competition). The effect is stronger as the value approaches 1 or -1. Table shows R_{II} and 95% CI
 448 for all treatments.

Response Variable	Treatment	Value, Mean \pm SE	R_{II} , Mean \pm SE	95% CI, Low	95% CI, High
Visit time/flower (s)	Low, No	5.05 ± 0.63	-0.28 ± 0.03	-0.33	-0.22
	Low, Yes	6.95 ± 0.57	-0.13 ± 0.03	-0.17	-0.08
	High, No	5.34 ± 0.66	-0.26 ± 0.03	-0.31	-0.21
	High, Yes	7.73 ± 1.91	-0.15 ± 0.04	-0.22	-0.08
Flowers visited/minute	Low, No	4.70 ± 0.51	0.18 ± 0.03	0.13	0.23
	Low, Yes	3.69 ± 0.41	0.04 ± 0.03	-0.02	0.10
	High, No	5.19 ± 0.74	0.20 ± 0.02	0.15	0.25
	High, Yes	4.08 ± 0.64	0.08 ± 0.03	0.02	0.14
Proportion bout nectar feeding	Low, No	0.24 ± 0.04	-0.19 ± 0.04	-0.27	-0.12
	Low, Yes	0.38 ± 0.09	-0.04 ± 0.03	-0.11	0.03
	High, No	0.34 ± 0.03	-0.01 ± 0.03	-0.06	0.05
	High, Yes	0.31 ± 0.04	-0.07 ± 0.04	-0.15	0.00

449 **Figure legends**

450 Figure 1. Decision tree showing the possible outcomes for nectar foragers under the conditions that
451 (A) secondary robbing or (B) legitimate foraging is a more efficient foraging strategy. Upper boxes
452 show environmental variables: primary robbing frequency (the frequency of robbing holes in
453 flowers) and nectar availability (whether primary robbed flowers have nectar). Lowest boxes show
454 outcomes weighing benefits and costs. Outcomes in which the benefit > cost suggest that primary
455 robbers facilitate secondary robbers; outcomes in which the benefit < cost suggest that facilitation
456 does not exist. In panel (B), legitimate foragers are not facilitated by primary robbers because they
457 do not utilize robbing holes. Outcomes show strong (benefit << cost) and weak (benefit < cost)
458 competition.

459
460 Figure 2. The effect of foraging strategy on mean \pm SE values for (A) Feeding time/flower, (B)
461 Flowers visited/minute, and (C) Proportion bout nectar feeding. For all graphs, $n = 39$ and 9 for the
462 number of individual *B. bifarius* foragers that adopted a legitimate foraging or secondary robbing
463 strategy, respectively. Asterisks indicate statistically significant ($p < 0.05$) values between foraging
464 strategies.

465
466 Figure 3. Mean \pm 95% CI R_{II} Values for each experimental treatment relative to the control. 95% CI
467 was generated using a randomization test. Panels represent R_{II} values for (A) Feeding time/flower,
468 (B) Flowers visited/minute, and (C) Proportion bout nectar feeding. Negative R_{II} values
469 significantly different from zero indicate a net negative effect of treatment on *B. bifarius* foraging
470 efficiency; Positive R_{II} values significantly different from zero indicate a net positive effect of
471 treatment on *B. bifarius* foraging efficiency.

Figure 1.

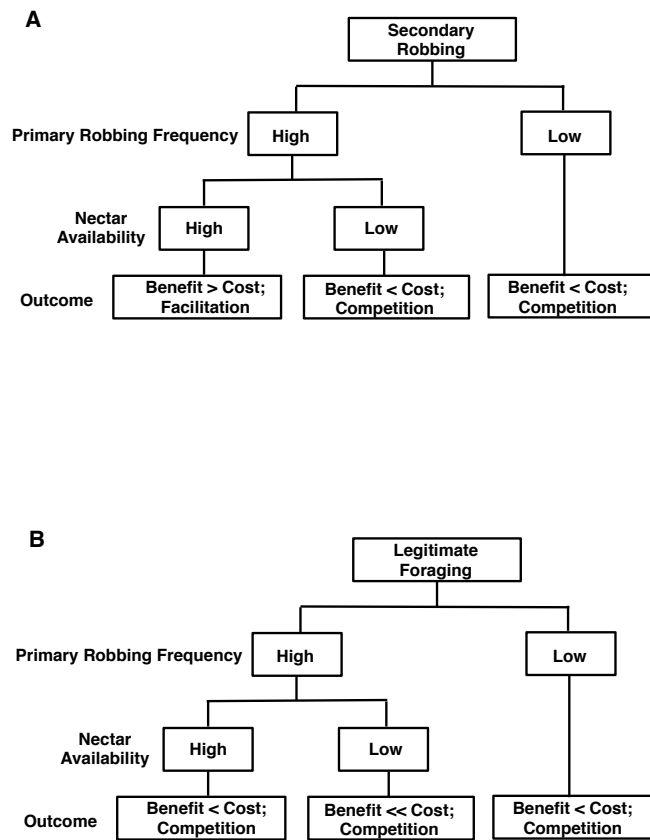


Figure 2

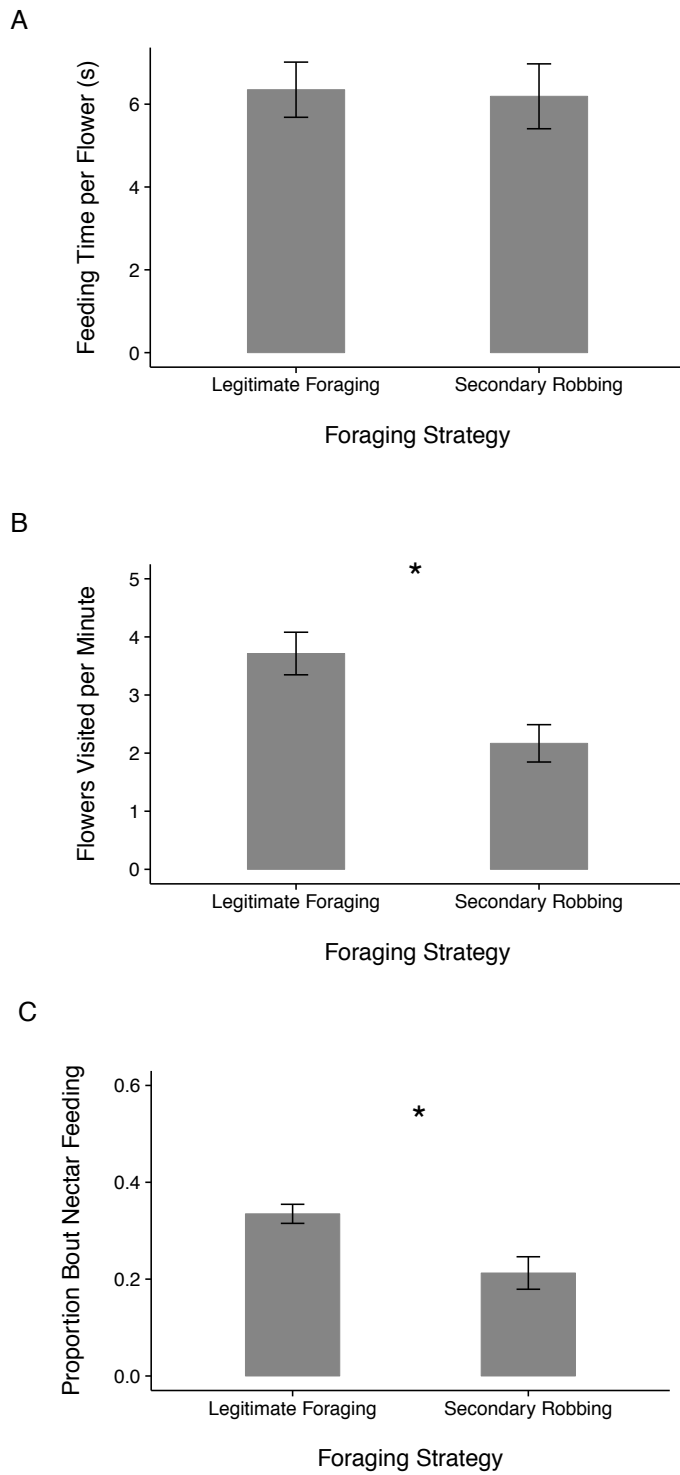


Figure 3

