Foraging strategy predicts foraging economy in a facultative secondary nectar robber

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

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

Why bees shift away from foraging legitimately is unknown. Nor are the environmental conditions that promote secondary robbing clear (Irwin et al. 2010). It is commonly thought that secondary robbing is a more efficient strategy relative to legitimate foraging (Deddej and Delaplane 2005). Specifically, because secondary robbing allows nectar robbers to circumvent a morphological mismatch with a flower that would otherwise make access to nectar difficult, it can reduce flower handling times and lead to increased nectar removal (Olesen 1996, Newman and Thomson 2005, Deddej and Delaplane 2005). If adopting a secondary robbing over a legitimate foraging strategy is more energetically efficient, it should alleviate some of the fitness costs associated with foraging, including energetic costs, predation risk and missed opportunity costs, such as those incurred when missing a mating opportunity (Brown et al. 1988). However, few studies
have tested this conventional wisdom (but see Thomson 2004).

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

By observing the foraging behavior of facultative secondary robbing bumble bees within floral arrays manipulated to mimic different effects of primary robbing (primary robbing rate and extent of nectar drainage from robbed flowers due to primary robbing), we tested the hypothesis that shifting to secondary robbing from legitimate foraging leads to higher individual foraging efficiency. From this initial hypothesis, three predictions follow:

1) if secondary robbing is a more efficient foraging strategy, we predict that secondary robbers will achieve higher foraging efficiency in patches with higher rates of primary robbing, as long as nectar standing crop in primary-robbed flowers is high, due to limited ‘secondary’ visits from primary robbers. In this case, we would expect that the benefits of primary robbers’ feeding activities (i.e. creating robbing holes) would outweigh the cost of competing with them for nectar, leading to facilitation (Fig. 1A).

2) If nectar standing crop in primary-robbed flowers is instead low, due to a high number of ‘secondary’ visits from primary robbers, we predict that secondary robbers will experience reduced foraging efficiency in the presence of primary robbers, as a result of having to spend more time finding rewarding flowers. In this case, the cost of competing with primary robbers should outweigh the benefit of access to robbing holes (Fig. 1A).

3) If legitimate foraging is a more efficient strategy than secondary robbing regardless of primary robbing rate or nectar drainage in flowers, foragers should be more likely to adopt this strategy. In this case, we predict that there will not be a facilitative benefit due to primary robbing, as legitimate foragers do not utilize robbing holes. Rather, we expect that legitimate foragers will only pay a competitive cost from interacting with primary robbers (Fig. 1B).

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

Material and methods

Study site and system

Experiments were performed in a 2.5 x 3 x 2.1 m flight cage at the Rocky Mountain Biological Laboratory (RMBL, elevation 2895 m), Gothic, CO, USA. The flight cage was outdoors, and was made of a metal frame covered with white canvas. Mesh windows on all sides allow for ambient light and temperature inside. We observed individual foraging bouts of the facultative secondary robbing bumble bee Bombus bifarius on arrays of the host plant Linaria vulgaris (Plantaginaceae, henceforth Linaria). Linaria is a long-lived, rhizomatous perennial that produces racemes of 15–30 zygomorphic flowers (Arnold 1982). Flowers are yellow with an orange palate and a nectar spur 15–20 mm in length (Stout et al. 2000). Nectar is continually produced, with flowers producing up to 2.8 μl in 48 h (Nepi et al. 2003). Linaria was introduced by European settlers into North America and is now widespread (Arnold 1982). In its North American range, Linaria has been incorporated into the foraging diet of a variety of pollinators, including bumble bees (Burkle et al. 2007). In addition, Linaria experiences primary nectar robbing by the bumble bee Bombus occidentalis, which uses its toothed mandibles to create holes in the nectar spurs. Bombus bifarius cannot primary rob but can secondary rob flowers primary-robbed by B. occidentalis. Both species
exhibit flexibility in foraging behavior. *B. occidentalis* often switches from primary robbing to secondary robbing as the rate of primary robbing holes in flowers increases, whereas *B. bifarius* can also legitimately forage from *Linaria* flowers for nectar and pollen (Newman and Thomson 2005). However, there is preliminary evidence that secondary robbing is a more efficient strategy for *B. bifarius* in field conditions (Newman and Thomson 2005). Workers possess short proboscies, making access to nectar through legitimate foraging difficult; furthermore, workers can consume more nectar per unit time by foraging from robbing holes (Newman and Thomson 2005).

**Collection of individuals for foraging observations**

We conducted foraging observations five days per week from 25 July 2014 to 26 August 2014. Each morning and afternoon, we collected 10–15 individual *B. bifarius* workers as they foraged from natural *Linaria* populations within the vicinity of the RMBL. Bees were collected in vials and immediately placed into a cooler before being transferred to a 10°C refrigerator for 1 h. Upon capture, we recorded the foraging strategy being employed (legitimate foraging or secondary robbing). All bees used the foraging strategy recorded at capture during the experimental trials.

**Experimental treatments**

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

We created primary robbing holes by piercing the nectar spur with a pair of fine-tipped forceps, creating the characteristic ‘u’-shaped perforation made by *B. occidentalis* (Richman unpubl.). When necessary for the experimental treatment, we removed all available nectar from flowers using a 10 ul microcapillary tube inserted into the robbing hole. This method removes nectar using capillary action and does not damage the floral tissue or reproductive structures (Irwin and Brody 1998, Irwin et al. 2015).

**Foraging bout observations**

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

We observed foraging bouts of individual *B. bifarius* on *Linaria* arrays, *n* = 10 bees/treatment, each bee given one array. Treatments were randomized by day of the week and time of day (morning or afternoon). Once a bee began foraging from the treatment stalks, we recorded its behavior using both a video recorder and a hand-held digital voice recorder. For each floral visit, we recorded the stalk number, how many flowers were visited per stalk, the time spent nectar-feeding from each flower, and the foraging strategy employed at each flower (legitimate foraging or secondary robbing). When possible, we recorded the reward collected at each visit (pollen or nectar). After a bee finished its foraging bout, signified by leaving the array and flying to the side or ceiling of the flight cage, we captured it and removed it from the arena. It has been shown in another system that across species, body size can predict bumble bees' decisions to legitimately forage or secondary rob, with smaller bees more likely to secondary rob (Ishii 2013). Consequently, we measured radial cell length (mm) of the right forewing using digital calipers (to the nearest 0.01 mm) as an estimate of bee size (Harder 1982). Before releasing a bee back to the field at its point of collection, we marked it with a unique numbered tag glued to its thorax using non-toxic glue. This method ensured that we did not re-use bees for foraging observations.

**Statistical analyses and interaction strength calculations**

To test whether treatment predicted foraging strategy, we generated a contingency table containing the number of bouts observed per foraging strategy, broken down by treatment. We performed a χ²-test of independence based on this contingency table. To test the hypothesis that foraging efficiency differed by foraging strategy, and that primary robbing frequency and nectar availability (whether primary robbed flowers were rewarding or unrewarding) affected foraging efficiency (predictions 1, 2), we calculated the following response variables: 1) feeding time per flower (s), calculated as (total time spent nectar feeding at flower (s))/total no. flowers visited; this time does not include time spent searching or probing for a robbing hole. 2) Flowers
Results

Foraging efficiency of secondary nectar robbing versus legitimate foraging

We observed a total of 48 bouts of Bombus bifarius foraging on 1009 flowers across the five treatments, 38 of which were from the four manipulative treatments. Average bout time was 6.37 ± 0.72 min. Opposite to our initial prediction, we found that legitimate foraging was a more efficient foraging strategy than secondary robbing. Bees that legitimately foraged visited an average of 0.75 more flowers/min than those that secondary robbed (F1,28 = 5.89, p = 0.02; Fig. 2B). There was a significant, positive effect of body size on the number of flowers visited/min (adjusted R2 = 0.14, p = 0.02). Legitimately foraging bees spent an average of 34.6% more time per bout nectar-feeding (as opposed to searching for flowers, searching for robbing holes or grooming) than did secondary robbers (χ2 = 10.47, p = 0.001, Fig. 2C), with no significant effect of body size on time spent nectar-feeding (p = 0.08). There was no effect of treatment on foraging strategy (χ2 = 2.68, p = 0.44).

Effect of primary robbing on foraging efficiency

Primary robbing frequency and nectar availability within the array did not significantly affect the length of time that bees spent nectar-feeding at flowers, the number of flowers they visited per minute (Table 1, 2), nor the proportion of each bout they spent nectar-feeding (primary robbing frequency χ2 = 1.23, p = 0.26; nectar availability χ2 = 0.10, p = 0.75). Nor was the interaction between primary robbing rate and nectar availability statistically significant for any of the three response variables (Table 1 for average time/flower, number of flowers visited/minute; proportion bout spent nectar feeding χ2 = 1.18, p = 0.28). Overall, neither foraging strategy nor body size significantly affected feeding time (Fig. 2A for foraging strategy).

Relative interaction intensity (RІІ)

There was an overall weak negative effect of primary robbing on RІІ associated with average feeding time per flower (s),
We tested the prediction, emerging from limited field studies (Dedej and Delaplane 2005, Newman and Thomson 2005), that the advantage of secondary robbing is that it allows a bee to make more frequent floral visits and consume more nectar per unit time than would foraging legitimately, resulting in increased foraging efficiency. Higher foraging efficiency, in turn, should decrease the costs and increase the benefits of secondary robbing, indicating that primary robbers facilitate secondary robbers (Fig. 1A). Interestingly, after testing this prediction under controlled conditions, we found the opposite. For the facultative secondary-robber Bombus bifarius foraging on Linaria vulgaris, secondary-robbing individuals visited significantly fewer flowers per minute and spent a lower proportion of their foraging bout consuming nectar than did legitimate foragers of the same species. Furthermore, 71% of bees tested chose legitimate foraging over secondary robbing. Consistent with our prediction for a scenario in which legitimate foraging is more efficient (Fig. 1B), we did not find a benefit for B. bifarius of increased foraging efficiency in response to primary robbing. In this scenario, the lack of benefits provided by primary robbers should produce an outcome of no facilitation of secondary robbers (Fig. 1B). Indeed, our findings indicate that primary robbers’ feeding activities do not facilitate the success of species that can secondary rob. Negative RII values for average feeding time per flower and the proportion of the foraging bout spent nectar feeding indicate the potential for high competition with primary robbers. While positive RII values for the number of flowers visited per minute indicate that primary robbing can benefit B. bifarius foraging efficiency, the interpretation of the results is confounded by the fact that bees that visited more flowers per minute also spent less time per flower nectar-feeding. This finding, that legitimate foraging is more efficient than secondary robbing, spurs interesting questions about the ecology of secondary robbing, particularly given that B. bifarius secondary robs Linaria commonly in nature.

Why be a secondary nectar robber?

If secondary robbing does not always maximize foraging efficiency, it becomes essential to consider other factors that could contribute to adoption of the behavior. One
hypothesis is that, due to cognitive constraints (Gegear and Laverty 2001), secondary robbing is ultimately more efficient, even though individuals can increase short-term efficiency if they foraged legitimately. For instance, robbing holes may serve as a search image for secondary robbers. Use of a search image can improve foraging efficiency by creating a ‘run’ effect, allowing foragers to find the same resource repeatedly (Tinbergen 1960, Bond and Riley 1991, Gegear and Laverty 2001), although no empirical evidence of this phenomenon exists for nectar robbers. Additionally, robbing holes may provide a visual stimulus that encourages learning of secondary robbing as a foraging strategy. *Bombus terrestris* legitimate foragers can learn to secondary rob through social transmission after foraging among flowers with robbing holes in a laboratory setting, and subsequently visit the nectary (rather than the floral opening) faster than bees that do not learn to rob (Leadbeater and Chittka 2008). Secondary robbers in our experiment often flew directly to the spur, sometimes making the mistake of probing an intact spur, indicating that they have at least made an association between the nectar spur and access to floral rewards. Similar behavior has been observed in other *Bombus* species foraging on the long-spurred plant *Corydalis caseana* in the field (Richman unpubl.).

Another explanation for why bees secondary-rob although it is less efficient than legitimate foraging is that asymmetric inter- or intraspecific competition forces individuals to choose secondary robbing, although they would prefer to forage legitimately. Body size, which was a significant factor affecting foraging efficiency in our study, as well as proboscis length have been shown to be important factors in structuring competitive hierarchies in *Bombus* spp., with longer-tongued species often competitively dominant (Inouye 1978, Ishii et al. 2008). Moreover, there is evidence that nectar-robbing *Bombus* individuals tend to have shorter tongues than legitimate foraging individuals (Ishii 2013). It is also plausible that individuals adopt secondary robbing as a foraging strategy in response to simultaneously interacting with a high density of foragers in a patch or on a stalk, and utilizing robbing holes rather than floral openings is a resource partitioning strategy that does not require the cognitive effort involved in switching to a new plant species. There is evidence for partitioning of this kind in the field: Newman and Thomson (2005) report that *Bombus* spp. individuals spatially segregate on floral stalks by foraging strategy (legitimate foraging and secondary robbing). Our experimental design prohibited us from being able to detect any effect of conspecific or heterospecific forager presence on *B. bifarius* foraging strategy because bees foraged alone. If *B. bifarius* experiences higher foraging efficiency by foraging legitimately, we would expect to see a high proportion of individuals using this strategy in the absence of other foragers. Our results are consistent with this expectation. Approximately 80% of bees used in the experiment foraged legitimately, a much higher proportion than is found in nature (Newman and Thomson 2005). However, it is unknown whether the difference in proportion of legitimate foragers in the flight cage versus in nature is indeed in

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

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Visit time/flower (s) Mean ± SE</th>
<th>Flowers visited/minute Mean ± SE</th>
<th>Proportion bout nectar feeding Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary rob frequency - High</td>
<td>6.47 ± 0.98</td>
<td>3.72 ± 0.54</td>
<td>0.33 ± 0.03</td>
</tr>
<tr>
<td>Primary rob frequency - Low</td>
<td>6.15 ± 0.47</td>
<td>2.97 ± 0.29</td>
<td>0.29 ± 0.03</td>
</tr>
<tr>
<td>Nectar available - no</td>
<td>5.21 ± 0.45</td>
<td>3.70 ± 0.49</td>
<td>0.29 ± 0.03</td>
</tr>
<tr>
<td>Nectar available - yes</td>
<td>7.30 ± 0.89</td>
<td>3.03 ± 0.38</td>
<td>0.23 ± 0.03</td>
</tr>
</tbody>
</table>

### Table 3. Mean ± SE values of *B. bifarius* foraging efficiency for all experimental treatment conditions. Treatments indicate the combinations of crossed factors: primary robbing frequency (low or high), nectar availability (whether primary robbed flowers are rewarding; yes or no). Mean ± SE values for the control condition are 6.68 ± 1.37, 3.35 ± 0.44 and 0.35 ± 0.04 for feeding time/flower (s), flowers visited/minute and proportion bout nectar feeding, respectively. RII (relative interaction intensity) is a measure of interaction strength ranging from –1 to 1. Positive values represent a net positive effect (facilitation); negative values represent a net negative effect (competition). The effect is stronger as the value approaches 1 or –1. Table shows RII and 95% CI for all treatments.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Treatment</th>
<th>Value, Mean ± SE</th>
<th>RII, Mean ± SE</th>
<th>95% CI, Low</th>
<th>95% CI, High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visit time/flower (s)</td>
<td>Low, no</td>
<td>5.05 ± 0.63</td>
<td>-0.28 ± 0.03</td>
<td>-0.33</td>
<td>-0.22</td>
</tr>
<tr>
<td></td>
<td>Low, yes</td>
<td>6.95 ± 0.57</td>
<td>-0.13 ± 0.03</td>
<td>-0.17</td>
<td>-0.08</td>
</tr>
<tr>
<td></td>
<td>High, no</td>
<td>5.34 ± 0.66</td>
<td>-0.26 ± 0.03</td>
<td>-0.31</td>
<td>-0.21</td>
</tr>
<tr>
<td></td>
<td>High, yes</td>
<td>7.73 ± 1.91</td>
<td>-0.15 ± 0.04</td>
<td>-0.22</td>
<td>-0.08</td>
</tr>
<tr>
<td>Flowers visited/minute</td>
<td>Low, no</td>
<td>4.70 ± 0.51</td>
<td>0.18 ± 0.03</td>
<td>0.13</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>Low, yes</td>
<td>3.69 ± 0.41</td>
<td>0.04 ± 0.03</td>
<td>0.02</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td>High, no</td>
<td>5.19 ± 0.74</td>
<td>0.20 ± 0.02</td>
<td>0.15</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>High, yes</td>
<td>4.08 ± 0.64</td>
<td>0.08 ± 0.03</td>
<td>0.02</td>
<td>0.14</td>
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<tr>
<td>Proportion bout nectar feeding</td>
<td>Low, no</td>
<td>0.24 ± 0.04</td>
<td>-0.19 ± 0.04</td>
<td>-0.27</td>
<td>-0.12</td>
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<tr>
<td></td>
<td>Low, yes</td>
<td>0.38 ± 0.09</td>
<td>-0.04 ± 0.03</td>
<td>-0.11</td>
<td>0.03</td>
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<tr>
<td></td>
<td>High, no</td>
<td>0.34 ± 0.03</td>
<td>-0.01 ± 0.03</td>
<td>-0.06</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>High, yes</td>
<td>0.31 ± 0.04</td>
<td>-0.07 ± 0.04</td>
<td>-0.15</td>
<td>0.00</td>
</tr>
</tbody>
</table>
response to other foragers being absent, or due to another factor, such as one connected with foraging in an artificial setting. We have no reason to expect that bees would forage differently in the fight cage than in nature, but it would be valuable to conduct a similar study in a field setting and compare foraging behaviors. Finally, in order to fully understand the dynamics of competition between forager types, it would be necessary to understand the behavior of facultative secondary nectar robbers in response to overall competitor density as well as the relative densities of conspecific and heterospecifics.

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