

1 **Running Head:** Mutualism exploitation: costs & benefits

2

3 **Title:** Costs and benefits of alternative food handling tactics help explain facultative exploitation
4 of pollination mutualisms

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18 **Abstract**

19 Many mutualisms are taken advantage of by organisms that take rewards from their partners but
20 provide no benefit in return. In the absence of traits that limit exploitation, facultative exploiters
21 (partners that can either exploit or cooperate) are widely predicted by mutualism theory to
22 choose an exploitative strategy, potentially threatening mutualism stability. However, it is
23 unknown whether facultative exploiters choose to exploit, and, if so, make this choice because it
24 is the most beneficial strategy for them. We explored these questions in a subalpine plant-insect
25 community in which individuals of several bumble bee species visit flowers both “legitimately”
26 (entering via the flower opening, picking up and depositing pollen, and hence behaving
27 mutualistically) and via nectar robbing (creating holes through corollas or using an existing hole,
28 bypassing stigmas and anthers). We applied foraging theory to (1) quantify handling costs,
29 benefits and foraging efficiencies incurred by three bumble bee species as they visited flowers
30 legitimately or robbed nectar in cage experiments, and (2) determine whether these efficiencies
31 matched the food handling tactics these bee species employed in the field. Relative efficiencies
32 of legitimate and robbing tactics depended on the combination of bee and plant species. In some
33 cases (*Bombus mixtus* visiting *Corydalis caseana* or *Mertensia ciliata*), the robbing tactic
34 permitted more efficient nectar removal. As both mutualism and foraging theory would predict,
35 in the field, *B. mixtus* visiting *C. caseana* were observed more frequently robbing than foraging
36 legitimately. However, for *Bombus flavifrons* visiting *M. ciliata*, the expectation from mutualism
37 theory did not hold: legitimate visitation was the more efficient tactic. Legitimate visitation to *M.*
38 *ciliata* was in fact more frequently observed in free-flying *B. flavifrons*. Free-flying *B. mixtus*
39 also frequently visited *M. ciliata* flowers legitimately. This may reflect lower nectar volumes in
40 robbed than unrobbed flowers in the field. These results suggest that a foraging ecology

41 perspective is informative to the choice of tactics facultative exploiters make. In contrast, the
42 simple expectation that exploiters should always have an advantage, and hence could threaten
43 mutualism persistence unless they are deterred or punished, may not be broadly applicable.

44

45 **Keywords**

46 Mutualism; pollination; cheating; exploitation; nectar robbing; foraging; food handling tactics;

47 *Bombus*

48

49 **Introduction**

50 Mutualisms, reciprocally beneficial interactions among species, are often taken advantage
51 of by species or individuals that use the resource or service offered by one mutualistic partner
52 without providing a benefit to that partner in return. This phenomenon has variously been termed
53 cheating, defection, parasitism, larceny, and exploitation (e.g., Soberon and Martinez del Rio
54 1985, Yu 2001, Bronstein 2001, Jones et al. 2015); we adopt the latter term here, as it de-
55 emphasizes motivations and mechanisms and focuses instead on its effects in the context of the
56 mutualism.

57 Associated with the study of exploitation has been a set of assumptions regarding its
58 benefits to the performer and its cost to the recipient. In particular, a large body of theoretical
59 research starts from the assumption that exploitation yields higher fitness than cooperating,
60 because exploiters should not suffer the costs of providing resources or services to a mutualistic
61 partner (Sachs 2015, Jones et al. 2015, Frederickson 2017). As a consequence, mutualists are
62 commonly predicted to exploit whenever exploitation is not effectively controlled (e.g., Pillai et
63 al. 2014, Sachs 2015). This logical argument fails, however, to explain the ubiquity in nature of
64 facultative exploitation, in which a single individual can perform both cooperative and
65 exploitative behaviors. For example, yucca moth individuals sometimes skip the behaviors used
66 to pollinate yucca flowers (Tyre and Addicott 1993), and ants sometimes eat the aphids they
67 usually protect (Sakata 1994). In systems in which mutualistic partners punish exploiters,
68 facultative exploitation may result when punishment threat by the partner is low (e.g., Pinto et al.
69 2011). Facultative exploitation can also be common in systems with no apparent sanctions
70 against exploiters, however, including ones in which the costs of being exploited are low or
71 absent (Bronstein 2001, Jones et al. 2015, Barker and Bronstein 2016).

72 Given the rarity or incomplete effectiveness of punishment and sanctions, why don't
73 mutualists with behavioral options always choose the exploitative strategy? Addressing this
74 question requires a shift away from the usual perspective on exploitation of mutualism, which
75 centers on the impact of exploitation on recipients (e.g., Richman et al. 2017a, Furukawa and
76 Kawakita 2017) and possible responses to it (Sachs 2015). Instead, we adopt here the much more
77 rarely considered perspective: that of the individual weighing the choice of whether to exploit or
78 cooperate with its partner.

79 Because most mutualisms are consumer-resource interactions (Holland et al. 2005),
80 insights derived from an animal foraging perspective have the potential to illuminate the costs
81 and benefits of alternative foraging tactics that represent cooperation and exploitation, thereby
82 testing whether exploitation yields higher net benefits than cooperating. In consumer-resource
83 systems, foraging theory predicts that natural selection acts on what, where and how an organism
84 eats (Hamilton 2010). Facultative exploitation provides an opportunity to test this third type of
85 decision: which of several alternative food handling tactics to use to extract resources. Here we
86 use the term "decision" as defined in behavioral ecology: selection of one option when at least
87 two options are available (Ydenberg 2010). Tests of foraging theory typically measure benefits
88 in terms of energy intake, and costs as time (search, handling, etc.) or energy expenditure. A
89 large body of literature shows that animals alter their behaviors over short time scales by, for
90 example increasing foraging efficiency or adopting alternative reproductive tactics that increase
91 reproduction. Thus, foraging theory suggests that facultative exploitation is the outcome of
92 flexible food-handling tactics deployed adaptively in response to local conditions.

93 Facultative nectar robbing provides an opportunity to test an idea implicit in recent
94 discussions of mutualism stability: exploitation is more advantageous than cooperation when

95 both options are available to an individual. Specifically, we use nectar robbing to look at whether
96 food handling tactics commonly viewed as exploitative (i.e., those that confer benefits only to
97 the forager) are more efficient than tactics commonly viewed as cooperative (those that confer
98 benefits to both partners). A nectar robber consumes nectar either by biting holes at the base of
99 flowers (primary robbing) or by using existing holes (secondary robbing), rather than by visiting
100 “legitimately” via the flower entrance (Inouye 1980). Nectar robbing is widespread, exhibited by
101 insects, birds and mammals, and is seen on most flowers with a tubular corolla or nectar spur
102 (Irwin et al. 2010). Because they remain outside the flower and typically do not contact anthers
103 or stigmas, most nectar robbers do not provide pollination services (but see, e.g., Higashi et al.
104 1988, Zhu et al. 2010). While nectar robbing has been well studied from the plant’s perspective,
105 it is less recognized that it is often a facultative behavior in which a flower visitor exhibits both
106 food handling tactics over time (on the same or different plant species) or even in the course of a
107 single foraging bout (Bronstein et al. 2017). Switching between tactics has been documented at
108 both the species (e.g., Dedej and Delaplane 2004, Ishii and Kadoya 2016) and individual levels
109 (e.g., Richardson and Bronstein 2012, Richman et al. 2017a). The gains that flower visitors
110 receive from each food handling tactic they can use, as well as the forces that might lead visitors
111 to choose between them, have been minimally explored.

112 To explore whether foraging theory can predict food handling tactics, and hence the
113 choice of whether to cooperate with or to exploit a partner, we experimentally quantified the
114 handling costs and benefits that several bumble bee species incur using their alternative foraging
115 tactics. Whether an individual visits a flower legitimately or robs should depend on the costs
116 required to access nectar with each tactic and how much nectar she is able to extract. We used
117 these costs and benefits to determine the foraging efficiencies of each tactic for four pairs of

118 bumble bee and plant species combinations. Second, we used field observations of free-flying
119 bees to ask whether these efficiencies match how frequently bumble bees exhibit each food
120 handling tactic in nature. We predicted that the most efficient flower handling tactic under a
121 given set of ecological conditions (e.g., bee-plant combination, benefit offered by a particular
122 flower) would be the predominant tactic employed in the field. Our results challenge the
123 commonly held assumption that behaviors termed “exploitative” yield higher benefits than those
124 viewed as “cooperative”.

125

126 **Materials and Methods**

127 Data and R scripts are available at [10.5281/zenodo.1243208](https://doi.org/10.5281/zenodo.1243208).

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129 *Study area and organisms*

130 This research was conducted during June-Aug 2015 in Gunnison County, CO, USA near
131 the Rocky Mountain Biological Laboratory (RMBL; 2886 m elevation). This region is
132 characterized by open meadows dominated by perennial flowering plant species that provide
133 food for pollinators, primarily bees. We studied flower handling behavior of three common,
134 native bumble bee species that are distinguishable based on pile markings: *Bombus bifarius*, *B.*
135 *flavifrons* and *B. mixtus* (Apidae) (Pyke 1982, Williams et al. 2014). The three species can each
136 obtain nectar from some flowers legitimately (Morris 1996, Newman and Thomson 2005).
137 *Bombus mixtus* can act as a primary nectar robber (Morris 1996) by using its toothed mandibles
138 (Fig. S1) to make holes in floral nectar spurs or at the base of tubular flowers to remove nectar.
139 All three species can also act as secondary robbers (e.g., Newman and Thomson 2005, Richman
140 et al. 2017a). Consistent with the behaviors each species can perform, experiments with *B.*

141 *mixtus* compared costs and benefits of legitimate visitation, primary robbing and secondary
142 robbing while experiments with *B. bifarius* and *B. flavifrons* compared costs and benefits of
143 legitimate visitation versus secondary robbing.

144 We focused on three herbaceous, perennial plant species that are visited legitimately and
145 nectar robbed by bumble bees (Maloof 2000, Newman and Thomson 2005; pers. obs.). *Corydalis*
146 *caseana* (Fumariaceae) has closed flower openings that bees push open with the head or body to
147 access nectar and pollen legitimately (Maloof 2000). These flowers produce 35% (g sugar/g
148 nectar, hereafter w/w) nectar sugar concentration at an average 2 μ l/day (Maloof 2000), which
149 collects in a spur beyond the nectary. In the study area, *C. caseana* typically flowers between
150 mid-June and early August (Maloof 2000). About 66% of *C. caseana* flowers were primary-
151 robbed in censuses conducted during July 2015 (unpublished data). *Mertensia ciliata*
152 (Boraginaceae) has a tubular flower that may limit how much nectar shorter-tongued bees are
153 able to obtain legitimately (Suzuki 1994). These flowers produce 37% (w/w) nectar sugar
154 concentration (unpublished data) at a rate of 1.4 μ L/day (Morris 1996), and on average 55% are
155 robbed (unpublished data, July-Aug 2014). Both *C. caseana* and *M. ciliata* are self compatible
156 but show increased seed set with insect visitation (Geber 1985, Maloof 2000). In the study area,
157 *M. ciliata* typically flowers from late June through late July. *Linaria vulgaris* (Plantaginaceae) is
158 non-native but has been in the study ecosystem for almost a century, flowering between July and
159 early September. Its flowers produce 37% (w/w) nectar sugar concentration (Arnold 1982) at a
160 rate of 1.4 μ L/day (unpublished data), which collects in a spur below the nectary. On average,
161 about 79% of flowers are robbed (Irwin and Maloof 2002). *Linaria vulgaris* is self-incompatible
162 but can spread clonally (Arnold 1982).

163 We used five study sites in which the focal plant and bee species were present and that
164 were separated from one another by at least 5 km (Appendix S2: Table S1). At all sites, we
165 verified that robbing holes were present on the focal plant species to ensure that bees had the
166 opportunity to learn to rob flowers before they were used in the experiment. We studied four
167 common species pairs: *B. mixtus* visiting *C. caseana* and *M. ciliata*, *B. flavifrons* visiting *M.*
168 *ciliata*, and *B. bifarius* visiting *L. vulgaris* (Appendix S2: Table S1). For each bee-plant pair, we
169 conducted 10 trials per food handling tactic.

170

171 *Foraging efficiency*

172 To quantify the costs, benefits and efficiencies of alternative food handling tactics
173 (legitimate visitation, primary robbing and secondary robbing) we collected bees and flowers
174 from field sites and measured their foraging behavior under standardized conditions in a 2.4 x
175 3.1 x 2.1 m outdoor flight cage (WeatherPort Shelter Systems, Delta, CO) at the RMBL.

176 *Bee and flower collection and preparation.* Each morning, we cut stalks of the focal plant
177 species. Stalks had been bagged in the field for at least 24 h to minimize presence of cues
178 indicating recent bee visitation, such as hydrocarbon “footprints” (Stout et al. 1998). To keep
179 flowers fresh throughout the day, we immediately placed cut stalks in floral water picks and
180 stored them in cool conditions. At the same site, we caught bees that were visiting the focal plant
181 species, and noted whether each individual was visiting legitimately or robbing. All bees were
182 stored in a refrigerator prior to experimentation to minimize stress and to ensure that bees were
183 sufficiently motivated to feed during experiments.

184 Each trial used three stalks of the same plant species, trimmed to bear five unrobbed,
185 open flowers. We selected flowers of similar color for trials with *M. ciliata*, whose flowers

186 change from pink to dark blue with age (Morris 1996). After trimming stalks, we removed all
187 floral nectar with filter paper (Whitman 3MM chromatography paper) and refilled each flower
188 with a standardized reward of 3 μ L of 35% (w/w) sucrose solution using a 10 μ L Hamilton
189 syringe. 35% sugar concentration is within the range produced by each species (Arnold 1982,
190 Maloof 2000; unpublished data). To ensure that a bee visited flowers using a single tactic, we
191 manipulated the flowers as follows. In legitimate visitation trials, we placed small pieces of clear
192 plastic drinking straws over the nectar spur or corolla of each flower. This technique successfully
193 prevents robbing (Irwin and Brody 1999, Richman et al. 2017b). For both robbing treatments, we
194 tacked shut the flower openings with a glue stick (Elmer's Disappearing Purple Glue Stick). In
195 secondary robbing trials, we used fine forceps to make holes mimicking those observed in the
196 field. These artificial holes adequately simulate natural nectar robbing by bumble bees, and do
197 not damage non-petal plant structures (e.g., Irwin and Brody 1999). We placed these holes where
198 the bees make them: close to the spur tip for *C. caseana* (mean 4.6 mm from the tip), near the
199 calyx of *M. ciliata* (mean 2.5 mm from the proximal end of the calyx), and part way down the
200 spur for *L. vulgaris* (mean 8.4 mm from the tip). Each stalk was only used in a single trial.

201 *Efficiency trials.* We conducted trials with free-flying bees inside the flight cage between
202 0930 and 1800, randomizing the order of both treatments and individual bees. When possible, we
203 matched the tactic bees were using when caught with the treatment. To start each trial, we placed
204 the three flower stalks with the same manipulation treatment in separate pots of soil, equidistant
205 from each other. We placed a bee, recently removed from the refrigerator, on one stalk and
206 allowed her to acclimate to the cage and to visit three flowers to adjust to experimental
207 conditions. We collected data from her fourth visit, which we filmed. We only collected data on
208 the fourth flower and not throughout a foraging bout because bee behaviors can vary across a

209 foraging bout as their honey crops fill and they lose their motivation to collect nectar. This point
210 is especially relevant in our study because we used wild bees collected from the field with
211 various crop loads. Thus, we focused on a single flower relatively early in the bout to ensure
212 similar motivations to forage for nectar. After the bee's fourth visit, we applied a dot of non-
213 toxic paint to her thorax to prevent re-using her and later released her at the original site of
214 capture. We then used 5 μ L microcapillary tubes (Drummond Scientific) to measure the volume
215 of sucrose solution remaining in the flower and thus how much of the 3 μ L of sucrose solution
216 the bee collected during her visit. In addition, we noted two factors that could potentially affect
217 foraging efficiency: whether the bee carried pollen (which she had collected in the field) in her
218 corbiculae during the trial, and a categorical age description of the fourth flower ("younger" or
219 "older", depending on whether petal tissue was beginning to languish). Limited flower
220 availability in the field prevented us from using exclusively younger flowers.

221 *Efficiency data analysis.* From the videos, we measured the total time each bee spent on
222 her fourth flower, and how long she spent with her proboscis in the flower opening or robbing
223 hole extracting sucrose solution. We then calculated gross energetic gain, feeding rate, handling
224 time, access time and foraging efficiency (described in Table 1). We calculated foraging
225 efficiency in two different ways: net energy intake rate (the most common measure of foraging
226 efficiency; Hamilton 2010) and net energy efficiency (a measure possibly maximized by
227 foraging bees; Schmid-Hempel et al. 1985). For *B. mixtus* foraging on *C. caseana*, we subtracted
228 the time a bee spent unsuccessfully biting the flower from handling and access time calculations.
229 Subtracting this time yielded qualitatively similar handling time and efficiency results as not
230 subtracting this time. Thus, we show only the former.

231 A bee's net energetic gain while visiting one flower is her gross gain minus metabolic
232 costs incurred while on the flower. To determine gross energetic gain, we converted the volume
233 of 35% sucrose solution she consumed (μL) to energy (Joules, J) consumed by first converting
234 the solution's concentration to $\mu\text{mol}/\mu\text{L}$ (Kearns and Inouye 1993) and then the volume to Joules
235 ($5.8 \text{ J}/\mu\text{mol}$, Kleiber 1961). We estimated walking mass-specific metabolic rate using the resting
236 metabolic rate of *B. vosnesenskii* workers (the only bumble bee species for which we could find
237 resting metabolic rates: average fresh weight 0.177 g) at temperatures similar to our experimental
238 conditions (Kammer and Heinrich 1974). We then multiplied this value by each species' average
239 fresh mass (*B. bifarius*: 0.1105 g , R. Cartar and S. O'Donnell, pers. comm.; *B. flavifrons*: 0.1514
240 g , R. Cartar, pers. comm.; *B. mixtus*: 0.1239 g , R. Cartar, pers. comm.; bees collected in Alberta,
241 Canada) to estimate species-specific walking metabolic rates and converted metabolic rates from
242 oxygen consumption to J ($20.09 \text{ J}/\text{mL O}_2$, Seeley 1994).

243 We analyzed effects of flower handling tactic on each response variable (Table 1) using
244 linear regression in R (R Core Team 2015), ensuring first that we met regression assumptions.
245 Models included tactic, site, corbicular pollen presence, flower age, and whether the bee walked
246 or flew to the fourth flower. For *B. mixtus* visiting *M. ciliata*, we also included which tactic the
247 bee was performing when caught. We did not include this variable for the other bee-plant
248 combinations because the bees were almost all robbing (*C. caseana*: 100% robbing) or visiting
249 legitimately (*B. bifarius*: 85% visiting legitimately, 10% no information; *B. flavifrons*: 95%
250 visiting legitimately). We ran analyses with bees performing the minority tactic included and
251 excluded and found similar results (results not shown), and so we present analyses of the full
252 dataset with all bees included. Due to a similar lack of variability, we excluded flower age and
253 how the bee arrived at the flower for trials involving *M. ciliata* (all flowers were younger and all

254 bees walked to flowers), and site and flower age from the *L. vulgaris* analyses (only one site and
255 all younger flowers were used). We then used AICc-based model selection (MuMIn package,
256 Barton 2014) to determine the best-fit models (see Appendix S2: Table S2 for AICc values and
257 weights for all models considered). In several cases, there were two best-fit models that agreed
258 qualitatively in their results. For *B. mixtus* analyses, we used post-hoc Tukey tests to evaluate
259 differences among treatments (multcomp package, Hothorn et al. 2015).

260

261 *Field observations*

262 To determine how bees handled flowers under natural conditions and whether flower
263 handling in the field matched predictions based on the foraging efficiencies, we observed bumble
264 bees foraging on *C. caseana*, *M. ciliata* and *L. vulgaris* between late June and mid-Aug 2015.
265 Observations occurred at the sites where we collected bees and flowers for experiments, plus one
266 additional *Mertensia* site (Appendix S2: Table S1). Three to five observers watched free-flying
267 bees for six h/day, five days/wk. An observer followed an individual bumble bee as she visited
268 the focal plant species, until she flew out of sight (referred to as a “bout”). We recorded which
269 tactic the bee used for each flower in the bout. We classified bouts as containing only legitimate
270 visits, only primary robbing, only secondary robbing or a mix of any tactic combination.

271 We assessed whether bees used the different food handling tactics with equal probability
272 using Friedman tests (*B. mixtus* data) and Wilcoxon signed-rank tests (*B. bifarius* and *B.*
273 *flavifrons* data) on the proportion of visits within each bout that were of each tactic. Our analyses
274 included field data only from the bee-plant combinations used in the foraging efficiency trials.
275 For *B. mixtus* data, we conducted pairwise comparisons among tactics with Nemenyi post-hoc
276 tests (Pohlert 2014).

277

278 **Results**279 *Foraging efficiency*

280 Benefits, costs and foraging efficiencies varied by bee-plant combination. We found that
281 foraging efficiency could be higher for nectar robbing, higher for legitimate visitation or equal
282 for each food handling tactic. Robbing tended to be a better handling tactic than legitimate
283 visitation for *B. mixtus* visiting *C. caseana* and *M. ciliata* across most (but not all) response
284 variables, whereas legitimate visitation tended to be a better tactic than secondary robbing for *B.*
285 *flavifrons* visiting *M. ciliata*. Foraging tactics did not differ for *B. bifarius* visiting *L. vulgaris*.

286 *Benefits and costs of alternative handling tactics.* Across the four bee-plant species pairs,
287 gross energetic gain (benefits of handling a flower) was either higher for robbing, or equal
288 between robbing and legitimate visitation (Appendix S2: Table S3). *Bombus mixtus* consumed
289 significantly more sucrose solution when primary or secondary robbing than when foraging
290 legitimately both on *C. caseana* (Fig. 1a) and *M. ciliata* (Fig. 1b). Individuals constrained to visit
291 *C. caseana* legitimately were unable to force the flower open and could not access the sucrose
292 solution in the flower nectar spur. However, for *B. flavifrons* foraging on *M. ciliata* (Fig. 1c) and
293 *B. bifarius* foraging on *L. vulgaris* (Fig. 1d), flower visitation tactic (secondary robbing or
294 visiting legitimately) did not significantly affect how much sucrose solution a bee extracted.

295 Another potential benefit of a given food handling tactic is the ability to more quickly
296 consume nutrients (i.e., to have a higher feeding rate). We identified differential feeding rates
297 across tactics only for *B. mixtus* (Appendix S2: Fig. S2, Table S3). On *C. caseana*, *B. mixtus* fed
298 more rapidly by secondary robbing than visiting legitimately or primary robbing (Appendix S2:

299 Fig. S2a). Conversely, for *B. mixus* on *M. ciliata*, extraction rates were higher for primary
300 robbing than legitimate visitation (Appendix S2: Fig. S2b).

301 Handling and access times indicate the costs of employing a food handling tactic.

302 Handling time, a bee's total time cost for one flower, never varied by tactic for any bee-plant
303 combination (Fig. S3; Appendix S2: Table S3). However, among-tactic patterns in access time
304 (time from an individual's arrival at a flower to feeding commencement) did vary (Appendix S2:
305 Table S3). For *B. mixtus* on *C. caseana*, access time was the same across tactics (Fig. 2a).

306 Further, the time it took a primary robber to bite a hole in the flower was short compared to total
307 handling times: 1.1 ± 0.1 s (mean \pm SE, for *B. mixtus* biting both *C. caseana* and *M. ciliata*
308 flowers). On *M. ciliata*, *B. mixtus* foragers required on average 5.4 s longer to access the sucrose
309 solution when primary robbing (7.2 ± 0.6 s) than when secondary robbing or visiting legitimately
310 (combined mean 1.9 ± 0.1 s) (Fig. 2b). *Bombus flavifrons* foragers showed even greater access-
311 time differences: 13.8 s longer for secondary robbing than when visiting legitimately (Fig. 2c). In
312 contrast, *B. bifarius* foragers visiting *L. vulgaris* required on average 4.2 s less to begin feeding
313 when secondary robbing than when visiting legitimately (Fig. 2d).

314 *Efficiencies of flower handling tactics.* Relative foraging efficiencies combine both the
315 benefits and costs of a given food handling tactic. Estimates of relative foraging efficiencies
316 varied by bee-plant combination (Appendix S2: Table S3). In all cases, net energy intake rate
317 and net foraging efficiency yielded qualitatively similar results. *Bombus mixtus* foragers'
318 inability to collect more than a negligible quantity of sucrose solution when constrained to
319 legitimate visitation resulted in low foraging efficiency on *C. caseana* (Fig. 3a, Appendix S2: Fig
320 S4a). For *B. mixtus* on *M. ciliata*, secondary robbing overall yielded higher foraging efficiency
321 than did visiting legitimately, while primary robbing foraging efficiencies overlapped with both

322 legitimate visitation and secondary robbing (Fig. 3b, Appendix S2: Fig. S4b). In contrast, *B.*
323 *flavifrons* secondary robbing from *M. ciliata* were less efficient than were legitimate visitors
324 (Fig. 3c, Appendix S2: Fig. S4c). Finally, *B. bifarius* showed equal foraging efficiency when
325 legitimately visiting and secondary robbing *L. vulgaris* flowers (Fig. 3d, Appendix S2: Fig. S4d).

326 *Covariates.* The presence of pollen in a bee's corbiculae was associated with less sucrose
327 solution extracted from *M. ciliata* flowers for *B. flavifrons* (0.75 ± 0.05 vs. 0.95 ± 0.01 ; Tables
328 S3, S4), and with lower foraging efficiency for *B. mixtus* visiting *C. caseana* flowers ($0.73 \pm$
329 0.13 vs. 0.96 ± 0.04 J/s; Appendix S2: Tables S3, S4). *Bombus bifarius* collected more sucrose
330 solution when flying to than when walking onto a *L. vulgaris* flower (0.94 ± 0.01 vs. 0.78 ± 0.04 ;
331 Appendix S2: Tables S3, S4). Finally, even after removing time spent unsuccessfully biting *C.*
332 *caseana* flowers by *B. mixtus*, foraging efficiency was lower for bees that selected an older
333 flower (0.60 ± 0.10 vs. 0.98 ± 0.04 ; Appendix S2: Tables S3, S4).

334

335 *Field observations*

336 The flower handling tactics that bees primarily employed in the field matched each
337 tactic's relative efficiency when measured under standardized conditions in three of the four bee-
338 flower combinations (Figs. 4, S5). When constrained in the experiment to visit legitimately, *B.*
339 *mixtus* individuals had very low foraging efficiency on *C. caseana* (Fig. 3a). Consistent with this
340 result, in the field *B. mixtus* visited *C. caseana* flowers legitimately significantly less often (0 of
341 135 bouts) than they robbed (Friedman test: $\chi_2^2 = 153.2$, $p < 0.0001$; Nemenyi post-hoc test: $p <$
342 0.0001 for all pairwise combinations). Similarly, *B. flavifrons*, which showed higher efficiency
343 on *M. ciliata* when visiting it legitimately in the experiment (Fig. 3c), visited it legitimately in
344 nearly all observed bouts (149 of 150 bouts; Wilcoxon signed-rank test: $W = 11249$, $p < 0.0001$).

345 Finally, in the field, *Bombus bifarius* foragers were equally likely to rob (7 bouts) and
346 legitimately visit (5 bouts) *L. vulgaris* flowers (Wilcoxon signed-rank test: $W = 32.5$, $p = 0.60$).
347 *Bombus bifarius* foraging efficiency for each tactic was equal under standardized experimental
348 conditions (Fig. 3d).

349 In contrast to the other bee-plant pairs, the foraging efficiency measured under
350 standardized conditions for *Bombus mixtus* on *M. ciliata* did not reflect what we observed in the
351 field. In the field, *B. mixtus* visited *M. ciliata* legitimately in 56% of bouts (Figs. 4, S5),
352 significantly more often than primary and secondary robbing (Friedman test: $\chi_2^2 = 52.8$, $p <$
353 0.0001 ; Nemenyi post-hoc test: legitimate visitation vs. primary robbing $p < 0.0001$, legitimate
354 visitation vs. secondary robbing $p < 0.0001$, primary vs. secondary robbing $p = 0.96$). They
355 employed secondary robbing in only 23% of bouts (Figs. 4, S5). In contrast, under standardized
356 experimental conditions, foraging efficiency for legitimate visitation was lower than for
357 secondary robbing (Fig. 3b).

358

359 Discussion

360 Mutualistic behaviors are commonly exhibited by species that could easily exploit their
361 partners. This paradoxical observation directly challenges the frequent, yet largely untested,
362 assumption that exploiting a partner yields higher fitness benefits than would cooperating with it.
363 Our results show that, for species that can forage in two ways commonly considered cooperative
364 and exploitative, there is no single answer to whether or not it pays to exploit one's partner.
365 Within a Colorado bumble bee community, net benefits of cooperative (pollinating) behaviors
366 are sometimes higher (*B. flavifrons* visiting *M. ciliata*) or equal (*B. bifarius* visiting *L. vulgaris*)
367 to those conferred by exploitative (nectar-robbing) behaviors. For other species pairs (*B. mixtus*

368 visiting *C. caseana* and *M. ciliata*), exploitation yields higher returns. In addition, in the field the
369 focal bee species visited *M. ciliata* and *L. vulgaris* legitimately much more frequently than the
370 usual assumption – that exploitation is preferred whenever it is possible – would have led us to
371 expect. Our results also demonstrate that food handling decisions can be guided by multiple
372 facets of bee and plant ecology, even with a single food type (here, nectar).

373 The assumption that exploiting pays more than cooperating underlies many studies of the
374 evolution of mutualism. Yet, this idea is not grounded upon a strong base of empirical data on
375 species that can pursue both tactics. Indeed, remarkably few studies of mutualism have studied
376 the choices of organisms that can alternatively cooperate with and exploit their partners; fewer
377 still have attempted to quantify costs and benefits of these alternative behaviors (but see below).
378 Adopting such an approach may help address a persistent puzzle about mutualism: the difficulty
379 of identifying mechanisms that enforce honesty in many exploited mutualisms (Bronstein 2001,
380 Jones et al. 2015, Frederickson 2017). One prevalent explanation is that exploiters inflict more
381 limited fitness costs to their partners than once believed, weakening selection to control their
382 behaviors (Jones et al. 2015). Here we focus on another explanation: exploitation may simply not
383 be as beneficial a strategy as cooperation, in some or all ecological contexts. We tested this idea
384 by adopting logic derived from foraging theory. Treating cooperation and exploitation more
385 neutrally, as simply alternative behaviors of animals faced with choices, we derived insights
386 previously hidden behind the loaded terminology found in much of the cooperation literature
387 (and which, for convenience and consistency, we have used here).

388 There is growing evidence that individuals acting cooperatively can indeed receive higher
389 net benefits than those that exploit their hosts. For example, at the same site as this study,
390 Newman and Thomson (2005) showed that *B. flavifrons* may gain a higher net benefit from

391 visiting *L. vulgaris* legitimately than from robbing it (although the small number of robbing
392 individuals prevented statistical testing). Likewise, honey bees (*Apis mellifera*) gained more
393 energy per flower through legitimate visitation than secondary robbing of *Vaccinium ashei* in
394 Georgia, at least on some days (Dedej and Delaplane 2004). Outside of nectar-robbing, a handful
395 of studies have delineated the conditions under which cooperation or exploitation is most
396 beneficial. For example, some animals switch between predation and participating in a
397 mutualism depending on short-term nutritional needs (e.g., ants engaged in a protection
398 mutualisms; Sakata 1994) or forest fragment size (seed-dispersing rodents: Jorge and Howe
399 2009). Continued efforts to quantify costs and benefits from the exploiter's perspective will
400 undoubtedly reveal additional systems and conditions where exploitation results in a smaller net
401 benefit than cooperating.

402 Costs and benefits of different food handling tactics can change in response to multiple
403 properties of both the food and the forager, or with the community setting, thereby altering the
404 tactics foragers employ or the degree to which they mix tactics. First, nectar robbing has
405 historically been viewed as a foraging tactic that allows visitors to overcome morphological
406 mismatch with flowers, thereby making new resources available (cf. Fisher and Hinde 1949).
407 Consistent with this interpretation, *B. mixtus* avoided legitimate visitation to flowers to which
408 their relatively small body size precluded nectar access (*C. caseana*). Temporal or spatial
409 variation in bee or plant morphology, including variation in bee body size, may alter the degree
410 of morphological mismatch and thus relative net benefits of different food handling tactics. For
411 example, while we found that *B. bifarius* were able to completely drain *L. vulgaris* flowers with
412 either handling tactic, earlier work in our study region found that *B. bifarius* that visited *L.*
413 *vulgaris* legitimately could not reach the nectar and mainly robbed it (Newman and Thomson

414 2005). Second, flowers' morphological adaptations that guide pollinators to the floral opening, or
415 simply the relatively large size of the floral opening compared to a robbing hole, may increase
416 efficiency of legitimate relative to exploitative visitation. For example, *B. flavifrons* in our study
417 took less time to find the large opening of *M. ciliata* flowers than to find the relatively small
418 robbing hole. This decreased access time is unlikely to reflect experience with robbing, since all
419 bees appeared to be familiar with robbing (pers. obs.). Third, nectar volume can also influence
420 bees' decisions whether to rob or visit legitimately both within (*B. mixtus* handling *M. ciliata* in
421 this study) and across (Rojas-Nossa et al. 2016) plant species. Nectar volume can be strongly
422 influenced by co-visitor foraging, with robbed flowers often having lower nectar volumes than
423 unrobbed flowers (e.g., Dedej and Delaplane 2004, Newman and Thomson 2005). For bees that
424 can secondary- but not primary rob, the lower nectar volume often found in robbed flowers may
425 influence the decision to secondary rob an already robbed flower or legitimately visit an
426 unrobbed one.

427 We found one instance in which experimental measures of foraging efficiency did not
428 predict behaviors used in the field: *B. mixtus* feeding from *M. ciliata*. Experimental foraging
429 efficiencies for this bee-plant pair were higher with nectar-robbing than legitimate visits, yet bees
430 in the field visited flowers legitimately 78% of the time. We also observed *B. mixtus* switching
431 between legitimate visitation and nectar robbing within foraging bouts on this species. We offer
432 one possible explanation for this discrepancy. We measured foraging efficiency with equal
433 nectar levels in all flowers. However, natural nectar standing crops are typically lower in robbed
434 than unrobbed flowers in our focal plant species (unpublished data) and in other plant systems
435 (e.g., Dedej and Delaplane 2004, Newman and Thomson 2005). Thus, regardless of their relative
436 handling times while visiting flowers, bees that secondary-rob will tend to obtain less nectar per

437 flower than bees that are legitimately visiting or are primary robbing previously unrobbed
438 flowers. Post-hoc analyses (Appendix S1) estimating foraging efficiencies of bumble bees
439 visiting legitimately and secondary robbing under field conditions show that unequal nectar
440 volumes might explain the mismatch between the measured foraging efficiencies of *B. mixtus*
441 visiting *M. ciliata*. Our calculations support the prediction that legitimate visitation is more
442 efficient than robbing when robbed flowers have less nectar than unrobbed flowers. This pattern
443 also holds for the other bee-plant combinations that we studied. However, unequal nectar
444 volumes may be particularly important for this combination. Under field conditions the estimated
445 foraging efficiency difference between legitimate visitation and secondary robbing was 0.27 J/s
446 for *B. mixtus* visiting *M. ciliata*, but only 0.07 J/s for *B. bifarius* visiting *L. vulgaris* flowers.
447 Further, nectar volumes are unlikely to affect food handling tactic decisions for bees that are not
448 able to feed legitimately (e.g., *B. mixtus* visiting *C. caseana*).

449 Two factors are important to note in interpreting our results. First, the study of nectar-
450 robbing bees has largely ignored pollen foraging by these insects (but see Scott et al. 2016), yet
451 both resources are important for the nutrition and health of bees and their offspring. In two cases,
452 individuals with pollen in their corbiculae during the experiment had lower energetic gains or
453 foraging efficiencies than did individuals without pollen. Although these differences were fairly
454 small, they suggest that pollen foraging may affect a nectar robbing bee's behavior. Given that
455 bumble bees exhibit mild task-specialization for collecting nectar or pollen (Russell et al. 2017),
456 if bees with corbicular pollen were specializing on pollen collection when we caught them, it
457 would be reasonable to predict that they would show lower nectar-collecting efficiency in our
458 experiment. Indeed, we found that *B. mixtus* collected nectar from *C. caseana* more efficiently
459 when they lacked corbicular pollen (Appendix S2: Tables S3, S4). Other results, however, ran

460 counter to this prediction: *B. bifarius* visiting *M. ciliata* collected more nectar when they had
461 pollen in their corbiculae. Second, flower age affected the efficiency of *B. mixtus* foraging on *C.*
462 *caseana*. Bees were less efficient when robbing older than younger flowers, presumably because
463 the former were more difficult to bite through, insert a proboscis into or extract nectar from.
464 Given that *B. mixtus* are unable to legitimately extract nectar from *C. caseana*, this likely has
465 little effect on our interpretation of relative foraging efficiencies for this bee-plant species pair.
466 However, this phenomenon could potentially alter foraging behavior of other bee species that can
467 legitimately visit *C. caseana*, inducing them to switch to legitimate visitation or to other plant
468 species as the *C. caseana* flower population begins to senesce.

469 Finally, this study focused specifically on the perspective of the floral visitor, i.e., the
470 species that could alternatively choose to cooperate with or exploit its partner. As we have
471 argued here, this approach provides information on the relative costs and benefits of different
472 food handling tactics, and offers insight into the choices foragers make. However, fully
473 understanding the effects and persistence of facultative exploitation will require integrating
474 perspectives of both the actor and the recipient. This integration is ripe for future research.

475

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597

598 **Table 1:** Definitions of the costs, benefits and efficiencies measured in this study, and relative
 599 values among food handling tactics for each bee-flower combination.

600

Measure of foraging behavior	Definition	How measured/calculated
Gross energetic gain	Benefits of handling a flower using a given tactic	Proportion ¹ of the 3 μ L sucrose solution ingested during one flower visit
Feeding rate	Potential benefit, through more rapid nutrient consumption	(Amount sucrose solution collected) \div (nectar extraction rate = time proboscis in flower opening or robbing hole)
Handling time	Total time cost, for one flower, of processing a food item	Total time on flower (looking for nectar, biting a hole, collecting sucrose solution, grooming, walking down the flower after feeding)
Access time	Time cost, for one flower, from when a bee has arrived at a flower but before beginning to feed	Time from when bee lands on flower to when proboscis enters corolla or robbing hole
Foraging efficiency	The degree to which a food handling tactic maximizes benefits and minimizes costs	Net energy intake rate = (net energy gain from food item in Joules) \div (handling time); Net energy efficiency = (net energy gain) \div (net energy costs, including metabolic costs, of handling food) ³

601 **Figure Legends**

602

603 **Figure 1:** Gross energetic gain of each food handling tactic for (a) *Bombus mixtus* visiting
604 *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting
605 *M. ciliata*, and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes span the 25th to 75th
606 percentiles, with a line at the median. Letters above boxes indicate statistically different feeding
607 efficiencies. Benefits of nectar robbing (“1° rob” and “2° rob”) were significantly higher than
608 those of legitimate visitation (“Legit”) for *B. mixtus* visiting both *C. caseana* and *M. ciliata* (a,b),
609 but significantly lower for *B. flavifrons* visiting *M. ciliata* (c) and equal for *B. bifarius* visiting *L.*
610 *vulgaris* (d) (GLMs, see Appendix 2: Table S3 for test results).

611

612 **Figure 2:** Access time (cost, measured in seconds) for each food handling tactic for (a) *Bombus*
613 *mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus*
614 *flavifrons* visiting *Mertensia ciliata* and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes and
615 letters as in Figure 1. Robbing incurred a significantly higher cost than legitimate visitation for
616 *B. mixtus* (primary robbing only) and *B. flavifrons* visiting *M. ciliata* (b,c) (LMs, see Appendix
617 2: Table S3 for test results).

618

619 **Figure 3:** Net energy intake rate (foraging efficiency – net benefit – measured in Joules/s) of
620 each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus*
621 visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *M. ciliata* and (d) *Bombus bifarius*
622 visiting *Linaria vulgaris*. Boxes and letters as in Figure 1. Nectar robbing yielded significantly
623 higher foraging efficiency than visiting legitimately for *B. mixtus* visiting *C. caseana* and *M.*

624 *ciliata* (a,b), but significantly lower efficiency for *B. flavifrons* visiting *M. ciliata* (c) and equal
625 efficiency for *B. bifarius* visiting *L. vulgaris* (d) (LMs, see Appendix 2: Table S3 for test results).

626

627 **Figure 4:** Proportion of single-tactic flower visitation bouts observed in meadows where the bee
628 used a given tactic. Observers watched free-flying bees and recorded 103 pure-tactic bouts by *B.*
629 *mixtus* on *C. caseana*, 63 by *B. mixtus* on *M. ciliata*, 149 by *B. flavifrons* on *M. ciliata* and 13 by
630 *B. bifarius* on *L. vulgaris*. *Bombus flavifrons* and *B. bifarius* are incapable of primary robbing, so
631 this tactic was not recorded for these two species.

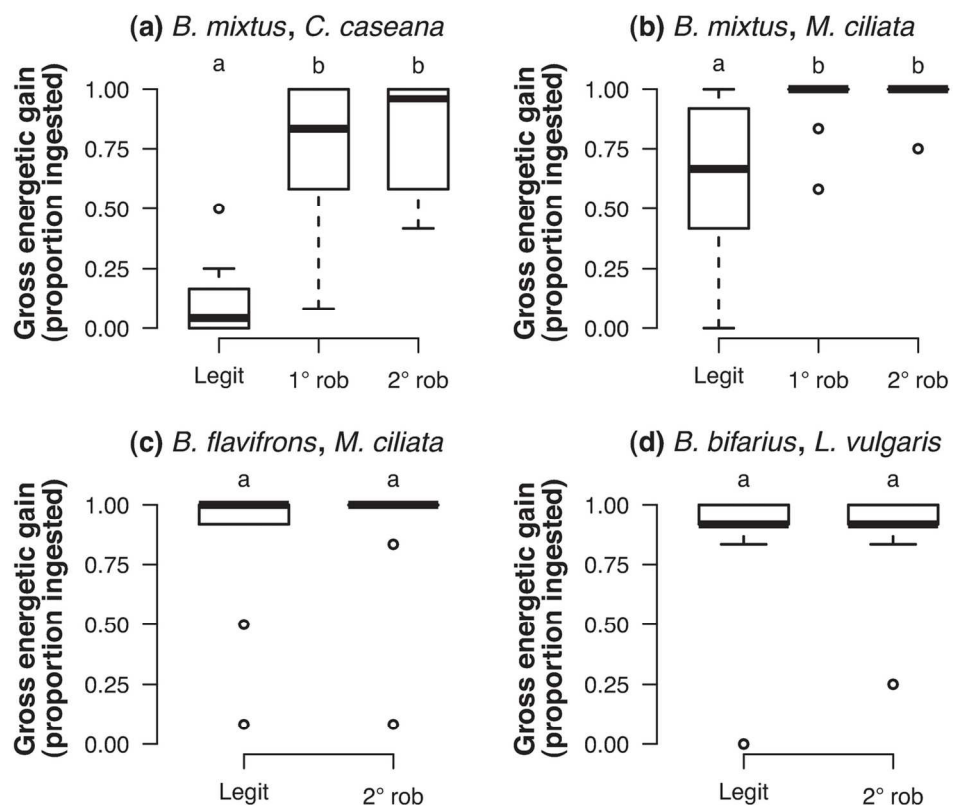


Figure 1: Gross energetic gain of each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *M. ciliata*, and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes span the 25th to 75th percentiles, with a line at the median. Letters above boxes indicate statistically different feeding efficiencies. Benefits of nectar robbing ("1° rob" and "2° rob") were significantly higher than those of legitimate visitation ("Legit") for *B. mixtus* visiting both *C. caseana* and *M. ciliata* (a,b), but significantly lower for *B. flavifrons* visiting *M. ciliata* (c) and equal for *B. bifarius* visiting *L. vulgaris* (d) (GLMs, see Appendix 2: Table S3 for test results).

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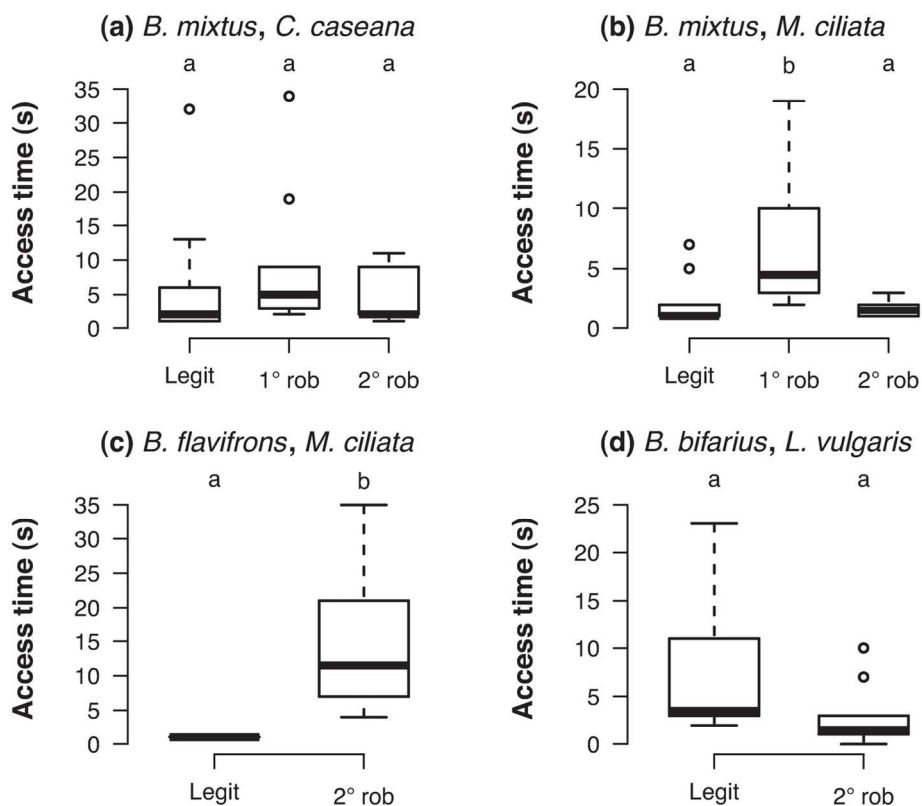


Figure 2: Access time (cost, measured in seconds) for each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *Mertensia ciliata* and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes and letters as in Figure 1. Robbing incurred a significantly higher cost than legitimate visitation for *B. mixtus* (primary robbing only) and *B. flavifrons* visiting *M. ciliata* (b,c) (LMs, see Appendix 2: Table S3 for test results).

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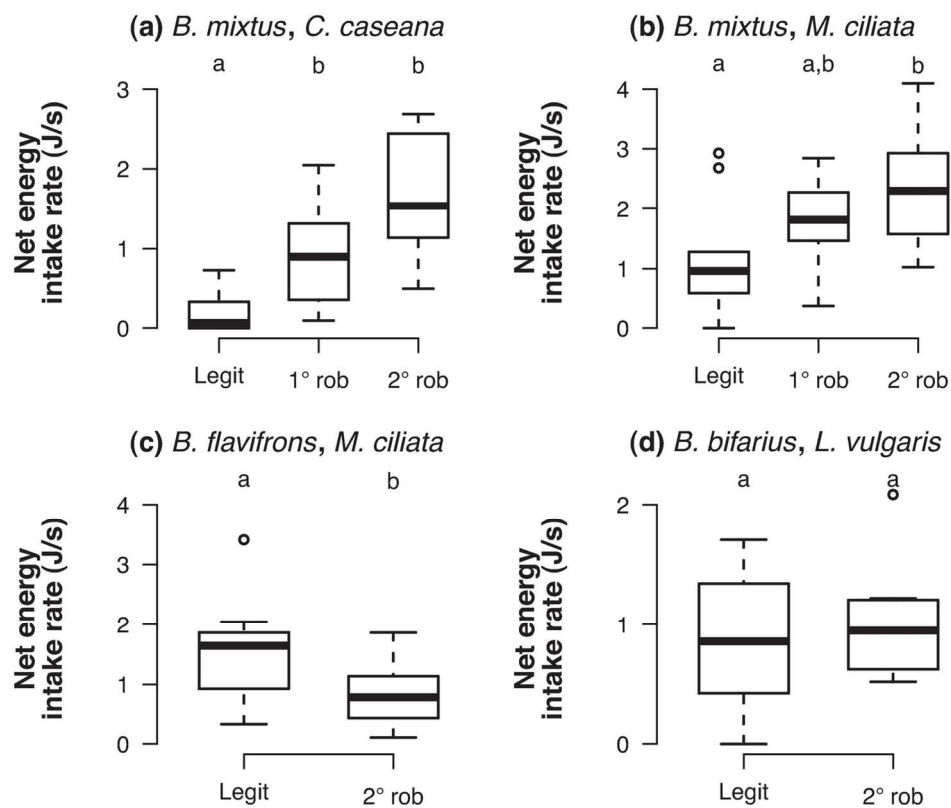


Figure 3: Net energy intake rate (foraging efficiency - net benefit - measured in Joules/s) of each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *M. ciliata* and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes and letters as in Figure 1. Nectar robbing yielded significantly higher foraging efficiency than visiting legitimately for *B. mixtus* visiting *C. caseana* and *M. ciliata* (a,b), but significantly lower efficiency for *B. flavifrons* visiting *M. ciliata* (c) and equal efficiency for *B. bifarius* visiting *L. vulgaris* (d) (LMs, see Appendix 2: Table S3 for test results).

127x105mm (300 x 300 DPI)

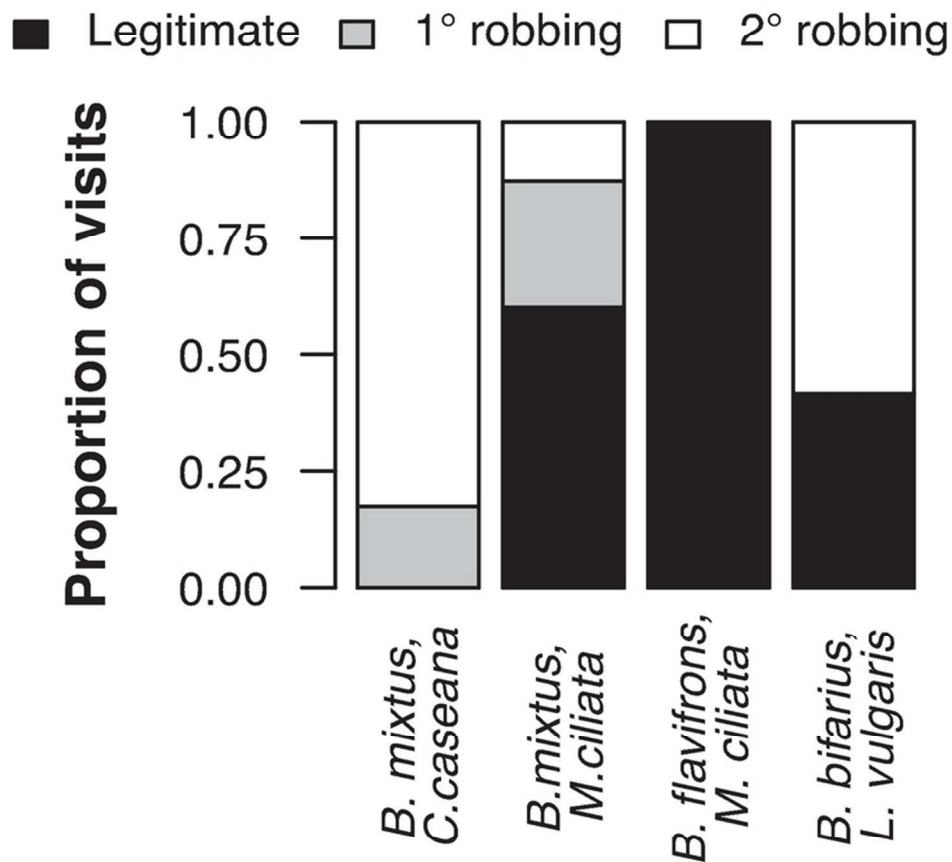


Figure 4: Proportion of single-tactic flower visitation bouts observed in meadows where the bee used a given tactic. Observers watched free-flying bees and recorded 103 pure-tactic bouts by *B. mixtus* on *C. caseana*, 63 by *B. mixtus* on *M. ciliata*, 149 by *B. flavifrons* on *M. ciliata* and 13 by *B. bifarius* on *L. vulgaris*. *Bombus flavifrons* and *B. bifarius* are incapable of primary robbing, so this tactic was not recorded for these two species.

76x76mm (300 x 300 DPI)