

Costs and benefits of alternative food handling tactics help explain facultative exploitation of pollination mutualisms

ELINOR M. LICHTENBERG ^{1,4,5} REBECCA E. IRWIN,^{2,3} AND JUDITH L. BRONSTEIN¹

¹Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

²Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695 USA

³Rocky Mountain Biological Lab, Crested Butte, Colorado 81224 USA

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

Key words: *Bombus*; cheating; exploitation; food handling tactics; foraging; mutualism; nectar robbing; pollination.

INTRODUCTION

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

Associated with the study of exploitation has been a set of assumptions regarding its benefits to the performer and its cost to the recipient. In particular, a large body of theoretical research starts from the assumption that exploitation yields higher fitness than cooperating, because exploiters should not suffer the costs of providing resources or services to a

mutualistic partner (Jones et al. 2015, Sachs 2015, Frederickson 2017). As a consequence, mutualists are commonly predicted to exploit whenever exploitation is not effectively controlled (e.g., Pillai et al. 2014, Sachs 2015). This logical argument fails, however, to explain the ubiquity in nature of facultative exploitation, in which a single individual can perform both cooperative and exploitative behaviors. For example, yucca moth individuals sometimes skip the behaviors used to pollinate yucca flowers (Tyre and Addicott 1993), and ants sometimes eat the aphids they usually protect (Sakata 1994). In systems in which mutualistic partners punish exploiters, facultative exploitation may result when punishment threat by the partner is low (e.g., Pinto et al. 2011). Facultative exploitation can also be common in systems with no apparent sanctions against exploiters, however, including ones in which the costs of being exploited are low or absent (Bronstein 2001, Jones et al. 2015, Barker and Bronstein 2016).

Given the rarity or incomplete effectiveness of punishment and sanctions, why don't mutualists with behavioral options always choose the exploitative strategy? Addressing this question requires a shift away from the usual perspective on exploitation of mutualism, which centers on the impact of exploitation on recipients (e.g., Furukawa and Kawakita 2017, Richman et al. 2017a) and possible responses to it

Manuscript received 15 November 2017; revised 24 March 2018; accepted 11 April 2018; final version received 7 May 2018. Corresponding Editor: Randall J. Mitchell.

⁴ Present address: Department of Integrative Biology, The University of Texas at Austin, Austin, Texas 78712 USA.

⁵ E-mail: elichten@utexas.edu

(Sachs 2015). Instead, we adopt here the much more rarely considered perspective: that of the individual weighing the choice of whether to exploit or cooperate with its partner.

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

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

To explore whether foraging theory can predict food handling tactics, and hence the choice of whether to cooperate with or to exploit a partner, we experimentally quantified the handling costs and benefits that several bumble bee species incur using their alternative foraging tactics. Whether

an individual visits a flower legitimately or robs should depend on the costs required to access nectar with each tactic and how much nectar she is able to extract. We used these costs and benefits to determine the foraging efficiencies of each tactic for four pairs of bumble bee and plant species combinations. Second, we used field observations of free-flying bees to ask whether these efficiencies match how frequently bumble bees exhibit each food handling tactic in nature. We predicted that the most efficient flower handling tactic under a given set of ecological conditions (e.g., bee-plant combination, benefit offered by a particular flower) would be the predominant tactic employed in the field. Our results challenge the commonly held assumption that behaviors termed “exploitative” yield higher benefits than those viewed as “cooperative”.

MATERIALS AND METHODS

Data and R scripts are available at <https://doi.org/10.5281/zenodo.1243208>.

Study area and organisms

This research was conducted during June–Aug 2015 in Gunnison County, CO, USA near the Rocky Mountain Biological Laboratory (RMBL; 2,886 m elevation). This region is characterized by open meadows dominated by perennial flowering plant species that provide food for pollinators, primarily bees. We studied flower handling behavior of three common, native bumble bee species that are distinguishable based on pile markings: *Bombus bifarius*, *B. flavifrons* and *B. mixtus* (Apidae) (Pyke 1982, Williams et al. 2014). The three species can each obtain nectar from some flowers legitimately (Morris 1996, Newman and Thomson 2005). *Bombus mixtus* can act as a primary nectar robber (Morris 1996) by using its toothed mandibles (Appendix S2: Fig. S1) to make holes in floral nectar spurs or at the base of tubular flowers to remove nectar. All three species can also act as secondary robbers (e.g., Newman and Thomson 2005, Richman et al. 2017a). Consistent with the behaviors each species can perform, experiments with *B. mixtus* compared costs and benefits of legitimate visitation, primary robbing and secondary robbing while experiments with *B. bifarius* and *B. flavifrons* compared costs and benefits of legitimate visitation vs. secondary robbing.

We focused on three herbaceous, perennial plant species that are visited legitimately and nectar robbed by bumble bees (Maloof 2000, Newman and Thomson 2005, *personal observation*). *Corydalis caseana* (Fumariaceae) has closed flower openings that bees push open with the head or body to access nectar and pollen legitimately (Maloof 2000). These flowers produce 35% (g sugar/g nectar, hereafter w/w) nectar sugar concentration at an average 2 μ L/day (Maloof 2000), which collects in a spur beyond the nectary. In the study area, *C. caseana* typically flowers between mid-June and early August (Maloof 2000). About 66% of *C. caseana* flowers were primary-robbed in censuses conducted during July 2015 (*unpublished data*). *Mertensia ciliata* (Boraginaceae) has a tubular flower that may limit how much nectar shorter-tongued bees are able to obtain legitimately (Suzuki 1994). These flowers produce 37% (w/w) nectar sugar

concentration (*unpublished data*) at a rate of 1.4 $\mu\text{L}/\text{day}$ (Morris 1996), and on average 55% are robbed (*unpublished data*, July–Aug 2014). Both *C. caseana* and *M. ciliata* are self compatible but show increased seed set with insect visitation (Geber 1985, Maloof 2000). In the study area, *M. ciliata* typically flowers from late June through late July. *Linaria vulgaris* (Plantaginaceae) is non-native but has been in the study ecosystem for almost a century, flowering between July and early September. Its flowers produce 37% (w/w) nectar sugar concentration (Arnold 1982) at a rate of 1.4 $\mu\text{L}/\text{day}$ (*unpublished data*), which collects in a spur below the nectary. On average, about 79% of flowers are robbed (Irwin and Maloof 2002). *Linaria vulgaris* is self-incompatible but can spread clonally (Arnold 1982).

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

Foraging efficiency

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

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

Each trial used three stalks of the same plant species, trimmed to bear five unrobbed, open flowers. We selected flowers of similar color for trials with *M. ciliata*, whose flowers change from pink to dark blue with age (Morris 1996). After trimming stalks, we removed all floral nectar with filter paper (Whitman 3MM chromatography paper) and refilled each flower with a standardized reward of 3 μL of 35% (w/w) sucrose solution using a 10 μL Hamilton syringe. 35% sugar concentration is within the range produced by each species (Arnold 1982, Maloof 2000, *unpublished data*). To ensure that a bee visited flowers using a single tactic, we manipulated the flowers as follows. In legitimate visitation trials, we placed small pieces of clear plastic drinking

straws over the nectar spur or corolla of each flower. This technique successfully prevents robbing (Irwin and Brody 1999, Richman et al. 2017b). For both robbing treatments, we tacked shut the flower openings with a glue stick (Elmer’s Disappearing Purple Glue Stick). In secondary robbing trials, we used fine forceps to make holes mimicking those observed in the field. These artificial holes adequately simulate natural nectar robbing by bumble bees, and do not damage non-petal plant structures (e.g., Irwin and Brody 1999). We placed these holes where the bees make them: close to the spur tip for *C. caseana* (mean 4.6 mm from the tip), near the calyx of *M. ciliata* (mean 2.5 mm from the proximal end of the calyx), and part way down the spur for *L. vulgaris* (mean 8.4 mm from the tip). Each stalk was only used in a single trial.

Efficiency trials.—We conducted trials with free-flying bees inside the flight cage between 09:30 and 18:00, randomizing the order of both treatments and individual bees. When possible, we matched the tactic bees were using when caught with the treatment. To start each trial, we placed the three flower stalks with the same manipulation treatment in separate pots of soil, equidistant from each other. We placed a bee, recently removed from the refrigerator, on one stalk and allowed her to acclimate to the cage and to visit three flowers to adjust to experimental conditions. We collected data from her fourth visit, which we filmed. We only collected data on the fourth flower and not throughout a foraging bout because bee behaviors can vary across a foraging bout as their honey crops fill and they lose their motivation to collect nectar. This point is especially relevant in our study because we used wild bees collected from the field with various crop loads. Thus, we focused on a single flower relatively early in the bout to ensure similar motivations to forage for nectar. After the bee’s fourth visit, we applied a dot of non-toxic paint to her thorax to prevent re-using her and later released her at the original site of capture. We then used 5 μL microcapillary tubes (Drummond Scientific) to measure the volume of sucrose solution remaining in the flower and thus how much of the 3 μL of sucrose solution the bee collected during her visit. In addition, we noted two factors that could potentially affect foraging efficiency: whether the bee carried pollen (which she had collected in the field) in her corbiculae during the trial, and a categorical age description of the fourth flower (“younger” or “older”, depending on whether petal tissue was beginning to languish). Limited flower availability in the field prevented us from using exclusively younger flowers.

Efficiency data analysis.—From the videos, we measured the total time each bee spent on her fourth flower, and how long she spent with her proboscis in the flower opening or robbing hole extracting sucrose solution. We then calculated gross energetic gain, feeding rate, handling time, access time and foraging efficiency (described in Table 1). We calculated foraging efficiency in two different ways: net energy intake rate (the most common measure of foraging efficiency; Hamilton 2010) and net energy efficiency (a measure possibly maximized by foraging bees; Schmid-Hempel et al. 1985). For *B. mixtus* foraging on *C. caseana*, we subtracted the time a bee spent unsuccessfully biting the flower from handling and

TABLE 1. Definitions of the costs, benefits and efficiencies measured in this study.

Measure of foraging behavior	Definition	How measured/calculated
Gross energetic gain	Benefits of handling a flower using a given tactic	Proportion of the 3 μL 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)

access time calculations. Subtracting this time yielded qualitatively similar handling time, access time and efficiency results as not subtracting this time. Thus, we show only the former.

A bee's net energetic gain while visiting one flower is her gross gain minus metabolic costs incurred while on the flower. To determine gross energetic gain, we converted the volume of 35% sucrose solution she consumed (μL) to energy (Joules, J) consumed by first converting the solution's concentration to $\mu\text{mol}/\mu\text{L}$ (Kearns and Inouye 1993) and then the volume to Joules (5.8 J/ μmol , Kleiber 1961). We estimated walking mass-specific metabolic rate using the resting metabolic rate of *B. vosnesenskii* workers (the only bumble bee species for which we could find resting metabolic rates: average fresh weight 0.177 g) at temperatures similar to our experimental conditions (Kammer and Heinrich 1974). We then multiplied this value by each species' average fresh mass (*B. bifarius*: 0.1105 g, R. Cartar and S. O'Donnell, *personal communication*; *B. flavifrons*: 0.1514 g, R. Cartar, *personal communication*; *B. mixtus*: 0.1239 g, R. Cartar, *personal communication*; bees collected in Alberta, Canada) to estimate species-specific walking metabolic rates and converted metabolic rates from oxygen consumption to J (20.09 J/mL O_2 , Seeley 1994).

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

2015) to determine the best-fit models (see Appendix S2: Table S2 for AICc values and weights for all models considered). In several cases, there were two best-fit models that agreed qualitatively in their results. For *B. mixtus* analyses, we used post-hoc Tukey tests to evaluate differences among treatments (multcomp package, Hothorn et al. 2017).

Field observations

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

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

RESULTS

Foraging efficiency

Benefits, costs and foraging efficiencies varied by bee-plant combination. We found that foraging efficiency could be higher for nectar robbing, higher for legitimate visitation or equal for each food handling tactic. Robbing tended to be a better handling tactic than legitimate visitation for *B. mixtus* visiting *C. caseana* and *M. ciliata* across most

(but not all) response variables, whereas legitimate visitation tended to be a better tactic than secondary robbing for *B. flavifrons* visiting *M. ciliata*. Foraging tactics did not differ for *B. bifarius* visiting *L. vulgaris*.

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

Another potential benefit of a given food handling tactic is the ability to more quickly consume nutrients (i.e., to have

a higher feeding rate). We identified differential feeding rates across tactics only for *B. mixtus* (Appendix S2: Fig. S2, Table S3). On *C. caseana*, *B. mixtus* fed more rapidly by secondary robbing than visiting legitimately or primary robbing (Appendix S2: Fig. S2a). Conversely, for *B. mixtus* on *M. ciliata*, extraction rates were higher for primary robbing than legitimate visitation (Appendix S2: Fig. S2b).

Handling and access times indicate the costs of employing a food handling tactic. Handling time, a bee's total time cost for one flower, never varied by tactic for any bee-plant combination (Appendix S2: Fig. S3, Table S3). However, among-tactic patterns in access time (time from an individual's arrival at a flower to feeding commencement) did vary (Appendix S2: Table S3). For *B. mixtus* on *C. caseana*, access time was the same across tactics (Fig. 2a). Further, the time it took a primary robber to bite a hole in the flower was short compared to total handling times: 1.1 ± 0.1 s (mean \pm SE, for *B. mixtus* biting both *C. caseana* and *M. ciliata* flowers). On *M. ciliata*, *B. mixtus* foragers required on average 5.4 s longer to access the sucrose solution when primary robbing (7.2 ± 0.6 s) than when secondary robbing or visiting legitimately (combined mean

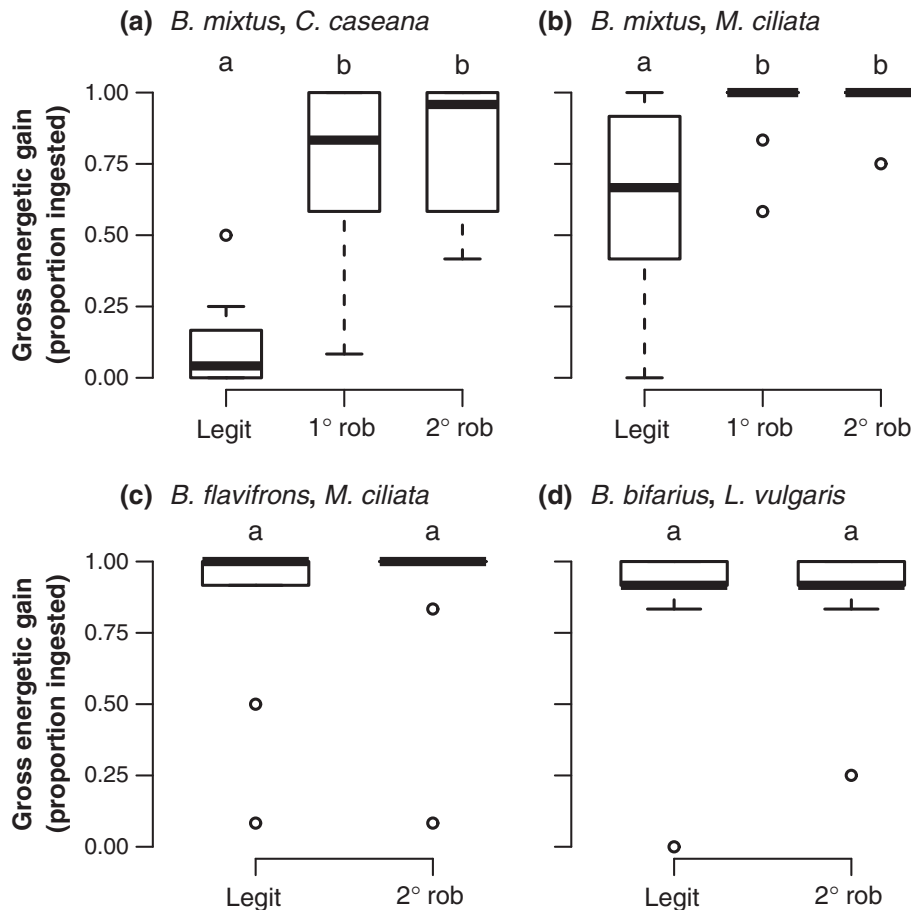


FIG. 1. Gross energetic gain of each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *M. ciliata*, and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes span the 25th to 75th percentiles, 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 S2: Table S3 for test results).

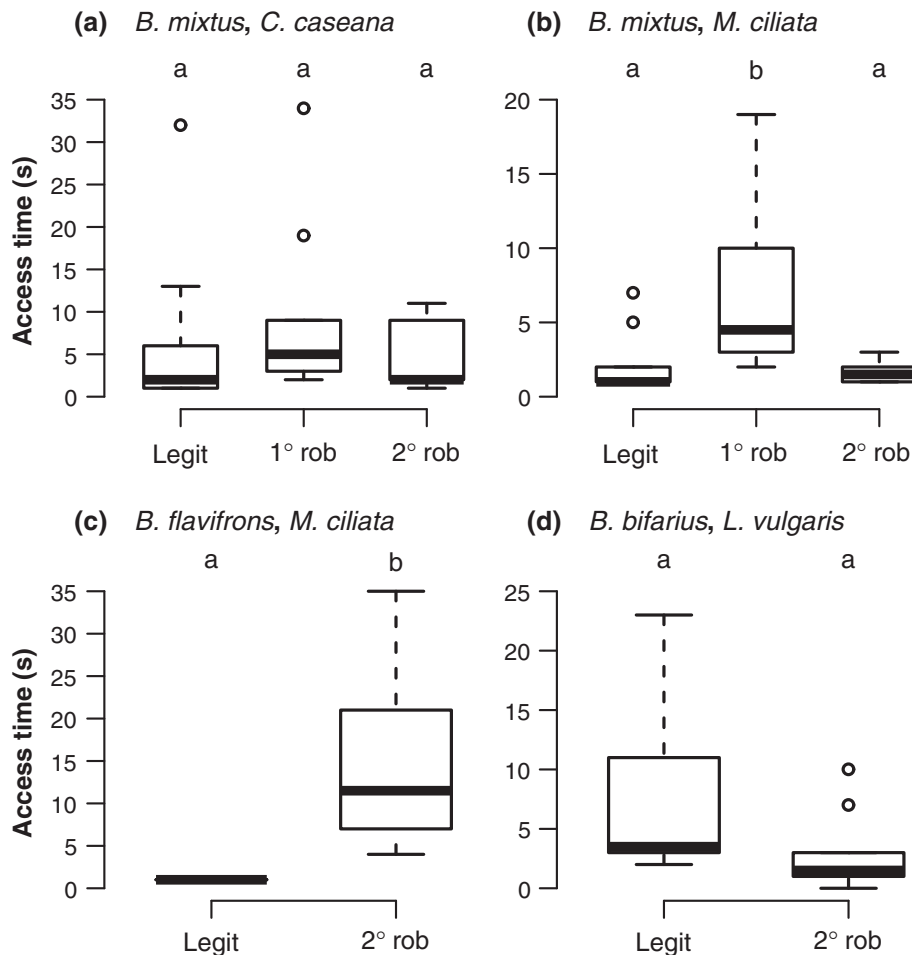


FIG. 2. Access time (cost, measured in seconds) for each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *M. ciliata* and (d) *Bombus bifarius* visiting *Linaria vulgaris*. Boxes and letters 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 S2: Table S3 for test results).

1.9 ± 0.1 s) (Fig. 2b). *Bombus flavifrons* foragers showed even greater access time differences: 13.8 s longer for secondary robbing than when visiting legitimately (Fig. 2c). In contrast, *B. bifarius* foragers visiting *L. vulgaris* required on average 4.2 s less to begin feeding when secondary robbing than when visiting legitimately (Fig. 2d).

Efficiencies of flower handling tactics.—Relative foraging efficiencies combine both the benefits and costs of a given food handling tactic. Estimates of relative foraging efficiencies varied by bee-plant combination (Appendix S2: Table S3). In all cases, net energy intake rate and net foraging efficiency yielded qualitatively similar results. *Bombus mixtus* foragers' inability to collect more than a negligible quantity of sucrose solution when constrained to legitimate visitation resulted in low foraging efficiency on *C. caseana* (Fig. 3a, Appendix S2: Fig. S4a). For *B. mixtus* on *M. ciliata*, secondary robbing overall yielded higher foraging efficiency than did visiting legitimately, while primary robbing foraging efficiencies overlapped with both legitimate visitation and secondary robbing (Fig. 3b, Appendix S2: Fig. S4b). In contrast, *B. flavifrons* secondary robbing from *M. ciliata* were less efficient than were legitimate visitors (Fig. 3c,

Appendix S2: Fig. S4c). Finally, *B. bifarius* showed equal foraging efficiency when legitimately visiting and secondary robbing *L. vulgaris* flowers (Fig. 3d, Appendix S2: Fig. S4d).

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

Field observations

The flower handling tactics that bees primarily employed in the field matched each tactic's relative efficiency when measured under standardized conditions in three of the four

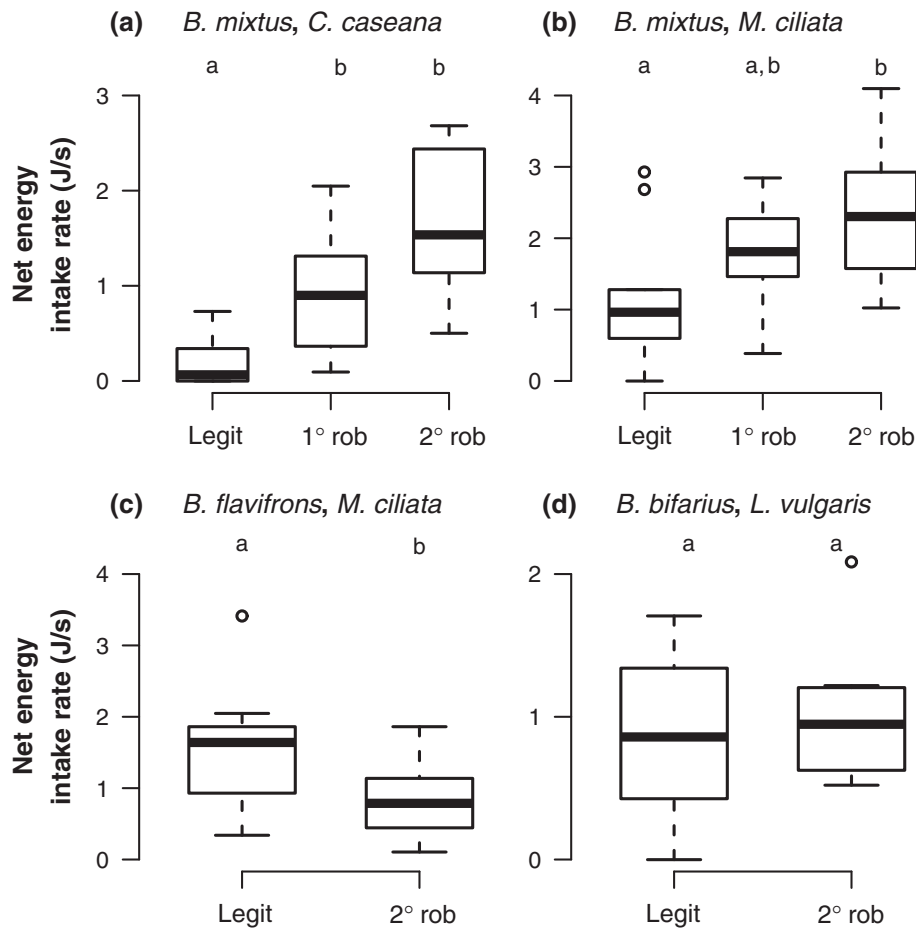


FIG. 3. Net energy intake rate (foraging efficiency – net benefit – measured in Joules/s) of each food handling tactic for (a) *Bombus mixtus* visiting *Corydalis caseana*, (b) *Bombus mixtus* visiting *Mertensia ciliata*, (c) *Bombus flavifrons* visiting *M. ciliata* and (d) *Bombus bifarius* visiting *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 S2: Table S3 for test results).

bee-flower combinations (Fig. 4, Appendix S2: Fig. S5). When constrained in the experiment to visit legitimately, *B. mixtus* individuals had very low foraging efficiency on *C. caseana* (Fig. 3a). Consistent with this result, in the field *B. mixtus* visited *C. caseana* flowers legitimately significantly less often (0 of 135 bouts) than they robbed (Friedman test: $\chi^2_2 = 153.2$, $P < 0.0001$; Nemenyi post-hoc test: $P < 0.0001$ for all pairwise combinations). Similarly, *B. flavifrons*, which showed higher efficiency on *M. ciliata* when visiting it legitimately in the experiment (Fig. 3c), visited it legitimately in nearly all observed bouts (149 of 150 bouts; Wilcoxon signed-rank test: $W = 11249$, $P < 0.0001$). Finally, in the field, *Bombus bifarius* foragers were equally likely to rob (seven bouts) and legitimately visit (five bouts) *L. vulgaris* flowers (Wilcoxon signed-rank test: $W = 32.5$, $P = 0.60$). *Bombus bifarius* foraging efficiency for each tactic was equal under standardized experimental conditions (Fig. 3d).

In contrast to the other bee-plant pairs, the foraging efficiency measured under standardized conditions for *B. mixtus* on *M. ciliata* did not reflect what we observed in the field. In the field, *B. mixtus* visited *M. ciliata* legitimately in 56% of bouts (Fig. 4, Appendix S2: Fig. S5), significantly

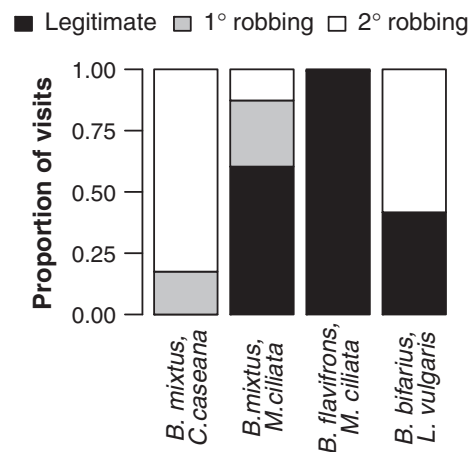


FIG. 4. Proportion of single-tactic flower visitation bouts observed in meadows where the bee used a given tactic. Observers watched free-flying bees and recorded 103 pure-tactic bouts by *B. mixtus* on *C. caseana*, 63 by *B. mixtus* on *M. ciliata*, 149 by *B. flavifrons* on *M. ciliata* and 13 by *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.

more often than primary and secondary robbing (Friedman test: $\chi^2_2 = 52.8$, $P < 0.0001$; Nemenyi post-hoc test: legitimate visitation vs. primary robbing $P < 0.0001$, legitimate visitation vs. secondary robbing $P < 0.0001$, primary vs. secondary robbing $P = 0.96$). They employed secondary robbing in only 23% of bouts (Fig. 4, Appendix S2: Fig. S5). In contrast, under standardized experimental conditions, foraging efficiency for legitimate visitation was lower than for secondary robbing (Fig. 3b).

DISCUSSION

Mutualistic behaviors are commonly exhibited by species that could easily exploit their partners. This paradoxical observation directly challenges the frequent, yet largely untested, assumption that exploiting a partner yields higher fitness benefits than would cooperating with it. Our results show that, for species that can forage in two ways commonly considered cooperative and exploitative, there is no single answer to whether or not it pays to exploit one's partner. Within a Colorado bumble bee community, net benefits of cooperative (pollinating) behaviors are sometimes higher (*B. flavifrons* visiting *M. ciliata*) or equal (*B. bifarius* visiting *L. vulgaris*) to those conferred by exploitative (nectar-robbing) behaviors. For other species pairs (*B. mixtus* visiting *C. caseana* and *M. ciliata*), exploitation yields higher returns. In addition, in the field the focal bee species visited *M. ciliata* and *L. vulgaris* legitimately much more frequently than the usual assumption – that exploitation is preferred whenever it is possible – would have led us to expect. Our results also demonstrate that food handling decisions can be guided by multiple facets of bee and plant ecology, even with a single food type (here, nectar).

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

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

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

Costs and benefits of different food handling tactics can change in response to multiple properties of both the food and the forager, or with the community setting, thereby altering the tactics foragers employ or the degree to which they mix tactics. First, nectar robbing has historically been viewed as a foraging tactic that allows visitors to overcome morphological mismatch with flowers, thereby making new resources available (cf. Fisher and Hinde 1949). Consistent with this interpretation, *B. mixtus* avoided legitimate visitation to flowers to which their relatively small body size precluded nectar access (*C. caseana*). Temporal or spatial variation in bee or plant morphology, including variation in bee body size, may alter the degree of morphological mismatch and thus relative net benefits of different food handling tactics. For example, while we found that *B. bifarius* were able to completely drain *L. vulgaris* flowers with either handling tactic, earlier work in our study region found that *B. bifarius* that visited *L. vulgaris* legitimately could not reach the nectar and mainly robbed it (Newman and Thomson 2005). Second, flowers' morphological adaptations that guide pollinators to the floral opening, or simply the relatively large size of the floral opening compared to a robbing hole, may increase efficiency of legitimate relative to exploitative visitation. For example, *B. flavifrons* in our study took less time to find the large opening of *M. ciliata* flowers than to find the relatively small robbing hole. This decreased access time is unlikely to reflect experience with robbing, since all bees appeared to be familiar with robbing (*personal observation*). Third, nectar volume can also influence bees' decisions whether to rob or visit legitimately both within (*B. mixtus* handling *M. ciliata* in this study) and across (Rojas-Nossa et al. 2016) plant species. Nectar volume can be strongly influenced by co-visitor foraging, with robbed flowers often having lower nectar volumes than unrobbed flowers (e.g., Dedaj and Delaplane 2004, Newman and Thomson 2005). For bees that can secondary- but not primary rob, the lower nectar volume often found in robbed flowers may influence the decision to secondary rob an already robbed flower or legitimately visit an unrobbed one.

We found one instance in which experimental measures of foraging efficiency did not predict behaviors used in the field: *B. mixtus* feeding from *M. ciliata*. Experimental foraging efficiencies for this bee-plant pair were higher with nectar-robbing than legitimate visits, yet bees in the field visited

flowers legitimately 78% of the time. We also observed *B. mixtus* switching between legitimate visitation and nectar robbing within foraging bouts on this species. We offer one possible explanation for this discrepancy. We measured foraging efficiency with equal nectar levels in all flowers. However, natural nectar standing crops are typically lower in robbed than unrobbed flowers in our focal plant species (*unpublished data*) and in other plant systems (e.g., Dedej and Delaplane 2004, Newman and Thomson 2005). Thus, regardless of their relative handling times while visiting flowers, bees that secondarily-rob will tend to obtain less nectar per flower than bees that are legitimately visiting or are primary robbing previously unrobbed flowers. Post-hoc analyses (Appendix S1) estimating foraging efficiencies of bumble bees visiting legitimately and secondary robbing under field conditions show that unequal nectar volumes might explain the mismatch between the measured foraging efficiencies of *B. mixtus* visiting *M. ciliata*. Our calculations support the prediction that legitimate visitation is more efficient than robbing when robbed flowers have less nectar than unrobbed flowers. This pattern also holds for the other bee-plant combinations that we studied. However, unequal nectar volumes may be particularly important for this combination. Under field conditions the estimated foraging efficiency difference between legitimate visitation and secondary robbing was 0.27 J/s for *B. mixtus* visiting *M. ciliata*, but only 0.07 J/s for *B. bifarius* visiting *L. vulgaris* flowers. Further, nectar volumes are unlikely to affect food handling tactic decisions for bees that are not able to feed legitimately (e.g., *B. mixtus* visiting *C. caseana*).

Two factors are important to note in interpreting our results. First, the study of nectar-robbing bees has largely ignored pollen foraging by these insects (but see Scott et al. 2016), yet both resources are important for the nutrition and health of bees and their offspring. In two cases, individuals with pollen in their corbiculae during the experiment had lower energetic gains or foraging efficiencies than did individuals without pollen. Although these differences were fairly small, they suggest that pollen foraging may affect a nectar robbing bee's behavior. Given that bumble bees exhibit mild task-specialization for collecting nectar or pollen (Russell et al. 2017), if bees with corbicular pollen were specializing on pollen collection when we caught them, it would be reasonable to predict that they would show lower nectar-collecting efficiency in our experiment. Indeed, we found that *B. mixtus* collected nectar from *C. caseana* more efficiently when they lacked corbicular pollen (Appendix S2: Tables S3, S4). Other results, however, ran counter to this prediction: *B. bifarius* visiting *M. ciliata* collected more nectar when they had pollen in their corbiculae. Second, flower age affected the efficiency of *B. mixtus* foraging on *C. caseana*. Bees were less efficient when robbing older than younger flowers, presumably because the former were more difficult to bite through, insert a proboscis into or extract nectar from. Given that *B. mixtus* are unable to legitimately extract nectar from *C. caseana*, this likely has little effect on our interpretation of relative foraging efficiencies for this bee-plant species pair. However, this phenomenon could potentially alter foraging behavior of other bee species that can legitimately visit *C. caseana*, inducing them to switch to legitimate visitation or to other plant species as the *C. caseana* flower population begins to senesce.

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

ACKNOWLEDGMENTS

We thank K. Brennan, E. Graber, R. Jones, C. Phillips for flight cage and field assistance; R. Cartar and S. O'Donnell for sharing bee mass data; and J. Francis, M.E. Frederickson, R. Mitchell and an anonymous reviewer for manuscript feedback. The RMBL and Gunnison National Forest provided access to field sites. This material is based upon work supported by the National Science Foundation under Grant No. DEB-1354061/1641243. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

LITERATURE CITED

- Arnold, R. M. 1982. Pollination, predation and seed set in *Linaria vulgaris* (Scrophulariaceae). *American Midland Naturalist* 107:360–369.
- Barker, J. L., and J. L. Bronstein. 2016. Temporal structure in cooperative interactions: what does the timing of exploitation tell us about its cost? *PLOS Biology* 14:e1002371.
- Barton, K. 2015. MuMIn: Multi-model inference. R package version 1.15.6.
- Bronstein, J. L. 2001. The exploitation of mutualisms. *Ecology Letters* 4:277–287.
- Bronstein, J. L., J. L. Barker, E. M. Lichtenberg, L. L. Richardson, and R. E. Irwin. 2017. Behavioral constancy of floral larceny. *Current Opinion in Insect Science* 21:14–18.
- Dedej, S., and K. S. Delaplane. 2004. Net energetic advantage drives honey bees (*Apis mellifera* L.) to nectar larceny in *Vaccinium ashei* Reade. *Behavioral Ecology and Sociobiology* 57:398–403.
- Fisher, J. B., and R. A. Hinde. 1949. The opening of milk bottles by birds. *British Birds* 42:347–357.
- Frederickson, M. E. 2017. Mutualisms are not on the verge of breakdown. *Trends in Ecology & Evolution* 32:727–734.
- Furukawa, S., and A. Kawakita. 2017. Limiting the cost of mutualism: the defensive role of elongated gynophore in the leafflower-moth mutualism. *Oecologia* 184:835–846.
- Geber, M. A. 1985. The relationship of plant size to self-pollination in *Mertensia ciliata*. *Ecology* 66:762–772.
- Hamilton, I. M. 2010. Foraging theory. Pages 177–193 in D. F. Westneat and C. W. Fox, editors. *Evolutionary behavioral ecology*. Oxford University Press, New York, New York, USA.
- Higashi, S., M. Ohara, H. Arai, and K. Matsuo. 1988. Robber-like pollinators: overwintered queen bumblebees foraging on *Corydalis ambigua*. *Ecological Entomology* 13:411–418.
- Holland, J. N., J. H. Ness, A. Boyle, and J. L. Bronstein. 2005. Mutualisms as consumer-resource interactions. Pages 17–33 in P. Barbosa and I. Castellanos, editors. *Ecology of predator-prey interactions*. Oxford University Press, New York, New York, USA.
- Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheibe. 2017. multcomp: Simultaneous Inference in General Parametric Models. R package version 1.4-7.
- Inouye, D. W. 1980. The terminology of floral larceny. *Ecology* 61:1251–1253.
- Irwin, R. E., and A. K. Brody. 1999. Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* 80:1703–1712.
- Irwin, R. E., and J. E. Maloof. 2002. Variation in nectar robbing over time, space, and species. *Oecologia* 133:525–533.

- Irwin, R. E., J. L. Bronstein, J. S. Manson, and L. Richardson. 2010. Nectar robbing: ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution, and Systematics* 41:271–292.
- Ishii, H. S., and E. Z. Kadoya. 2016. Legitimate visitors and nectar robbers on *Trifolium pratense* showed contrasting flower fidelity versus co-flowering plant species: could motor learning be a major determinant of flower constancy by bumble bees? *Behavioral Ecology and Sociobiology* 70:377–386.
- Jones, E. I., et al. 2015. Cheaters must prosper: reconciling theoretical and empirical perspectives on cheating in mutualism. *Ecology Letters* 18:1270–1284.
- Jorge, M. L. S. P., and H. F. Howe. 2009. Can forest fragmentation disrupt a conditional mutualism? A case from central Amazon. *Oecologia* 161:709–718.
- Kammer, A. E., and B. Heinrich. 1974. Metabolic rates related to muscle activity in bumblebees. *Journal of Experimental Biology* 61:219–227.
- Kearns, C. A., and D. W. Inouye. 1993. *Techniques for pollination biologists*. University Press of Colorado, Niwot, Colorado, USA.
- Kleiber, M. 1961. *The fire of life; an introduction to animal energetics*. Wiley, New York, New York, USA.
- Maloof, J. E. 2000. Reproductive biology of a North American subalpine plant: *Corydalis caseana* A. Gray ssp. *brandegei* (S. Watson) G. B. Ownbey. *Plant Species Biology* 15:281–288.
- Morris, W. F. 1996. Mutualism denied? Nectar-robbing bumble bees do not reduce female or male success of bluebells. *Ecology* 77:1451–1462.
- Newman, D. A., and J. D. Thomson. 2005. Effects of nectar robbing on nectar dynamics and bumblebee foraging strategies in *Linaria vulgaris* (Scrophulariaceae). *Oikos* 110:309–320.
- Pillai, P., T. C. Gouhier, and S. V. Vollmer. 2014. The cryptic role of biodiversity in the emergence of host–microbial mutualisms. *Ecology Letters* 17:1437–1446.
- Pinto, A., J. Oates, A. Grutter, and R. Bshary. 2011. Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology* 21:1140–1144.
- Pohlert, T. 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). R package version 4.2.
- Pyke, G. H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* 63:555–573.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson, L., and J. L. Bronstein. 2012. Reproductive biology of pointleaf manzanita (*Arctostaphylos pungens*) and the pollinator-nectar robber spectrum. *Journal of Pollination Ecology* 9:115–123.
- Richman, S. K., R. E. Irwin, and J. L. Bronstein. 2017a. Foraging strategy predicts foraging economy in a facultative secondary nectar robber. *Oikos* 126:1250–1257.
- Richman, S. K., R. E. Irwin, C. J. Nelson, and J. L. Bronstein. 2017b. Facilitated exploitation of pollination mutualisms: fitness consequences for plants. *Journal of Ecology* 105:188–196.
- Rojas-Nossa, S. V., J. M. Sánchez, and L. Navarro. 2016. Nectar robbing: a common phenomenon mainly determined by accessibility constraints, nectar volume and density of energy rewards. *Oikos* 125:1044–1055.
- Russell, A. L., S. J. Morrison, E. H. Moschonas, and D. R. Papaj. 2017. Patterns of pollen and nectar foraging specialization by bumblebees over multiple timescales using RFID. *Scientific Reports* 7:42448.
- Sachs, J. L. 2015. The exploitation of mutualisms. Pages 93–106 in J. L. Bronstein, editor. *Mutualism*. Oxford University Press, Oxford, UK.
- Sakata, H. 1994. How an ant decides to prey on or to attend aphids. *Researches on Population Ecology* 36:45–51.
- Schmid-Hempel, P., A. Kacelnik, and A. I. Houston. 1985. Honeybees maximize efficiency by not filling their crop. *Behavioral Ecology and Sociobiology* 17:61–66.
- Scott, Z., H. S. Ginsberg, and S. R. Alm. 2016. Native bee diversity and pollen foraging specificity in cultivated highbush blueberry (*Ericaceae: Vaccinium corymbosum*) in Rhode Island. *Environmental Entomology* 45:1432–1438.
- Seeley, T. D. 1994. Honey bee foragers as sensory units of their colonies. *Behavioral Ecology and Sociobiology* 34:51–62.
- Soberon, J., and C. Martinez del Rio. 1985. Cheating and taking advantage in mutualistic associations. Pages 192–216 in D. H. Boucher, editor. *The biology of mutualism*. Oxford University Press, New York, New York, USA.
- Stout, J. C., D. Goulson, and J. A. Allen. 1998. Repellent scent-marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). *Behavioral Ecology and Sociobiology* 43:317–326.
- Suzuki, K. 1994. Pollinator restriction in the narrow-tube flower type of *Mertensia ciliata* (James) G. Don (Boraginaceae). *Plant Species Biology* 9:69–73.
- Tyre, A. J., and J. F. Addicott. 1993. Facultative non-mutualistic behaviour by an “obligate” mutualist: “cheating” by yucca moths. *Oecologia* 94:173–175.
- Williams, P. H., R. W. Thorp, L. L. Richardson, and S. R. Colla. 2014. *Bumble bees of North America: an identification guide*. Princeton University Press, Princeton, New Jersey, USA.
- Ydenberg, R. 2010. Decision theory. Pages 131–147 in D. F. Westneat and C. W. Fox, editors. *Evolutionary behavioral ecology*. Oxford University Press, New York, New York, USA.
- Yu, D. W. 2001. Parasites of mutualisms. *Biological Journal of the Linnean Society* 72:529–546.
- Zhu, X.-F., J.-P. Wan, and Q.-J. Li. 2010. Nectar robbers pollinate flowers with sexual organs hidden within corollas in distylous *Primula secundiflora* (Primulaceae). *Biology Letters* 6:785–787.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2395/supinfo>

DATA AVAILABILITY

Data, R scripts and analysis output files are available at <https://doi.org/10.5281/zenodo.1243208>.