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Bumble bees are constant to nectar-robbing behaviour despite low switching costs

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Individuals sometimes exhibit striking constancy to a single behaviour even when they are capable of short-term behavioural flexibility. Constancy enables animals to avoid costs such as memory constraints, but can also inflict significant opportunity costs through behaviour–environment mismatch. It is unclear when individuals should exhibit behavioural constancy and which types of costs most strongly influence such behaviour. We use a case in which individuals within a population exhibit more than one handling tactic for a single food type to investigate whether costs associated with switching among tactics constrain expression of intra-individual variation. Using wild bumble bees (*Bombus* spp.) that feed on nectar through flower openings (legitimate visits) or through holes at the base of flowers (robbing), we asked three questions. (1) Do individual bees exhibit tactic constancy within and across foraging bouts? (2) Are individuals willing to switch their food-handling tactics? (3) Is constancy in food-handling tactics maintained by costs associated with switching tactics? We measured energetic costs in addition to handling times. We found that bees freely foraging in meadows were highly constant to a single food-handling tactic both within and across bouts. However, experiments with individual captive bees showed that these bees were willing to switch tactics and experienced minimal costs in doing so. Thus, switching costs do not drive the observed constancy in food-handling tactics of bumble bees within and across foraging bouts.
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Selective use of flexible behaviours to match current conditions is a core theme in behavioural ecology (Dall, Houston, & McNamara, 2004; Ghalambor, Angeloni, & Carroll, 2010; Snell-Rood, 2013). However, individuals also can remain constant to a single behaviour or tactic, exhibiting it exclusively or almost exclusively. This can occur even in situations where individuals can perform multiple tactics over a short period and under relatively consistent conditions, i.e. they are capable of 'intra-individual variation'. The proximate causes and functional significance of intra-individual variation and its inverse, constancy, remain virtually ignored despite potentially large adaptive and ecological impacts (Stamps, 2016; Westneat, Wright, & Dingemanse, 2015). Theory and limited empirical evidence predict that constancy enables individuals to avoid both direct costs (e.g. neural investment, memory constraints, physical costs of assessing new resources, predation) and indirect costs (e.g. time spent assessing rather than feeding) associated with closely matching behaviour to local conditions via frequent assessment (Dunlap, Papaj, & Dornhaus, 2017; Stephens, 1987; Ydenberg & Prins, 2012). However, constancy may also impose significant opportunity costs if animals remain constant to a behaviour that is a poor match to local conditions (Dunlap et al., 2017). Given the potential for high costs of either behavioural constancy or variation through environmental assessment, it is unclear which types of costs most strongly influence expression of intra-individual variation. Here we use a common type of foraging behaviour – food-handling tactics – to investigate whether costs associated with switching among tactics constrain expression of intra-individual variation. Flexibility in food handling is well documented (e.g. Bozinovic & Vásquez, 1999; Helfman, 1990), particularly in situations in which an individual or species handles food of different types or sizes with different tactics. However,

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much of this research measures handling errors or handling times, rather than energetic costs. We focus on energetic costs in the intriguing case in which individuals use more than one handling tactic for a single food type.

Costs and benefits of handling different food types often drive individuals of a given species to vary their food-handling tactics (reviewed in Helfman, 1990). For example, handling costs are likely the primary drivers of floral constancy, i.e. visiting a single flower species even though more than one is available (Chittka & Thomson, 1997; Gegear & Laverty, 2005; Goulson, 1999). Individual food items are often heterogeneous, and thus the net benefits of a given food-handling tactic can change over very short timescales – with each food item a forager encounters – and also as environmental conditions change. Foragers exhibiting high food-handling flexibility therefore may face high variability in expected payoffs, requiring them to assess the quality of each food item they encounter. Foraging theory often assumes that collecting information about food in order to track local conditions is key to adaptive foraging behaviour (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; e.g. McNamara & Houston, 1985). However, collecting information about each individual food item (Austin, Horack, & Dunlap, 2019), as well as learning and memory constraints (Raine & Chittka, 2007), may impose significant costs and thus favour constancy to a single food-handling tactic.

Handling one flower species in several ways likely magnifies costs of closely matching food handling to every food item encountered, relative to handling different flower species in several ways, as assessment prior to handling a food item may not be possible. Many nectar foragers can access nectar by biting holes at the base of flowers (primary nectar robbing) or by using existing holes (secondary nectar robbing), in addition to visiting 'legitimately' via the flower opening (Inouye, 1980). Legitimate visits commonly result in pollination (Appendix, Fig. A1, Supplementary Video S1), whereas robbing generally does not (Irwin, Bronstein, Manson, & Richardson, 2010). Nectar robbing, exhibited by a wide variety of insects, birds and mammals, is common on flowers with tubular corollas or nectar spurs (Irwin et al., 2010). Nectar robbing is often facultative, with an individual forager capable of exhibiting both robbing and legitimate visits (Bronstein, Barker, Lichtenberg, Richardson, & Irwin, 2017; Richman, Irwin, & Bronstein, 2017). There is no evidence of innate preferences for either legitimate visits or nectar robbing. Previously naïve bees can learn preferences for legitimate visits or nectar robbing (Barker, Dornhaus, Bronstein, & Muth, 2018). Furthermore, the bee species observed in this and a related study (Lichtenberg, Richman, Irwin, & Bronstein, 2020) varied their preferred tactic across plant species and environmental conditions. Several behavioural and ecological factors likely influence which tactic a forager uses. Secondary robbing can only occur in a community where primary robbers have bitten holes. Foraging energetics also likely influence foragers' decisions. Robbing is often assumed to be faster, or to enable consumption of more of a flower's nectar, than legitimate visits, since the holes through which robbers feed are often closer to the nectary (Irwin et al., 2010). However, robbed flowers may provide lower benefits since they typically contain less nectar than unrobbed ones (e.g. Heiling et al., 2018; Newman & Thomson, 2005). The limited data currently available indicate that, in some cases, robbing is more efficient than legitimate visits, whereas in others, robbing is equally or less efficient (Dedej & Delaplane, 2004; Lichtenberg, Irwin, & Bronstein, 2018; Newman & Thomson, 2005). These relative efficiencies likely vary with nectar standing crop or availability of holes for secondary robbing (Bronstein et al., 2017). Several studies report constancy to nectar robbing by wild bees (Free, 1968; Marzinzig et al., 2018; Mayer et al., 2014; Stout, Allen, & Goulson, 2000), although with low sample sizes or with handling tactic constancy not differentiated from floral constancy.

Here we investigate whether foragers exhibit constancy in food-handling tactic decisions and, if they do, then why. We used an observational study and a manipulative experiment in a subalpine meadow system in which several bumble bee species visit several plant species both legitimately and as nectar robbers. In the observational study, we observed free-flying bees in meadows to ask (1) do individual bumble bees exhibit food-handling tactic constancy within and across foraging bouts? Based on previous reports of food-handling tactic constancy by bees at the individual (Free, 1968; Ishii & Kadoya, 2016; Mayer et al., 2014) and population (Marzinzig et al., 2018; Stout et al., 2000) levels, we expected to observe high tactic constancy. In the experiment, we manipulated individual bees to visit flowers either legitimately or via secondary robbing, then switched the tactic they had to use to access food (Video S1). The experiment measured foraging behaviour under standardized conditions, and addressed two questions. (2) Are individuals willing to switch their food-handling tactics? We expected no constraints to the use of either foraging tactic, given that at least some individual bees are known to readily switch between nectar robbing and legitimate visits (Mayer et al., 2014; R. E. Irwin, personal observation) and that bumble bees can learn to nectar-rob (Barker et al., 2018; Leadbeater & Chittka, 2008). Willingness to switch when the current tactic's net benefit decreases has not previously been quantified, however. (3) Do costs of switching tactics maintain food-handling tactic constancy? For floral constancy, these costs arise at least in part from delays and errors as learned handling procedures are recalled from long-term memory during switching (Gegear & Laverty, 2005; Raine & Chittka, 2007). Handling one flower species in more than one way may be as cognitively complex as handling separate flower species and impose similar costs (Bronstein et al., 2017). We thus predicted that bees induced to switch tactics would show short-term reductions in foraging performance, including (a) increased food handling and access times and (b) decreased foraging efficiencies. Because our previous research showed that the focal bee species collects nectar from the focal plant species more efficiently via secondary robbing than via legitimate visits (Lichtenberg et al., 2018), we also predicted that (c) switching from robbing to legitimate visits would cause larger reductions in foraging performance than would switching from legitimate visits to robbing.

METHODS

Study System

Research was conducted during June–August 2014–2016 in Gunnison County, Colorado, U.S.A. near the Rocky Mountain Biological Laboratory (RMBL; 2886 m elevation). Lichtenberg et al. (2018) describe the system in detail. Briefly, the region is characterized by open meadows dominated by perennial flowering plant species that provide floral food resources for pollinators, especially bees. Native bumble bees are common and frequently rob several plant species.

Observational Study Field Methods (Question 1)

We used field observations to determine whether individual bumble bees exhibit food-handling tactic constancy within and across foraging bouts. We quantified tactic constancy of three bumble bee species: *Bombus bifarius*, *Bombus flavifrons* and *Bombus mixtus*. These species are readily distinguishable in the field based

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on pile markings (Pyke, 1982; Williams, Thorp, Richardson, & Colla, 2014). All three bee species can both visit legitimately and act as secondary nectar robbers (Appendix, Fig. A1) on three focal plant species: *Corydalis caseana* (Fumariaceae), *Linaria vulgaris* (Plantaginaceae) and *Mertensia ciliata* (Boraginaceae) (Lichtenberg et al., 2018; Maloof, 2000; Newman & Thomson, 2005; Richman, Irwin, & Bronstein, 2017). All three plant species have tubular flowers or nectar spurs, and they produce nectar with similar sugar concentrations (35–37% g sugar/g nectar; Arnold, 1982; Irwin, Lichtenberg, Heiling, & Bronstein, n.d.; Maloof, 2000) at similar rates (1.4–2 μl/day; Irwin et al., n.d.; Maloof, 2000; Morris, 1996). *Bombus mixtus* is also capable of primary robbing (Morris, 1996).

To determine how often bees are constant to a single food-handling tactic within and across foraging bouts, we observed the three bumble bee species foraging on *C. caseana*, *M. ciliata* and *L. vulgaris* between late June and mid-August in 2014–2016 at 20 sites (see Appendix, Table A1). Three to five observers watched free-flying bees for 6 h/day, 5 days/week, throughout each plant species' blooming season. An observer followed an individual bumble bee as she visited the focal plant species until she flew out of sight, a visit sequence here referred to as a 'bout'. We recorded which foraging tactic the bee used for each flower in each bout. In 2015 and 2016, the first time we observed each bee, we caught her in a vial and marked her by gluing a unique numbered tag (Betterbee, Greenwich, NY, U.S.A., https://www.betterbee.com) to her thorax. This enabled us to track individual bees across multiple bouts.

Observational study data analysis

We used field records of flower visits to classify each observed bout as containing (1) only legitimate visits, (2) only primary robbing, (3), only secondary robbing or (4) any mix of these three tactics. The first three types of bouts were categorized as constant, and the last as not constant. Because most bouts consisted entirely or almost entirely of one tactic, we could not use constancy indices (Bateman, 1951; Gegear & Thomson, 2004). We determined within-bout constancy using data from all 3 years. Among-bout constancy was assessed only for the years in which we individually marked bees: 2015 and 2016. For both types of constancy, we calculated the percentage of bouts or individuals, respectively, that were constant. In a second analysis we considered constancy of nectar robbing (primary + secondary) by *B. mixtus*. Primary and secondary robbing are more similar to each other than either is to a legitimate visit, and *B. mixtus* shows similar foraging behaviour and efficiency when primary and secondary robbing *M. ciliata* flowers under experimental conditions (Lichtenberg et al., 2018). All analyses were conducted in R v.3.5.0 (R Core Team, 2018).

Although we recorded data for all observed bumble bees, we limited the present analyses to bouts by workers, since workers, queens and males may have different foraging motivations. We also constrained analyses to bouts in which the bee fed from at least five flowers (following Pohl, Wyk, & Campbell, 2011; 55% of *C. caseana* bouts, 57% of *M. ciliata* bouts, 63% of *L. vulgaris* bouts). Furthermore, we constrained analyses to bee–plant species pairs for which we observed at least eight bouts (when quantifying within-bout constancy) or eight individuals (when quantifying among-bout constancy) that met the above criteria. In addition, we constrained among-bout constancy assessment to (1) data from 2015 and 2016, when bees were marked, and (2) bees that we observed for at least five bouts of five or more flowers (16% of *B. mixtus* foragers visiting *C. caseana*, 23% of *B. flavifrons* foragers visiting *M. ciliata*, 19% of *B. mixtus* foragers visiting *M. ciliata*). This yielded 441 bouts for *C. caseana*, 659 bouts for *M. ciliata* and 293 bouts for *L. vulgaris*.

Experimental Methods (Questions 2 and 3)

We conducted an experiment in 2016 to determine whether individuals are willing to switch food-handling tactics (question 2) and whether food-handling tactic constancy is maintained due to costs associated with switching tactics (question 3). The experiment induced wild-caught *B. mixtus* foragers to switch from one feeding tactic to another while visiting *M. ciliata* flowers (Video S1). Each morning, we went to one of three sites (see Appendix, Table A1) and caught bees that were visiting *M. ciliata* flowers. At each of these sites, we verified that robbing holes were present on the focal plant species so that bees likely had learned how to rob flowers before they were used in the experiment. We noted the foraging tactic of each bee when we caught her. All bees were stored in a refrigerator prior to experimentation to minimize stress and to ensure that they were sufficiently motivated to feed (i.e. not satiated) during experiments. At the same location, we cut *M. ciliata* stalks that had been bagged in the field for at least 24 h to minimize the presence of cues on plants that indicate recent bee visits, such as hydrocarbon 'footprints' (Stout, Goulson, & Allen, 1998). To keep flowers fresh throughout the day, we immediately placed cut stalks in floral water picks and stored them in cool conditions.

We conducted trials with free-flying bees at the RMBL inside a 2.4 × 3.1 × 2.1 m outdoor flight cage (WeatherPort Shelter Systems, Delta, CO, U.S.A., https://weatherport.com) between 1030 and 1600 hours, randomizing the order of both treatments and individual bees. Each trial consisted of two phases that differed in the handling tactic the bee was able to adopt. In phase 1, we presented a bee with flowers from which she could only successfully access nectar using one tactic (either legitimate visits or secondary robbing). When possible, we matched the tactic bees were using when caught in the field with the tactic they were able to use in phase 1. To start each trial, we placed three flower stalks that were trimmed to each bear five unrobbed, open flowers in separate pots, equidistant from each other. Immediately prior to the trial, we removed all floral nectar with filter paper (Whatman 3MM chromatography paper) and refilled each flower with a standardized reward of 3 μl of 35% (w/w) (6.83 J) (Kearns & Inouye, 1993; Kleiber, 1961) sucrose solution using a 10 μl Hamilton syringe. We then placed a bee, recently removed from the refrigerator, on one stalk and allowed her to visit three flowers to acclimate. Phase 1 continued until the bee had fed from at least five flowers and more when possible (median 10). In phase 2, we induced the bee to switch food-handling tactics by replacing the flowers from phase 1 with a set of flowers at which she could only successfully access nectar using the other tactic. We made this switch while the bee was freely flying in the cage, to minimize disruption. Phase 2 continued until the bee stopped visiting the flowers after having fed from multiple flowers, or until she went 10 min without feeding if she visited no or few flowers. All trials were videotaped (Sony HDR-SR11). Thirty-one bees were used in phase 1 (17 robbing, 14 feeding legitimately), and 27 of those 31 also fed in phase 2.

Flower manipulation

We manipulated flowers as follows to allow only legitimate visits or secondary robbing. In legitimate visit phases, we placed small pieces of clear plastic drinking straws over the corolla of each flower. This technique successfully prevents robbing (Irwin & Brody, 1999; Richman, Irwin, Nelson et al., 2017). In robbing phases, we tacked the flower openings shut with a glue stick (Elmer's Disappearing Purple Glue Stick, Westerville, OH, U.S.A.) and used fine forceps to make holes mimicking those observed in the field. These artificial holes adequately simulate natural nectar-robbing holes made by bumble bees and do not damage nonpetal floral structures (Irwin & Brody, 1999). We placed these holes where the

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bees make them while robbing: on average, 2.5 mm from the proximal end of the calyx. Each stalk was only used in a single trial.

After each trial, we used 5 µl microcapillary tubes (Drummond Scientific, Broomall, PA, U.S.A., www.drummondsci.com) to measure the volume of sucrose solution remaining in each flower and, thus, how much of the 3 µl of sucrose solution the bee collected during the trial. Following the trial, we applied a dot of nontoxic paint to the bee's thorax to prevent reusing her and later released her at the original site of capture.

Experimental data analysis

From the videos, we recorded for each floral visit (1) whether the bee walked or flew onto the flower, (2) the part of the flower on which she landed (floral opening, bell or tube; see Fig. 1), (3) the part of the flower to which she moved to after landing, (4) whether the bee made buzzing sounds while feeding and (5) the times at which the bee landed on the flower, inserted her proboscis into the flower opening or the robbing hole to extract sucrose solution, removed her proboscis from those openings and left the flower. We included bees that buzzed, possibly while collecting pollen, because almost half our bees (44%) buzzed at least once. However, buzzing across all flower visits was rare (8% of visits), and buzzing did not affect foraging performance. We used these times and our measurements of sucrose solution consumption to calculate (1) handling time, defined as the total time a flower visit lasted, (2) access time, defined as the time from when a bee landed on a flower to when she first started to feed, and (3) foraging efficiency, defined as net energy intake rate, i.e. the net energy gain per unit time spent on the flower (Hamilton, 2010). Foraging efficiency calculations followed methods in Lichtenberg et al. (2018), incorporating the volume of sucrose solution a bee drank (converted to its caloric value), *B. mixtus*' metabolic costs while on a flower, and each bee's handling time. We did not calculate flight time between successive flowers because this can be highly influenced by bees' motivational states (primarily hunger levels).

We quantified willingness to switch food-handling tactics (question 2) in two ways. First, for the 31 bees that fed in phase 1, we determined whether the bee fed using the new food-handling tactic in phase 2. Second, we quantified the location where bees began to search for nectar (flower opening versus tube) after landing on a flower, after they had been induced to switch tactics (i.e. during phase 2). We included floral visits in which a bee either did or did not feed, but limited this analysis to visits in which a bee landed on the flower's bell (Fig. 1) and thus was not already at one of the two potential feeding locations ($N = 95$ visits across 22 bees). This avoided confounding effects from bees deciding where to feed prior to landing versus landing or walking on the most convenient part of the flower. We defined searching as walking from the bell to either the flower opening or the calyx. We first used a chi-square goodness-of-fit test against a uniform distribution to ask whether bees were more likely to walk towards the opening or tube of the flower during phase 2. We then assessed via logistic regression whether the portion of the flower the bee first investigated varied with the tactic that enabled nectar access and the tactic the bee was using when caught in the field (fixed effects), with trial as a random effect ('lme4' package; Bates, Mächler, Bolker, & Walker, 2015). We ensured that we met model assumptions by visually inspecting diagnostic plots of residuals (Quinn & Keough, 2002) and checked for overdispersion by comparing the sum of Pearson residuals to the residual degrees of freedom (Bolker et al., 2020). For all mixed models (questions 2 and 3), we assessed significance of model terms via likelihood ratio tests.



Figure 1. Parts of a *Mertensia ciliata* flower (left) and photo of a *Bombus flavifrons* forager approaching a *Mertensia ciliata* flower (right).

To determine whether switching food-handling tactics altered foraging performance (question 3), we conducted three types of regressions for each foraging measure (handling time, access time and foraging efficiency) with trials where bees fed from multiple flowers in both phase 1 and phase 2 ($N = 27$ trials). The first set of regressions compared foraging performance during phases 1 and 2. They included trial as a random effect and the following fixed effects: the interaction between phase and tactic permitted during that phase, which tactic the bee was using when caught and whether the bee was audibly buzzing. The second set of regressions included the same fixed and random effects, but compared foraging performance during phase 1 with performance only during the first three flowers a bee fed from during phase 2. This let us determine whether switching tactics causes an immediate reduction in foraging performance. The third set of regressions simultaneously investigated two things. First, in general, did bees improve their foraging performance across a phase under our experimental conditions? Second, did foraging performance change across phase 2, as the bee gained more experience with the new food-handling tactic? Here, we regressed each foraging measure on the three-way interaction including the tactic the bee was using, where in the sequence of feeding visits the flower was and the phase, which tactic the bee was using when caught and whether the bee was audibly buzzing as fixed effects and trial as a random effect. To address the first question, we assessed significance of the phase term. For the second question, we conducted a planned contrast post hoc test that determined the effect of food item sequence on foraging performance within phase 2 ('phia' package; De Rosario-Martinez, 2013). We used a second planned contrast to test whether changes across phase 2 varied by food-handling tactic. Both post hoc tests used a sequential Bonferroni correction (Holm, 1979). We ensured that we met model assumptions by visually inspecting diagnostic plots of residuals (Quinn & Keough, 2002). We omitted two long access times that showed noticeably higher Cook's distances than other data points (Quinn & Keough, 2002). Retaining these outliers did not qualitatively alter results.

Ethical Note

Ethical approval is not required for bumble bee research, but we took care to reduce any possible suffering by individuals and impacts to wild populations. Our observational study involved little interaction between bee and observer, with bees being briefly restrained once (in 2015 and 2016) to apply tags with bee-safe glue. Our experimental bees were caught in the field (by gently placing a vial around them while feeding), kept in the dark to minimize stress at all times other than during a trial, fed overnight and returned the following day to the site where they were caught. Field site access and bee collecting were conducted under U.S. Fish and Wildlife permits held by the Rocky Mountain Biological Lab.

RESULTS

Observational Study: Do Individual Bumble Bees Exhibit Food-handling Tactic Constancy Within and Across Foraging Bouts?

Free-flying bumble bees generally showed high tactic constancy within foraging bouts. At least 86% of bouts or individuals exhibited

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just one tactic, or a mix of primary and secondary robbing, for all species pairs except *B. mixtus* visiting *M. ciliata* (Table 1). *Bombus bifarius* and *B. flavifrons* mainly fed from *C. caseana* flowers via secondary robbing and from *M. ciliata* flowers legitimately. *Bombus flavifrons* visited *L. vulgaris* flowers legitimately, while *B. bifarius* individuals were mainly constant to either legitimate visiting or secondary robbing. *Bombus mixtus* exhibited either only primary robbing or only secondary robbing (the predominant tactic) in 66.1% of bouts on *C. caseana*, and a mixture of the two types of robbing in an additional 32.6% of bouts. Thus, while this bee species was only somewhat constant to a single food-handling tactic, it tended to be constant to robbing. The one case in which bees frequently mixed legitimate visiting with primary or secondary robbing (53.0% of bouts) was *B. mixtus* visiting *M. ciliata*. When this bee species was constant in its handling of *M. ciliata* flowers, it mainly visited legitimately.

Food-handling tactic constancy across foraging bouts varied by bee and plant species (Table 1). Each bee was observed over 6.3 ± 1.0 days (mean $\pm$ SE) on *C. caseana* and 4.6 ± 0.5 days on *M. ciliata*. *Bombus flavifrons* foragers mainly (86.4% of individuals) remained constant to single-tactic legitimate visiting bouts when visiting *M. ciliata* flowers. The *B. mixtus* that we observed multiple times on *C. caseana* mainly mixed primary and secondary robbing both within and among bouts (83.3% of individuals). On *M. ciliata*, *B. mixtus* also tended to mix tactics within and across bouts, but mainly mixed robbing with legitimate visits (87.5% of individuals).

Experiment: Will Individuals Switch Food-handling Tactics?

Despite the high tactic constancy observed in the field, under experimental conditions, *B. mixtus* foragers exhibited a high willingness to switch food-handling tactics (question 2). Thirteen of the 17 bees (76.5%) that fed by robbing in phase 1 and 12 of 14 bees (85.7%) that visited flowers legitimately in phase 1 also fed – using the new tactic – in phase 2.

Looking into switching behaviour in more detail, we found that bees exhibited a preference for attempting to rob flowers in phase 2, after the handling tactic that they had been using became impossible. Bees that flew onto the bell of a *M. ciliata* flower were more likely to next walk towards the part of the flower where robbing occurs (near the calyx; 86.3% of visits) than to walk towards the flower opening, where legitimate visiting occurs (16.7% of visits) (chi-square test of independence: $\chi^2_1 = 9.16$, $P = 0.003$). Bees in both types of trials exhibited this preference, although it was somewhat weaker for bees that fed legitimately during phase 2 (74.4% of visits) than for bees that robbed during phase 2 (97.9% of visits) (GLMM: $\chi^2_1 = 10.15$, $P = 0.001$; Appendix, Tables A2, A3).

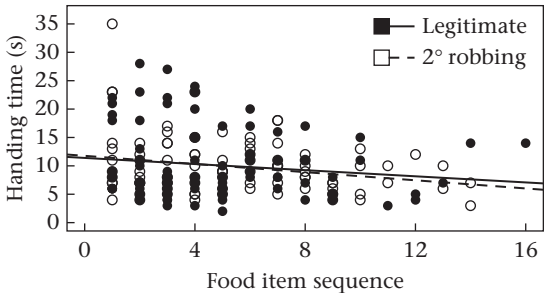

Figure 2. Handling time of *Bombus mixtus* foragers using legitimate and robbing tactics on *Mertensia ciliata* flowers across phase 2. Black dots indicate legitimate visits; white dots indicate robbing visits. Food item sequence is number of visits after the induced tactic switch.

Experiment: Is Food-handling Tactic Constancy Maintained by Costs Associated with Switching Tactics?

Overall, we found minimal reductions in foraging performance when we induced bumble bees to change their food-handling tactic (question 3). *Bombus mixtus* foragers showed only slight increases in handling and access times in phase 2, and no change in foraging efficiency. Whether the bee buzzed while visiting the flower and how the bee was feeding when caught had no significant impact on feeding metrics (Appendix, Tables A3–A5). Bees also showed no evidence of improving their foraging performance within a phase, when we considered both phases together (Appendix, Table A5, phase term).

Food-handling time reflects costs associated with assessing, remembering how to access, accessing and consuming a food item. *Bombus mixtus* foragers exhibited equal handling times during phase 1 (mean $\pm$ SE: 10.0 ± 0.5 s), phase 2 (10.2 ± 0.4 s) and the first three visits of phase 2 (11.2 ± 0.8 s) ($P = 0.93$ and 0.61, respectively; Appendix, Fig. A2, Tables A3, A4). These bees decreased their handling time across phase 2, as they visited more flowers after switching food-handling tactics ($P = 0.02$; Fig. 2, Appendix, Table A6). Across phase 2, bees spent approximately 0.2 s less on each successive flower they visited. This decrease occurred independent of the tactic a bee was using (Appendix, Table A7).

Switching food-handling tactics caused a slight (mean 0.5 s) increase in access times, which reflects costs of assessing food properties that correlate with profitability and costs of the forager positioning herself to feed. *Bombus mixtus* foragers took significantly longer to access nectar in phase 2 (1.9 ± 0.2 s) than during phase 1 (1.4 ± 0.1 s) ($P = 0.009$; Fig. 3, Appendix, Table A3). Access time did not change between phase 1 and the first three visits of phase 2 (1.9 ± 0.2 s; $P = 0.07$; Appendix, Fig. A3a, Table A4) or across phase 2 ($P = 0.48$; Appendix, Fig. A3b, Tables A5, A6).

Table 1
Number of bouts (within) or bees (among) observed for each plant–bee species combination exhibiting each tactic or combination of tactics

Plant species	Bee species	Bout	Legitimate visits	1° robbing	2° robbing	Legitimate + robbing	1° + 2° robbing
C. caseana	*B. bifarius*	Within	2	NA	51	5	NA
C. caseana	*B. flavifrons*	Within	1	NA	165	2	NA
C. caseana	*B. mixtus*	Within	0	6	136	3	70
M. ciliata	*B. bifarius*	Within	87	NA	1	9	NA
M. ciliata	*B. flavifrons*	Within	399	NA	11	19	NA
M. ciliata	*B. mixtus*	Within	57	4	1	70	1
L. vulgaris	*B. bifarius*	Within	121	NA	68	22	NA
L. vulgaris	*B. flavifrons*	Within	66	NA	9	7	NA
C. caseana	*B. mixtus*	Among	0	0	1	1	10
M. ciliata	*B. flavifrons*	Among	19	NA	0	3	NA
M. ciliata	*B. mixtus*	Among	1	0	0	7	0

'Within bout' refers to switches within foraging bouts; 'among bout' refers to switches by marked bees across foraging bouts.

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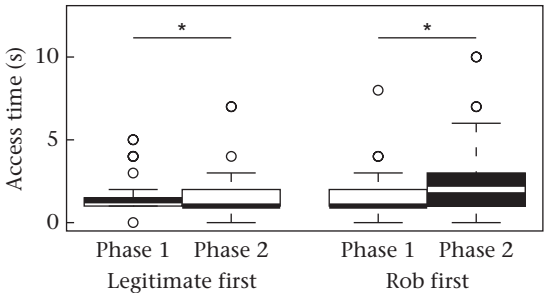

Figure 3. Food access times of *Bombus mixtus* foragers using legitimate and robbing tactics during phases 1 and 2. Black boxes correspond to legitimate visits; white boxes correspond to robbing visits. Asterisks indicate statistically significant differences ($P < 0.05$). Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

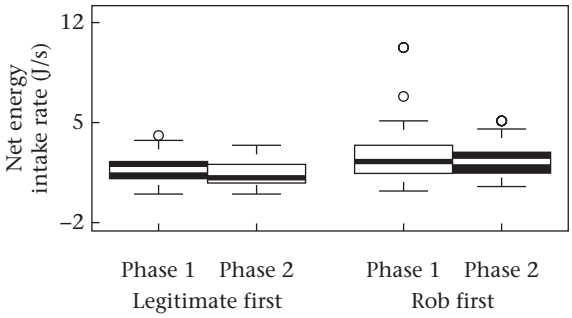

Figure 4. Foraging efficiency of legitimate and robbing tactics used by *Bombus mixtus* on *Mertensia ciliata* flowers during phases 1 and 2. Black boxes correspond to legitimate visits; white boxes correspond to robbing visits. Asterisks indicate statistically significant differences. Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

Even though a forced switch in food-handling tactic increased handling and access times, it did not decrease foraging efficiency. *Bombus mixtus* foragers consumed nectar with equal efficiency in phase 1 (2.3 ± 0.2 s), in phase 2 (2.0 ± 0.1 s), in the first three visits of phase 2 (2.0 ± 0.2 s) and as they gained more experience during phase 2 ($P = 0.33$, 0.33 and 0.24, respectively; Fig. 4, Appendix, Fig. A4, Tables A3–A6). Also, *B. mixtus* foraged more efficiently on *M. ciliata* flowers via nectar robbing than via legitimate visits ($P < 0.0001$, $P = 0.02$ and $P = 0.0008$, respectively; Appendix, Fig. A5, Tables A3–A5).

DISCUSSION

Foragers must balance costs of frequent environmental assessment against opportunity costs associated with behavioural constancy. Behaviour theory highlights this trade-off (McNamara & Houston, 1985), but empirical determination of when and why individuals should exhibit short-term behavioural constancy remains limited. Nectar robbing, the focus of this study, is an excellent system for exploring such questions because its ecology is fairly well documented (reviewed in Irwin et al., 2010) and because of the ease in observing many flower visits by a single individual. Our results show that bumble bees capable of handling flowers in two or three distinct ways exhibit high tactic constancy in nature, as predicted. We observed constancy both within and across foraging bouts. This constancy occurs even though the focal species are capable of switching food-handling tactics. However, our experimental data were largely inconsistent with the hypothesis that costs associated with switching promote the tactic constancy we observed. Taken together, the results indicate high food-handling tactic constancy, but that costs associated with switching are not the mechanistic driver. Other unmeasured factors, such as foraging payoffs, likely drive high food-handling tactic constancy.

The degree of food-handling tactic constancy observed in this study was strikingly high, with typically at least 90% of bouts or bees including only one food-handling tactic (or a combination of primary and secondary robbing of *C. caseana* by *B. mixtus*). This matches previous reports of high constancy to robbing or legitimate visits (Free, 1968; Marzinzig et al., 2018; Mayer et al., 2014; Stout et al., 2000), as well as constancy to a specific flower colour (e.g. Briggs, Graham, Switzer, & Hopkins, 2018) or plant species (Gegear & Laverty, 2001), by bumble bees and honey bees. Our study extends this basic understanding of tactic or floral constancy by assessing the behaviour of large numbers of individuals and by explicitly considering food-handling tactic constancy separately from the plant species being visited. High behavioural constancy is common, as exhibited by the breadth of systems in which personality or behavioural syndromes exist (Bell, Hankison, & Laskowski, 2009). While it is not possible to directly compare behavioural constancy as measured in the current study (and floral constancy research) and 'repeatability' measures used to detect behavioural syndromes (which compare among- to within-individual variation), assessing intra-individual constancy in the latter body of literature would provide an intriguing analysis.

The high constancy we observed in the field is particularly striking given individuals' willingness to switch tactics in the experiment. This contrast between our observational and experimental results is consistent with previously reported higher behavioural repeatability (lower within- than among-individual variability in a behaviour) in the field than in the laboratory (Bell et al., 2009). For example, male cricket calling behaviour was two to three times more repeatable when crickets called in fields than in the laboratory (Kolluru, 1999), and field-reared spiders exhibit a boldness–aggressiveness syndrome while laboratory-reared individuals do not (Sweeney et al., 2013).

Our experimental results are not consistent with the hypothesis that switching costs drive high food-handling tactic constancy. The small increases in handling and access time we measured did not impact bees' foraging efficiencies. Furthermore, we found minimal switching costs even when bees switched to the less efficient tactic (legitimate visit). Because nectar robbing tends to occur on complex flowers with tubes or nectar spurs, we originally predicted that switching between nectar robbing and legitimate visiting would incur costs similar to those that drive floral constancy of bees feeding on complex flowers (Gegear & Laverty, 2005). However, in the present study, the increase in handling time was similar in magnitude to the relatively small changes in handling time seen in floral constancy experiments using simple flowers that are easy for bees to handle (reviewed in Gegear & Laverty, 2001). Our flower alterations potentially reduced switching costs by covering the cues that bees use to assess whether to rob or visit legitimately. We rarely saw free-flying bees hover to assess flowers before deciding where to land or which direction to walk after landing, however. Thus, bees are most likely using both their ability to access the nectar and the nectar volume or quality they encounter as cues; cues that drive other bee foraging decisions (e.g. Dukas & Real, 1993a; Gegear & Thomson, 2004) and that were present (if modified) in our experiment. Future work clarifying how bees assess whether to rob or visit legitimately would provide the data necessary to determine how our manipulations may have altered switching costs.

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It is possible that field conditions magnify switching costs enough to drive constancy and, more broadly, to explain higher behavioural repeatability in the field than in the laboratory (Bell et al., 2009). (1) The small handling and access time differences we measured could impact bees' foraging decisions when summed across hundreds of flower visits. However, Gegear and Laverty (1995) estimated that, during long foraging bouts in the field, access time reductions of ~2 s (slightly larger than those found here) would only minimally decrease bumble bee foraging efficiency at moderate switching rates. Furthermore, the increase in access time we found did not translate to an increase in handling time or a decrease in foraging efficiency. Additional research could provide insights into whether and how much foraging performance changes measured on a small number of flowers translate to changes in colony productivity or fitness. (2) Bees' visual environments are also significantly more complex in meadows than in our experiment, with many flowers in close proximity to each other. Diverse animals increase foraging times or choosiness when food items are cryptic compared to when food items strongly contrast with their backgrounds (e.g. Goulson, 2000; Jones, Krebs, & Whittingham, 2006). Likewise, high environmental heterogeneity can increase assessment costs (Stephens, 1987) and reduce learning rates (Dukas & Real, 1993b). (3) Floral rewards are typically lower in the field than in our experiment (Lichtenberg et al., 2020). Smaller nectar volumes may promote efficiency-enhancing behaviours such as selecting the most rewarding food-handling tactic (the focus of this study) or flower species (Gegear & Thomson, 2004). In a similar vein, spiders eat at a more constant rate at lower prey densities (Michalko, Košulič, Pung, & Vichitbandha, 2018). Lower nectar rewards may also reflect higher competition levels (Pleasants, 1981), which increase floral constancy (Brosi & Briggs, 2013) but can also reduce individuals' niche specialization (Araújo, Bolnick, & Layman, 2011). However, competition levels have little impact on nectar robbing constancy (Lichtenberg et al., 2020). Lower nectar volumes could also drive constancy to nectar robbing, as nectar will be located deeper in the flower and thus might be accessible only via robbing. Thus, we think it is possible that field conditions magnify switching costs.

One alternative possibility is that foragers remain constant to a tactic with higher payoff. Our results are partially consistent with this hypothesis. Most of the bee species that we observed had a preferred food-handling tactic on a given plant species. These preferences matched the food-handling tactic that is most efficient for *B. mixtus* visiting *C. caseana*, and for *B. flavifrons* visiting *M. ciliata* (efficiencies determined by Lichtenberg et al., 2018). Furthermore, bees in the current experiment switched to a less efficient tactic (legitimate visit) when we manipulated the more efficient tactic to have zero benefit. However, in nature, *B. bifarius* visiting *L. vulgaris* receive equal payoffs when foraging legitimately and robbing (Lichtenberg et al., 2018). In the current study, these bees mainly remained constant to a single tactic within bouts but failed to show a population level preference for a single tactic. This suggests that payoffs from different tactics vary at a finer scale than we investigated, or that something else drives short-term, intra-individual variation.

Food-handling tactic constancy may also be a by-product of other behavioural drivers (or states, Sih et al., 2015), such as body condition and predation or competition levels. For example, individual body condition impacts the degree of feeding site constancy that brown pelicans, *Pelecanus occidentalis*, exhibit (Geary, Walter, Leberg, & Karubian, 2019), and predation risk alters fish behavioural constancy (Bell & Sih, 2007). Higher resource diversity increases foraging specialization at the individual level in several species (Araújo et al., 2011). These factors can alter bee foraging behaviour (e.g. Foster & Cartar, 2011; Wang, Chittka, & Ings, 2018). However, their potential impacts on bee foraging constancy remain unknown. These factors were unlikely to have influenced the experimental results presented here, because there was no predation, competition levels were standardized and low, and bees only participated in the experiment when they were sufficiently hungry.

In conclusion, we found that switching costs did not promote high constancy in food-handling tactic use in flower-foraging bumble bees. Our observational data lent mixed support to the hypothesis that foragers remain constant to the food-handling tactic with the higher payoff. A hypothesis consistent with our results is that foraging payoffs are a primary driver of food-handling tactic constancy, but that payoffs can vary at a smaller scale (e.g. individual, day) than has been investigated so far. More detailed investigation of how payoffs and constancy vary among environmental conditions (Auld, Agrawal, & Relyea, 2010), individuals and taxa may be a fruitful avenue of research to shed light on why we observe intra-individual variation that has previously been classified as random noise (Westneat et al., 2015).

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Supplementary Material

Supplementary video related to this article can be found at https://doi.org/10.1016/j.anbehav.2020.09.008.

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Appendix

Table A1
Sites used in this study and the data collected at each

Valley	Site	Latitude	Longitude	Tactic-switching experiment	Plant species field observations
East	401 Trail	39.018	-107.044	Yes	*M. ciliata*
East	403 Trail	38.981	-107.011	No	*M. ciliata*
East	Avery	38.976	-106.996	No	*M. ciliata*
East	Bellview Bench	39.051	-107.031	No	*M. ciliata*
East	Gothic	38.959	-106.990	No	*L. vulgaris*
East	Schofield Pass	39.016	-107.049	No	*M. ciliata*
East	Townsite	38.866	-107.095	No	*L. vulgaris*
Kebler	Kebler Campground	38.862	-107.104	No	*M. ciliata*
Kebler	Irwin Town Site	38.866	-107.095	No	*M. ciliata*
Kebler	Kebler Pass	38.865	-107.106	Yes	*C. caseana*, *M. ciliata*
Kebler	Lower South Kebler	38.867	-107.104	No	*M. ciliata*
Kebler	Ohio Road	38.846	-107.099	Yes	No data
Kebler	South Kebler Pass	38.864	-107.106	No	*C. caseana*
Poverty	Lower Poverty Gulch	38.954	-107.023	No	*C. caseana*
Poverty	Middle Poverty Gulch	38.956	-107.078	No	*C. caseana*
Poverty	Upper Poverty Gulch	38.958	-107.080	No	*C. caseana*
Slate	Kapushion	38.887	-106.985	No	*L. vulgaris*
Slate	Lower Loop	38.904	-107.026	No	*L. vulgaris*
Slate	Wildbird	38.891	-106.996	No	*L. vulgaris*
Washington	Lower Washington Gulch	38.941	-107.023	Yes	*C. caseana*, *M. ciliata*
Washington	Middle Washington Gulch	38.940	-107.029	No	*C. caseana*
Washington	Upper Washington Gulch	38.960	-107.034	No	*C. caseana*, *M. ciliata*

Table A2
Test statistics for model assessing bees' willingness to switch tactics, as determined by where they moved (calyx or flower opening) after landing on the bell

Measure of foraging performance	Model term	Value coefficient indicates	Coefficient	Coefficient standard error	Likelihood ratio χ^2	*df*	*P*
Where moved after bell	Intercept		1.22	0.59			
Where moved after bell	Tactic	Rob	2.84	1.11	8.67	1	0.003
Where moved after bell	How visited in field	Both tactics	-0.64	0.83	0.77	2	0.68
Where moved after bell	How visited in field	Rob	0.001	0.78			

Generalized linear model used a logit link.

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Table A3
Test statistics for models assessing foraging performance during phase 1 vs phase 2

Measure of foraging performance	Model term	Value coefficient indicates	Coefficient	Coefficient standard error	Likelihood ratio χ^2	*df*	*P*
Handling time	Intercept		10.24	1.03			
	Tactic	Rob	0.46	1.64	0.09	2	0.96
	Phase	Phase 2	0.21	1.59	0.15	2	0.93
	How visited in field	Both tactics	-0.26	1.77	1.83	2	0.40
	How visited in field	Rob	-2.15	1.75			
	Buzz while feeding	Yes	1.42	1.11	1.46	1	0.23
	Tactic:phase	Rob, phase 2	-0.76	2.92	0.08	1	0.77
Access time	Intercept		1.45	0.33			
	Tactic	Rob	-0.09	0.51	2.15	2	0.34
	Phase	Phase 2	0.32	0.49	9.41	2	0.009
	How visited in field	Both tactics	0.22	0.50	0.22	2	0.90
	How visited in field	Rob	0.06	0.52			
	Buzz while feeding	Yes	-0.48	0.41	1.39	1	0.24
	Tactic:phase	Rob, phase 2	0.70	0.84	0.81	1	0.37
Foraging efficiency	Intercept		1.73	0.26			
	Tactic	Rob	0.40	0.41	19.40	2	<0.0001
	Phase	Phase 2	-0.52	0.42	2.21	2	0.33
	How visited in field	Both tactics	0.23	0.46	4.61	2	0.10
	How visited in field	Rob	0.92	0.45			
	Buzz while feeding	Yes	-0.50	0.32	2.49	1	0.11
	Tactic:phase	Rob, phase 2	0.66	0.75	0.93	1	0.34

General linear models used the identity link.

Table A4
Test statistics for models assessing foraging performance during phase 1 vs the first three flowers fed from in phase 2

Measure of foraging performance	Model term	Value(s) coefficient indicates	Coefficient	Coefficient standard error	Likelihood ratio χ^2	*df*	*P*
Handling time	Intercept		10.20	1.14			
	Tactic	Rob	1.18	1.84	0.51	2	0.77
	Phase	Phase 2	1.44	1.90	1.00	2	0.61
	How visited in field	Both tactics	-0.78	2.11	2.95	2	0.23
	How visited in field	Rob	-3.22	2.01			
	Buzz while feeding	Yes	1.87	1.54	1.35	1	0.25
	Tactic:phase	Rob, phase 2	-1.54	3.45	0.24	1	0.62
Access time	Intercept		1.45	0.25			
	Tactic	Rob	0.09	0.40	0.71	2	0.70
	Phase	Phase 2	0.34	0.41	5.28	2	0.07
	How visited in field	Both tactics	0.31	0.45	1.81	2	0.41
	How visited in field	Rob	-0.30	0.43			
	Buzz while feeding	Yes	-0.57	0.36	2.60	1	0.11
	Tactic:phase	Rob, phase 2	0.16	0.74	0.05	1	0.82
Foraging efficiency	Intercept		1.80	0.28			
	Tactic	Rob	0.31	0.44	7.69	2	0.02
	Phase	Phase 2	-0.64	0.49	2.21	2	0.33
	How visited in field	Both tactics	0.14	0.51	5.35	2	0.07
	How visited in field	Rob	1.04	0.48			
	Buzz while feeding	Yes	-0.88	0.50	3.09	1	0.08
	Tactic:phase	Rob, phase 2	0.72	0.83	0.86	1	0.35

General linear models used the identity link.

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Table A5
Test statistics for models assessing foraging performance across phases

Measure of foraging performance	Model term	Value coefficient indicates	Coefficient	Coefficient standard error	Likelihood ratio χ^2	*df*	*P*
Handling time	Intercept		10.48	2.49			
	Tactic	Rob	2.48	3.30	0.71	4	0.95
	Food item sequence		-0.04	0.30	8.78	4	0.07
	Phase	Phase 2	1.14	2.91	2.6	4	0.62
	How visited in field	Both tactics	-0.13	1.81	2.30	2	0.32
	How visited in field	Rob	-2.34	1.79			
	Buzz while feeding	Yes	1.86	1.12	2.49	1	0.32
	Tactic:sequence	Rob	-0.24	0.37	0.48	2	0.79
	Tactic:phase	Rob, phase 2	-2.11	4.30	0.24	2	0.89
	Sequence:phase	Phase 2	-0.23	0.35	0.55	2	0.76
	Tactic:sequence:phase	Handling time	0.15	0.43	0.10	1	0.76
Access time	Intercept		2.07	0.66			
	Tactic	Rob	0.09	0.86	5.65	4	0.23
	Food item sequence		-0.09	0.08	3.96	4	0.41
	Phase	Phase 2	-0.45	0.75	4.63	4	0.33
	How visited in field	Both tactics	0.25	0.37	1.90	2	0.39
	How visited in field	Rob	-0.30	0.38	0.44	1	0.51
	Buzz while feeding	Yes	-0.19	0.30			
	Tactic:sequence	Rob	-0.007	0.10	0.30	2	0.86
	Tactic:phase	Rob, phase 2	0.69	1.05	0.62	2	0.73
	Sequence:phase	Phase 2	0.08	0.10	1.01	2	0.60
	Tactic:sequence:phase	Handling time	-0.04	0.12	0.16	1	0.69
Foraging efficiency	Intercept		2.26	0.60			
	Tactic	Rob	-0.14	0.82	18.85	4	0.0008
	Food item sequence		-0.07	0.07	3.47	4	0.48
	Phase	Phase 2	-1.29	0.73	3.98	4	0.41
	How visited in field	Both tactics	0.16	0.47	4.83	2	0.09
	How visited in field	Rob	0.93	0.46			
	Buzz while feeding	Yes	-0.53	0.34	2.50	1	0.11
	Tactic:sequence	Rob	0.07	0.09	0.52	2	0.77
	Tactic:phase	Rob, phase 2	1.16	1.10	1.24	2	0.54
	Sequence:phase	Phase 2	0.12	0.09	2.52	2	0.28
	Tactic:sequence:phase	Handling time	-0.07	0.11	0.26	1	0.61

General linear models used the identity link.

Table A6
Post hoc planned contrast testing whether foraging performance changed over phase 2

Measure of foraging performance	Phase	Likelihood ratio χ^2	*df*	*P*
Handling time	1	0.75	1	0.39
	2	6.89	1	0.02
Access time	1	2.79	1	0.19
	2	0.49	1	0.48
Foraging efficiency	1	0.52	1	0.47
	2	2.44	1	0.24

P values are adjusted using a sequential Bonferroni correction.

Table A7
Post hoc planned contrast testing whether foraging performance changed differently when bees were robbing or visiting legitimately during phase 2

Measure of foraging performance	Phase	Likelihood ratio χ^2	*df*	*P*
Handling time	1	0.42	1	1
	2	0.14	1	1
Access time	1	0.01	1	1
	2	0.27	1	1
Foraging efficiency	1	0.60	1	0.88
	2	0.003	1	0.96

P values are adjusted using a sequential Bonferroni correction.

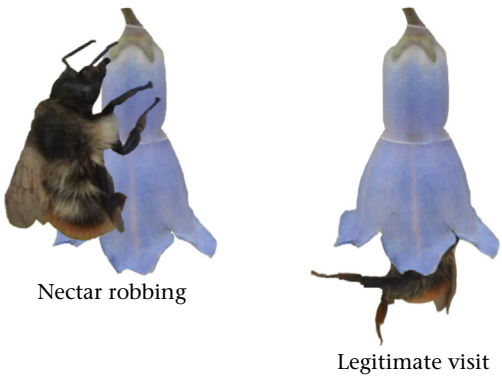

Figure A1. Legitimate visit versus nectar robbing of *Mertensia ciliata* flowers. Photos: copyright Jessica Barker, and used with permission.

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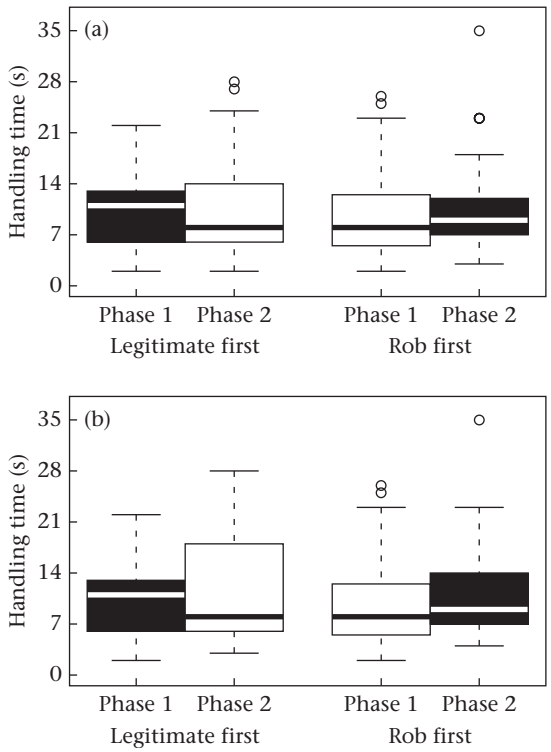

Figure A2. Handling times of *Bombus mixtus* foragers on *Mertensia ciliata* flowers (a) during phase 1 and phase 2 and (b) during phase 1 and the first three visits in phase 2. Black boxes correspond to legitimate visits, white boxes to robbing visits. Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

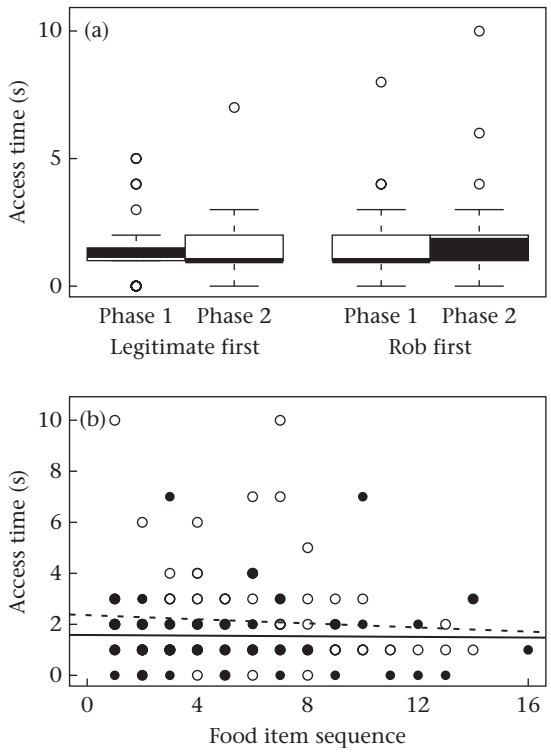

Figure A3. Access times of *Bombus mixtus* foragers on *Mertensia ciliata* flowers (a) during phase 1 and the first three visits of phase 2 and (b) across phase 2. Black boxes and points and solid lines correspond to legitimate visits. White boxes and points and dashed lines correspond to robbing visits. Asterisks indicate statistically significant differences. Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

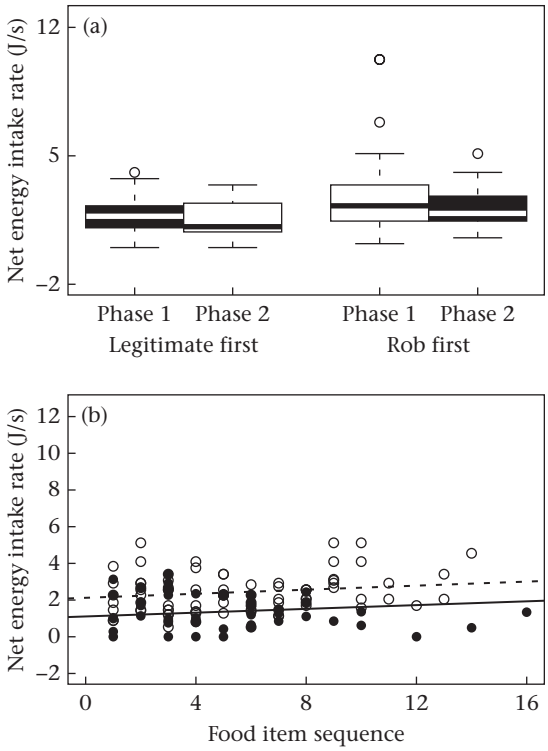

Figure A4. *Bombus mixtus* foragers on *Mertensia ciliata* exhibited equal foraging efficiencies (a) during phase 1 and the first three visits of phase 2 and (b) across phase 2. Black boxes and points, and solid lines, correspond to legitimate visits. White boxes and points, and dashed lines, to robbing visits.

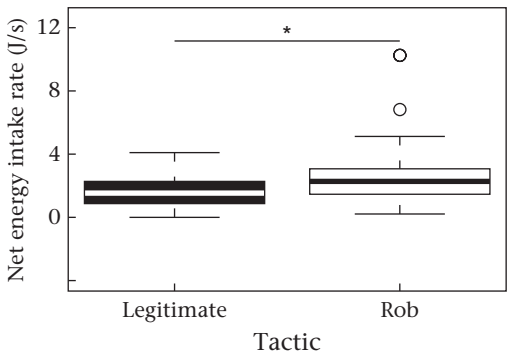

Figure A5. Foraging efficiencies of *Bombus mixtus* foragers visiting *Mertensia ciliata* flowers legitimately or by secondary robbing. Asterisks indicate statistically significant differences.

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