

THE TACTIC AND FLORAL CONSTANCY OF FORAGING BUMBLEBEES: PURE  
LEGITIMATE FORAGERS, PURE NECTAR-ROBBERS, AND MIXED TACTIC INDIVIDUALS  
VISITING ONE OR MORE HOST SPECIES

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## **Abstract**

Floral visitors in a Colorado bumblebee community engage in two main foraging tactics: nectar-robbing and legitimate foraging. An individual may employ one tactic consistently throughout a foraging bout or switch and may visit one constant host species or multiple. In order to understand foraging strategies, tactic and floral constancy must jointly be investigated with pollen and nectar foraging. I do so in this second ever study to compare floral visit observations with pollen load compositions. I found that nectar-robbers carried pollen less or as often as legitimate foragers, depending on robber and host species. This suggests that pollen-carrying robbers are mixed tactic individuals that could, in one foraging bout, cheat and cooperate with its plant partner. Visitors were observed switching tactic within a host species and switching tactic between host species. Both robbers and legitimate foragers carried pollen from the same host species they visited for nectar when that host species could be both robbed for nectar and legitimately foraged for pollen. These results suggest that tactic switching is more common than previously thought and that floral constancy is frequently maintained across tactic switches, unless host floral morphology constrains behavior and forces a host switch.

## **Background**

Pollinators are animals that transport plants' male gametes (pollen) from the pollen-bearing anthers to the female reproductive organs (ovule-bearing stigmas). For the most successful fertilization and production of viable seeds, pollen removal and receipt must occur in the same species: on the same plant or even within the same flower in self-compatible species, or preferably, between different plants, as this increases genetic diversity of the offspring. Plant-pollinator relationships are usually considered mutualistic since both partners, the plant and the animal vector, generally benefit. The plant partner gains reproductive services. The pollinator gains a food reward (nectar and/or pollen).

The magnitudes of benefits are variable, however. Species produce nectar and pollen of varying quality, while the amount of resources an individual flower has depends on the rate of depletion, nectar replenishment, and anther dehiscence. While some floral visitors may be pollinators, others may waste the plant's male gametes by delivering them to the wrong species. Visitors may also simply take nectar and pollen without pollinating. From the visitors' perspective, food rewards are still gained in this scenario, potentially at a discounted energy expenditure. From the plants' perspective, however, non-pollinating behaviors reduce fitness. Floral visitors suspected of taking rewards without pollinating are considered "cheaters" of the mutualism that can potentially harm the plant partner and/or its legitimate pollinators.

One classic "cheating" behavior is nectar robbery, in which nectar is taken through an alternative opening, bypassing the floral entrance and often, the anthers and stigma

(Inouye 1980a). Species whose nectar accumulates at the base of long tubular flowers or in the tips of nectar spurs are often the targets of a form of nectar robbery in which nectar is taken through a hole made in the corolla (Irwin & Maloof 2002). Nectar-robbing is often contrasted with "legitimate" foraging, in which visitors take nectar through the floral entrance, often while positioned to contact the anthers and stigma in the process. Where nectar robbery tends to only yield the nectar resource (though see Higashi et al. 1988, and Navarro 2000 for examples of a robber-pollinators), legitimate foraging often yields both nectar and pollen and facilitates pollination.

Nectar-robbers can significantly deplete a flower's nectar, even removing all the available nectar, without pollinating. As such, nectar-robbing is often framed as detrimental to plants and legitimate visitation as beneficial. In reality, floral visitors' and especially nectar-robbers' impacts on plant fitness can be difficult to discern. Maloof and Inouye (2000) and Irwin et al. (2010) found that robbers' direct and indirect impacts on plant reproduction range from negative to positive effects on male and female reproduction. Conversely, legitimate visits are not always beneficial, i.e., they do not necessarily result in successful pollination. For example, a morphological mismatch between a floral visitor and a flower not adapted for that visitor may thwart pollen transfer (Hargreaves et al. 2009). Value-laden terms like "legitimate" and "robber" are a convention in the literature that prematurely assign dichotomous "good" versus "bad" roles to floral visitors. In this thesis, I continue to use these established terms, but acknowledge their problems and prioritize clarity and specificity.

In many plant species, *Bombus* (bumblebee) species act as important pollinators in the course of foraging for nectar and pollen from flowers. Nectar is bumblebees' primary carbohydrate, while pollen is the protein source for their developing offspring. Worker bees fly around visiting flowers and lapping nectar up from the nectaries with their tongues, consuming some as their own energy source and storing the rest in their crops. They collect pollen by covering their bodies with pollen from floral anthers, then groom the loose pollen into a ball-like load which is packed on their hind legs' corbiculae. These pollen loads are evenly distributed between the two hind legs and built up from multiple floral visits over the course of a single foraging bout. At the end of a bout, workers bring their pollen loads and crop nectar back to the nest to feed the colony.

*Bombus* are known to perform both legitimate foraging and nectar robbery. Individual bees may specialize in one behavior or the other for durations ranging from a day to a lifetime (e.g. O'Donnell et al. 2000, Russell et al. 2017). Alternatively, individuals may switch between foraging behaviors in the midst of a bout (e.g. Morris 1996, Mayer et al. 2014). Bronstein et al. (2017) called the short-term fidelity of individuals to one behavior "tactic constancy". Tactic constancy builds on an existing framework called "floral constancy" which describes a behavior in which visitors consistently visit only one species despite the presence and potential advantages of other co-flowering species (Waser 1986). Tactic and floral constancy are especially useful when considered together, as floral visitor tactics are diverse and dynamic within and/or between host species as well as during and/or between foraging bouts.

Bees that switch foraging tactic challenge the assumption that floral visitors are always either a legitimate forager or always a nectar-robber on a host species. This introduces a difficulty in the pollination ecology terminology, as terms such as “legitimate forager” and “nectar-robber” can falsely suggest pure strategies instead of fluid behaviors. When I use “robber” or “legitimate forager”, I am referring the *current foraging tactic* performed by an individual on the *current floral host*, unless otherwise stated.

While floral constancy is documented in multiple systems, tactic constancy has been little studied, and the rules that govern both are hardly understood. As Bronstein et al. (2017) note, most studies focus on nectar foraging and only record the host species visited, with very few studies recording tactic use and even fewer including pollen foraging. This ignores the potential and likely interaction between nectar and pollen foraging, especially given how floral visitors may collect both resources in the same bout and potentially even on the same flower. For a more holistic understanding of *Bombus*’ floral use and foraging behavior, studies need to integrate the frameworks of tactic and host constancy for both nectar and pollen foraging.

The goal of this study was to further elucidate the contexts and patterns of tactic and host constancy in *Bombus*’ nectar and pollen foraging. In a system where nectar-robbing and legitimately foraging are the only visitor behaviors, an individual bee must employ one of three tactic strategies: pure nectar-robbing (always robbing), pure legitimate foraging (always foraging legitimately), or mixed tactics (switching between the two behaviors). Additionally, an individual can exhibit one of two host strategies: constant host (foraging only from one species) and mixed hosts (foraging from multiple species). Table 1a shows the possible combinations of host and tactic strategies an individual could exhibit.

Table 1a: The six different overall strategies an individual bee can theoretically utilize regarding floral host and foraging tactic during a foraging bout. Legitimate foraging is abbreviated “LF” and nectar-robbing “NR”. One asterisk (\*) indicates strategies the author predicted would be rare while two (\*\*) indicates ones predicted to occur frequently. Tactical strategies include “pure nectar-robbing”, “pure legitimate foraging”, and “mixed tactics” (switching between robbing and legitimate foraging). Floral strategies include “constant host” where the individual only visits one species or “mixed host” where multiple species are visited.

		Tactical strategy		
		Pure NR	Pure LF	Mixed tactics
Floral strategy	Constant host	Pure NR on constant host**	Pure LF on constant host**	Mixed tactics on constant host
	Mixed hosts	Pure NR on mixed hosts	Pure LF on mixed hosts	Mixed tactics on mixed hosts *

This study included pollen foraging by examining the species composition of *Bombus* workers’ pollen loads in addition to conducting floral visit observations. Given the difficulty and time investment necessary to observe individuals’ entire foraging bouts to

track host and tactic constancy, pollen loads offer valuable bout-long records of the host species that pollen-carrying individual have previously visited (probably legitimately foraged) for pollen. Coupling these records of past hosts that were legitimately foraged upon from pollen load compositions with the snapshots of current tactics performed on current hosts from floral visit observations, I was able to partially track host and tactic histories.

To search for evidence of tactic and host switches, I asked the following questions:

*1) Do nectar-robbers carry pollen as often as do legitimate foragers?*

Question 1 relates to tactic constancy, because under the assumption that robbing yields only nectar whereas legitimate foraging can simultaneously yield nectar and pollen, nectar-robbers that carry pollen are tactic switchers, which, according to the literature (e.g. Stout et al. 2000, Ishii and Kadoya 2016), is infrequent. Finding out whether individuals ever exhibited mixed tactics was an important first step. Following the literature, I predicted that in general, pollen-carrying nectar-robbers, i.e., mixed-tactic individuals, would be less common than pollen-carrying legitimate foragers (which I predicted were mostly pure legitimate foragers).

*2) Do pollen-carrying nectar-robbers and legitimate foragers differ in whether their loads contain pollen from the species they are currently visiting?*

Question 2 investigates host constancy by comparing an individual's current host species, as seen during floral visit observations, with their previous pollen hosts, as determined from pollen load compositions. I predicted that legitimate foragers carry pollen from the plant species upon which they are legitimately foraging, while nectar-robbers carry pollen from plant species other than the host they are robbing: i.e., legitimate foragers were more host constant than nectar-robbers.

Based on multiple studies' findings that bumblebees exhibit high floral constancy (e.g. Free 1970, Heinrich 1977, Gegear and Lavery 2004), I predicted that pollen-carrying legitimate foragers would have previously legitimately foraged upon and collected pollen from their current host species. Furthermore, I predicted that host species' flowers would have corolla lengths that matched the legitimate foragers' proboscis lengths, based on findings that bumblebees preferentially legitimately forage flowers with corolla lengths which match their proboscis length (Inouye 1980b, Pyke et al. 2012).

I predicted that pollen-carrying nectar-robbers would have previously legitimately foraged upon and collected pollen from a plant species other than the host they were currently robbing. Studies have found that short-tongued bees tend to rob long-corolla species (e.g. Newman and Thomson 2005), and to be more efficient at legitimately foraging short-corolla species (Inouye 1980b). Therefore, when a tactic switch occurs, I predicted there will also be a corresponding host switch. For instance, I expected that a bee will switch between robbing one longer-corolla species and legitimately foraging upon another shorter-corolla one, as Ishii and Kadoya (2016) saw.

To my knowledge, Ishii and Kadoya (2016) is the only previous study that has ever examined pollen load composition alongside floral visit observations to describe patterns in pollinator behavior. Furthermore, this is the first study to consistently integrate the two methods throughout the study period, as Ishii and Kadoya only collected pollen loads on one day out of their field season from one of their sites and even then mostly relied on data from visit observations.

## Methods

### Study Species: Bees

*Bombus bifarius* and *Bombus mixtus* are both eusocial bumblebees native to North America and have similar ranges throughout western Canada and Alaska, and across the western United States. *Bombus mixtus* has disjunct populations in the Great Lakes region and Atlantic coast from Maine up into eastern Canada (Koch et al. 2012, Williams et al. 2014). Both species live in a variety of habitats including prairies, chaparral, riparian woodlands, montane meadows, and tundra (Mayer et al. 2000, Kearns & Oliveras 2009, Cook et al. 2010, Wilson et al. 2010, Miller-Struttman and Galen 2014). In Colorado, where this study was conducted, *B. bifarius* are found at elevations from 7500 to 10,000 ft while *B. mixtus* occurred from 9000 to 11,000 ft. Both species are considered common throughout most of their ranges and are classified "Least Concern" by the International Union for Conservation of Nature (Hatfield et al. 2014a and b).

In the Rocky Mountains, *B. bifarius* and *B. mixtus* have been observed foraging from a variety of plant hosts including species of *Astragalus*, *Cirsium*, *Epilobium*, *Erigeron*, *Linaria*, *Lupinus*, *Mertensia*, *Monardella*, *Pedicularis*, *Penstemon*, *Phacelia*, *Rudbeckia*, *Sisyrinchium*, and *Trifolium* (Macior 1974). Both *Bombus* species are active from May to September, though *B. bifarius* starts earlier (April) and ends later (October) and *B. mixtus* starting to forage as early as March (Williams et al. 2014).

My study species are relatively small for bumblebees: *Bombus bifarius* workers are 8-14 mm long and *B. mixtus* workers 10-14mm long (Koch et al. 2012, Williams et al. 2014). Both species are considered "short-tongued", or having proboscises < 9mm long (*B. bifarius* workers: 5.8 mm, Pyke et al. 2012; *B. mixtus* workers: 3.96 mm, Wang, *pers. obs.*).

*Bombus bifarius* has two color morphs. The Rocky Mountain region's form has considerable red hair on terga 2 and 3. The other form lacks red on terga 2 and 3 and is more common in the rest of *B. bifarius'* range (Thorp et al. 1983). *Bombus bifarius* workers are distinguished by the wedge of black pile on the thorax that creates a "V" with the tip projecting towards tergum 2, where a lateral black line bisects the abdomen banded with red, yellow, and black pile ending on tergum 5. *Bombus mixtus* workers have a distinctive black band on tergum 3 between its yellow (terga 1-2) and orange bands (terga 4-5) (Koch et al. 2012, Williams et al. 2014).

I chose to focus on these bee species because both are polylectic generalists known to carry pollen and nectar back to their colonies. Furthermore, both species are known to legitimately forage and nectar-rob.

### Study Species: Plants

Three focal plant species, all monoecious herbaceous perennials, were chosen because all three focal bee species foraged from them, they were all abundantly blooming during the study at their respective study sites, and they have tubular flowers known to frequently be robbed, especially by smaller, short-tongued bees such as my study species.

*Corydalis caseana* ssp. *brandegeei* (Papaveraceae), is the Colorado-native subspecies of *C. caseana* (Kaye 2001). *Corydalis caseana* is a self-compatible montane shrub, growing multiple hollow stems from the ground up to over 5 ft tall. Leafy stalks terminate in dense racemes that bear 50 or more flowers that bloom June through August. Flowers in a raceme are densely stacked in an inflorescence 10 cm long. Flowers are staggered and bloom in ascending order. Outer petals are light pink to white and crested; inner petals are purple tipped. Nectar is produced in the spur at the end of the sympetalous corolla and angled above the floral opening (Gray 1874). Bronstein measured *C. caseana* flowers at Washington Gulch near Gothic, CO in 2015 and found flower length to have a mean of 26.1 mm, with a standard deviation of 1.9mm (*unpublished data*). *Corydalis caseana* is pollinated mostly by long-tongued large bumblebees and robbed (without pollination) by smaller bumblebees. Maloof found that *C. caseana* robbers (*B. occidentalis*) did not deter its pollinators (*B. appositus*) or have a negative effect on fruit or seed set. Robbers perhaps even had a positive effect in causing pollinators to fly farther for nectar and so transport pollen greater distances (Maloof 2001).

*Mertensia ciliata* (Boraginaceae) is native to the western U.S. and usually grows in the montane zone (recorded elevational range: 1680-3960 m) in moist habitats such as stream sides and wet meadows. The self-compatible shrub grows up to 1 m tall. Peduncles off main stems support inflorescences of loosely clustered flowers that hang with the floral opening facing down. Inflorescences at any given time may contain buds alongside open flowers and nutlets. Blooms are lightly fragrant and radially symmetric bells with rounded lobes that start blue and turn pink with age. The corolla is 10-17 mm long and nectar collects at the base of the corolla (Pelton 1961). Flowers bloom from June to August before nutlets seeds begin to form (Williams 1937). *Mertensia ciliata* is mostly visited and pollinated by *Bombus*. Pelton also noted *Osmia* and *Colletes* species cutting holes to nectar rob without pollinating (1961).

*Linaria vulgaris* (Plantaginaceae) is a ruderal invasive from Eurasia that is now found in both Americas, Africa, and Australia. It was introduced to the United States as an ornamental and is now found in all 50 states. Sutton et al. (2007) found that in the Colorado Rocky Mountains, *L. vulgaris* was most likely to invade open sites, along trails, and areas with higher species diversity, which indicates the species' ability to threaten native species and biodiversity. *Linaria vulgaris* plants grow as erect stems 20-80 cm

tall. Inflorescences consist of racemes with densely packed yellow flowers that bloom in ascending order. The flower is snapdragon-like with a lanceolate upper and lower lobe. The bottom lobe or "lip" has a darker yellow "guide" coloration. The lip covers the floral opening and must be pulled down to legitimately access the flower. The corolla is 15 mm long and the slightly curved spur is also 15 mm long. Flowers bloom from June to September. *Linaria vulgaris* is self-incompatible and requires insect pollinators. However, it is very successful at vegetative propagation due to an extensive root system (Saner et al. 1995). Bumblebees are among the visitors strong enough to push past the flower's lip and enter the corolla. Stout et al. (2000) observed that long-tongued bees were the main pollinators while short-tongued species robbed the spur without pollinating. They concluded that robbers did not reduce *L. vulgaris* reproduction since pollinators were not deterred. Newman and Thomson (2005) observed short-tongued bees also legitimately foraging *L. vulgaris* to drink trace amounts of nectar from the sides of the spur, on account of not being able to reach all the way down the spur. They also suggest that *L. vulgaris*' flower and inflorescence morphology are "tolerance traits" against robbing. Other pollinators in the U.S. include *Halictus* and *Dialictus* species (Arnold 1982).

### Study Sites

I conducted this study near Crested Butte, Colorado. From July 20 to August 2, 2016, I worked with a field team at the Kebler West (KW) site, a wet montane meadow just west of Kebler Pass Road (KW site: 38°51'53.9"N 107°06'23.4"W). From August 3 to August 17, 2016, we worked at the Lower Loop (LL) site off the Lower Loop Trail in Gunnison National Forest (LL site: 38°53'59.2"N 107°01'08.2"W). LL was approximately 10 m uphill from the trail itself. LL was drier than KW and was mostly grassland that was recently grazed by cattle. All three bee species were commonly present at both sites. KW had 36 species blooming during the study period there, of which *C. caseana* and *M. ciliata* were the two most abundant, while LL had only 13 species blooming, of which *L. vulgaris* was the most abundant.

### Foraging Observations and Pollen Load Collection

Foraging observations and pollen load collection occurred between 9am and 4pm in conditions that ranged from sunny and cloudless to windy to overcast and cool. Field team members only observed bees that were currently visiting the three focal plant species. We would start by sighting a bee and observing it visit 2-5 flowers before netting it. We observed and caught workers and males of the following species: *B. bifarius*, *B. mixtus*, *B. flavifrons*, *B. occidentalis*, *B. californicus*, and *B. rufocinctus*. For the purposes of answering my questions, here I only address data from workers of the two focal bee species. Once caught, the bee was gently pressed by a "bee squeezer" (sponge plungers in a mesh-topped tube) to immobilize it. We then identified the bee to species and caste. We also recorded the time the bee was caught, the plant species of the flowers it visited, number of flowers visited, whether it was legitimately foraging or nectar-robbing those flowers, and whether or not the bee was carrying pollen. For each focal species, every other worker with pollen loads in their corbiculae had one of its

loads taken with forceps. Individual pollen loads were kept in Eppendorf tubes that were labelled to match them to the corresponding foraging observation. Tubes with pollen loads inside were kept in a cooler with ice packs while in the field and transferred to a laboratory freezer until analysis. We made 303 observations of the focal species and collected 98 pollen load samples by the end of the field season.

### Determination of Species Composition of Pollen Loads

To determine the species composition of individual pollen loads, I made microscope slides of pollen loads and viewed them under a compound light microscope. I identified the grains I saw to plant species.

While still in the field, I collected pollen from each of the blooming species at each site to build a reference collection. First I collected flowers from each blooming species at each site. The KW reference samples were collected August 8, 2016 (at the end of the study period there) while the LL samples were collected August 11, 2016 (middle of study period there).

Individual flowers were placed in Eppendorf tubes and transported in a cooler to the laboratory where each flower's anthers were rubbed with a cube of fuchsin gel to bind the pollen to the staining gel. The gel was then placed on a microscope slide and melted at low heat on a hot plate. A slide cover was immediately placed on the liquefied gel and firmly pressed and swirled to spread the pollen in an even layer on the slide. Instruments (e.g. forceps and scalpel for handling and cutting the fuchsin gel) were sterilized and wiped clean between samples.

I viewed reference slides under 40x magnification to categorize the species' pollen grain morphology as either spherical, cocci, spiky, or other (e.g. *M. ciliata* pollen has a distinct two lobed form). I also noted other distinguishing characteristics such as relative size and splitting pattern (many grains split in three triangular cuts, others in a single large "Pac man" cut).

Slides of bees' pollen loads were made with the same procedure, starting with rubbing a subsample from each load onto a small cube of fuchsin gel. The slides were labelled with a number that corresponded to the foraging observation record of the bee from which that load was taken. I did not refer to the foraging observations while I performed pollen identification. In total, I examined 90 pollen load slides.

I viewed each slide for at least five minutes at 10x magnification, sweeping my view up and down the sample along five transects. I switched to 40x each time I saw a pollen grain novel to the slide to identify its species by comparison to reference slides. More time was spent on pollen grains that were difficult to identify, either because I did not have a match in my reference collection ("Unknown #" was designated to unknown morphospecies) or because the pollen morphology matched multiple species in the reference. For example, many of the spiky pollen grains were lumped together under the plant family Asteraceae because of morphological similarity. Fortunately, the most

common pollen grains I saw in loads were morphologically distinct from other species at each site, and I am confident in my identification of *M. ciliata* and *L. vulgaris* pollen.

For each pollen load, I recorded which species were present and their rank abundance. Most loads were composed of only a single species. Second, third, or fourth species were sometimes present, though only as one to ten grains out of hundreds of total grains. After Ritchie et al. (2016), I considered these “incidental” species, most likely from contamination. Dropping incidental species’ pollen, I identified the loads’ predominant species compositions to *M. ciliata*, *L. vulgaris*, Asteraceae, or four unknown pollen types: Unknown #2, #4, #5, and #6.

I categorized pollen loads that contained pollen from the plant species the individual was currently visiting as a “match”. Loads with pollen from species other than the one the individual was currently visiting were called “mismatches”.

### Statistical Analyses

I ideally would have observations and pollen load slides from two focal bee species performing two foraging behaviors on each of three focal plant species. However, only four subsets had sufficient sample sizes for analysis: *B. bifarius* robbers of *L. vulgaris*, *B. bifarius* legitimate foragers of *L. vulgaris*, *B. mixtus* robbers of *M. ciliata*, and *B. mixtus* legitimate foragers of *M. ciliata*.

To address Question 1, I calculated the proportion of all individuals observed that were carrying pollen. To test the hypothesis that robbers carried pollen less often than did legitimate foragers, I used a one-tailed Fisher’s Exact Test to compare robbers’ proportions to legitimate foragers’ proportions.

Focusing only on pollen-carrying visitors for Question 2, I calculated the proportion of “match” pollen loads out of total pollen loads for robbers versus legitimate foragers. To test the hypothesis that robbers would have a lower proportion of “matches” than would legitimate foragers, I again used a one-tailed Fisher’s Exact Test to compare robbers’ proportions to legitimate foragers’ proportions.

## **Results**

### Pollen Collection by Nectar-robbers and Legitimate Foragers

1) *Do nectar-robbers carry pollen as often as legitimate foragers?*

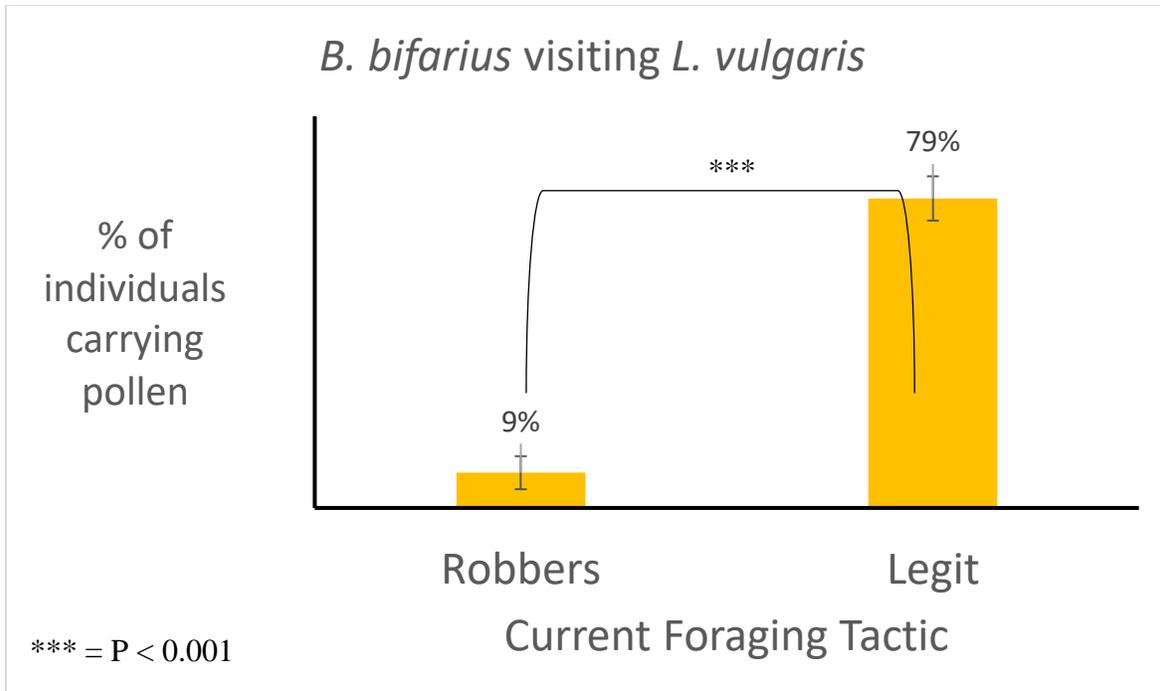


Figure 1: *Bombus bifarius* seen visiting *L. vulgaris*: proportionately fewer nectar-robbers ( $n = 46$ ) carried pollen compared to legitimate foragers ( $n = 52$ ); left-tailed Fisher's Exact Test:  $\alpha = 0.05$ ,  $p$ -value =  $5.479E-13$ . Error bars indicate  $\pm 1$  S.D.

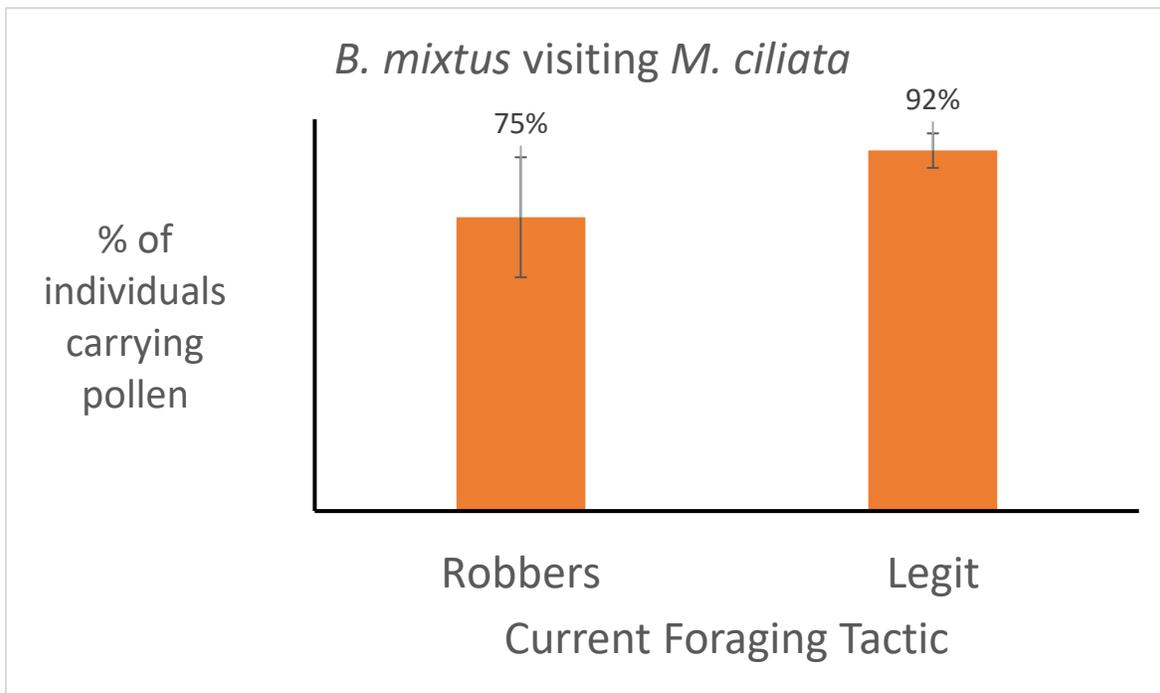


Figure 2: *Bombus mixtus* seen visiting *M. ciliata*: The proportion of nectar-robbers (n = 8) and legitimate foragers (n = 38) that carried pollen loads did not differ significantly; left-tailed Fisher's Exact Test:  $\alpha = 0.05$ , p-value = 0.203. Error bars indicate  $\pm 1$  S.D.

I compared the presence/absence of pollen loads in observed visitors of both foraging strategies. The proportion of nectar-robbers (n = 8) and legitimate foragers (n = 38) that carried pollen loads did not differ significantly (left-tailed Fisher's Exact Test: p-value = 0.203). *Bombus bifarius* visitors of *L. vulgaris* were consistent with my hypothesis that robbers would carry pollen loads less often than legitimate foragers. In contrast, I cannot reject the null hypothesis with *B. mixtus* visitors of *M. ciliata* because both legitimate foragers and robbers had similarly high proportions of individuals carrying pollen loads.

Floral Constancy in Nectar-robbers and Legitimate Foragers

Flowering species were identified usually to species or at least genus. At KW, a total of 13 morphospecies plus Asteraceae were found in pollen loads; at LL, 3 morphospecies plus Asteraceae. Table 2 lists the flowering species for both sites that I observed.

Table 2: The blooming plant species present for each site; in descending order of abundance. These same species are represented in each site's reference collection of pollen slides. Species were observed at KW on 8 August 2016 and at LL on 11 August 2016. Bolded species' pollen were identified to the Asteraceae family.

Plant species present at KW	Plant species present at LL
<i>Corydalis caseana</i>	<i>Linaria vulgaris</i>
<i>Mertensia ciliata</i>	<i>Potentilla fruticosa</i>
<i>Delphinium barbeyi</i>	<i>Achillea millefolium</i>
<i>Heracleum maximum</i>	<i>Agoseris glauca</i>
<i>Ligusticum porteri</i>	<b><i>Erigeron speciosus</i></b>
<b><i>Solidago multiradiata</i></b>	<i>Agastache urticifolia</i>
<i>Veratrum californicum</i>	<b><i>Aster foliaceus</i></b>
<i>Castilleja sulphurea</i>	<b><i>Viguiera multiflora</i></b>
<i>Aconitum columbianum</i>	<b><i>Hymenoxys hoopseii</i></b>
<i>Linum lewisii</i>	<i>Campanula rotundiflora</i>
<i>Geranium richardsonii</i>	<i>Vicia americana</i>
<i>Pedicularis racemosa</i>	<i>Penstemon strictus</i>
<i>Polemonium pulcherrimum</i>	<i>Castilleja sulphurea</i>
<i>Trifolium repens</i>	
<b><i>Viguiera multiflora</i></b>	
<b><i>Hymenoxys hoopseii</i></b>	
<b><i>Helianthella</i></b>	
<b><i>quinquenervis</i></b>	
<b><i>Senecio serra</i></b>	
<b><i>Senecio triangularis</i></b>	

<i>Erigeron elatior</i>
<i>Erigeron speciosus</i>
<i>Erigeron coulteri</i>
<i>Lathyrus sp.</i>
<i>Aquilegia coerulea</i>
<i>Erythranthe guttatus</i> (syn.: <i>Mimulus guttatus</i> )
<i>Ipomopsis aggregata</i>
<i>Lupinus argenteus</i>
<i>Vicia Americana</i>
<i>Achillea millefolium</i>
<i>Galium boreale</i>
<i>Heterotheca villosa</i>
<i>Senecio bigelovii</i>
<i>Arenaria congesta</i>
<i>Arnica parryi</i>
<i>Potentilla rubricaulis</i>
<i>Taraxacum officinale</i>

2) Do pollen-carrying nectar-robbers and legitimate foragers differ in whether their loads contain pollen from the species they are currently visiting?

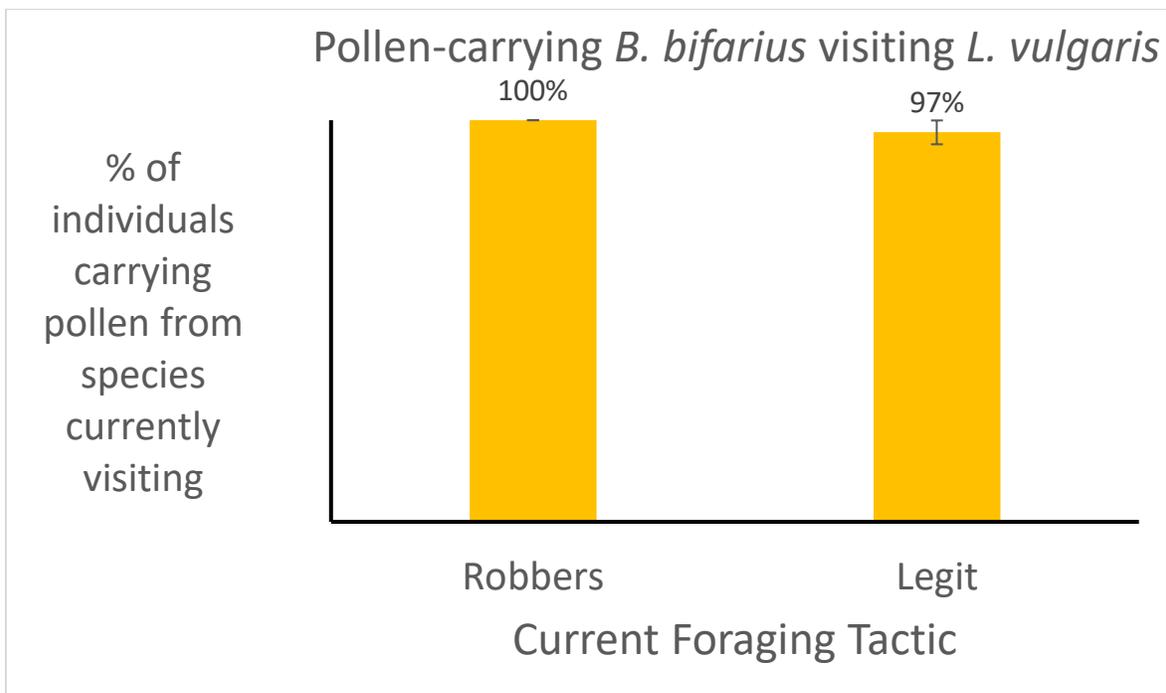


Figure 3: Pollen loads of *B. bifarius* visiting *L. vulgaris*: the proportion of nectar-robbers (n = 5) and legitimate foragers (n=33) carrying pollen from the species they were visiting (carrying “match” pollen

loads) were statistically similar; left-tailed Fisher's Exact Test:  $\alpha = 0.05$ ,  $p\text{-value} = 1$ . Error bars indicate  $\pm 1$  S.D.

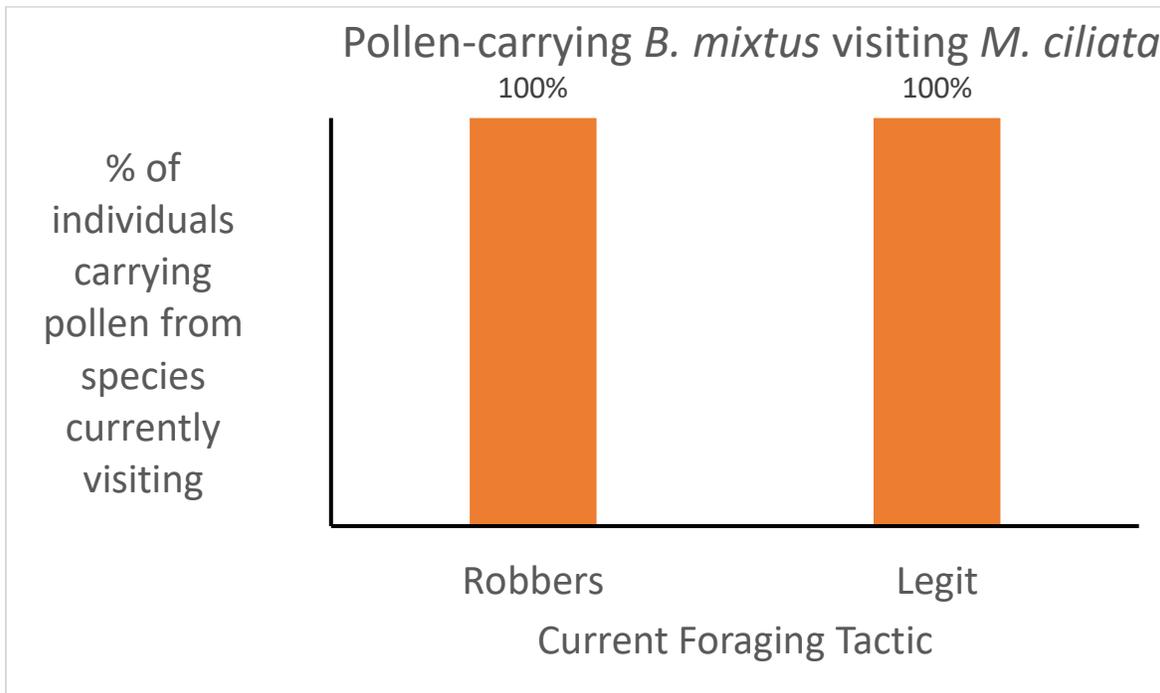


Figure 4: Pollen loads of *B. mixtus* visiting *M. ciliata*: the proportion of nectar-robbers ( $n = 5$ ) carrying pollen from the species they were visiting (carrying "match" pollen loads) was statistically similar to that of legitimate foragers ( $n = 17$ ); left-tailed Fisher's Exact Test:  $\alpha = 0.05$ ,  $p\text{-value} = 1$ . Error bars indicate  $\pm 1$  S.D.

With neither species combination (*B. bifarius* on *L. vulgaris* and *B. mixtus* on *M. ciliata*), could I reject the null hypothesis, as robbers and legitimate foragers did not differ significantly in their proportions of carriers of "match" pollen (left-tailed Fisher's Exact Test: *B. bifarius*  $p\text{-value} = 1$ ; *B. mixtus*  $p\text{-value} = 1$ ). Robbers and legitimate foragers were almost always found carrying pollen from the species they were currently visiting, indicating that within the same bout, they previously visited that same species in a manner that allowed pollen collection.

#### Floral Constancy in *C. caseana* Nectar-robbers' Loads

Though not one of my original questions, the previous result led me to ask if the same pattern held across plant species:

3) Across different robbed species, do nectar-robbers tend to carry pollen from the species they rob?

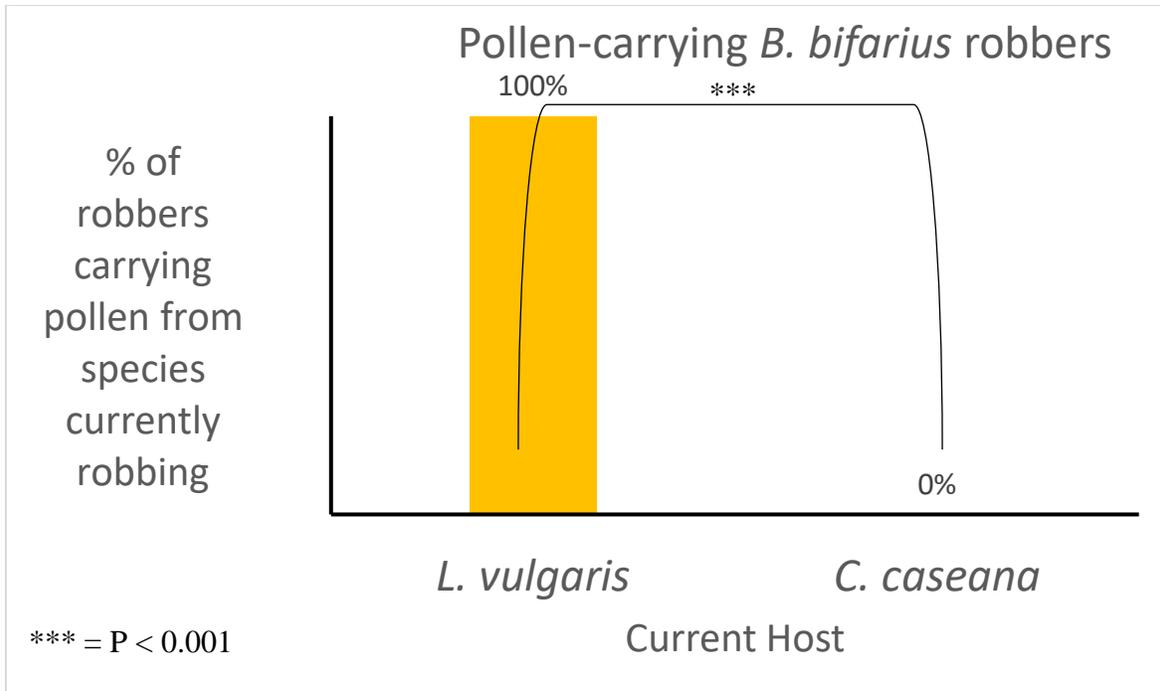


Figure 5: Pollen loads of *B. bifarius* robbers: the proportion of *L. vulgaris* nectar-robbers (n = 5) carrying pollen from the species they were visiting (carrying “match” pollen loads) significantly differed from that of *C. caseana* robbers (n = 10); two-tailed Fisher’s Exact Test:  $\alpha = 0.05$ , p-value = 3.330E-4. Note that most individuals carried one species’ pollen only (excluding incidental species).

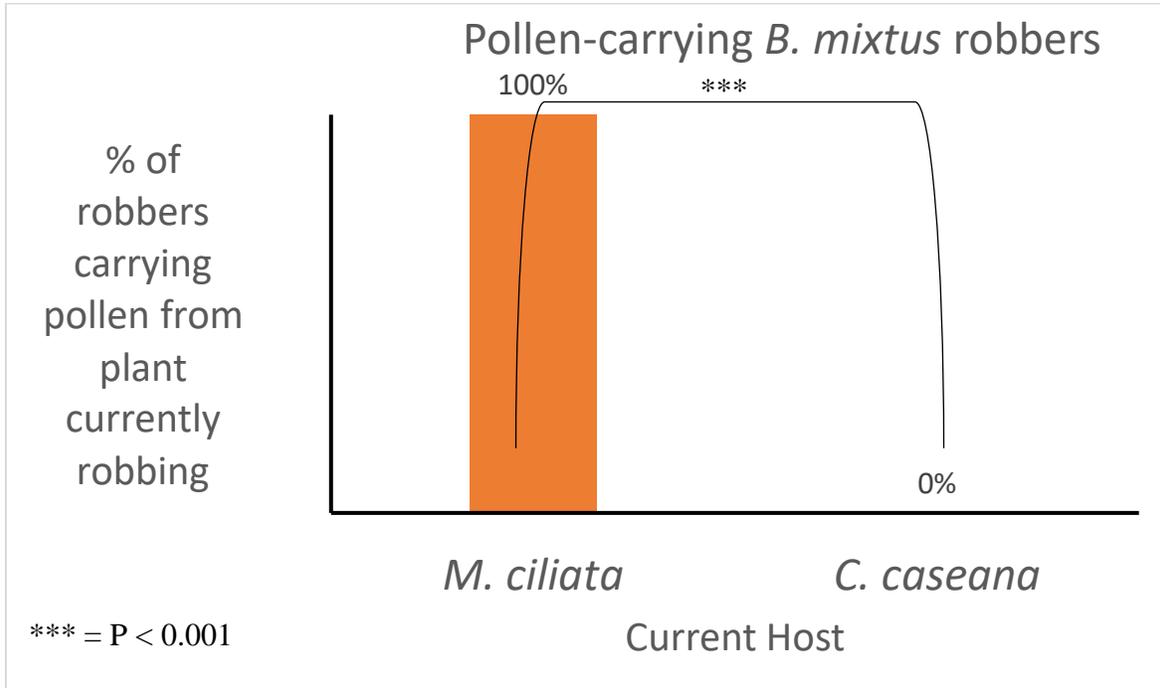


Figure 6: Pollen loads of *B. mixtus* robbers: the proportion of *M. ciliata* robbers (n = 5) carrying pollen from the species they were visiting (carrying “match” pollen loads) significantly differed from that of *C. caseana* robbers (n = 20); two-tailed Fisher’s Exact Test:  $\alpha = 0.05$ , p-value = 1.882E-5. Note that most individuals carried one species’ pollen only (excluding incidental species).

The proportion of *B. bifarius* robbers that carried “match” pollen differed significantly between the two host species (*L. vulgaris* or *C. caseana*) on which individuals were initially caught robbing (two-tailed Fisher’s Exact Test: p-value = 3.330E-4). The same was true of *B. mixtus* robbers initially caught robbing either *M. ciliata* or *C. caseana* (two-tailed Fisher’s Exact Test: p-value = 1.882E-5). Furthermore, regardless of robber species, pollen-carrying robbers of *L. vulgaris* and *M. ciliata* always carried those species’ pollen (often, exclusively); robbers of *C. caseana*, showed the opposite pattern of never carrying *C. caseana* pollen. I never saw loads containing even incidental amounts of *C. caseana* pollen. *C. caseana* visitors were also always observed nectar-robbing, never legitimately foraging.

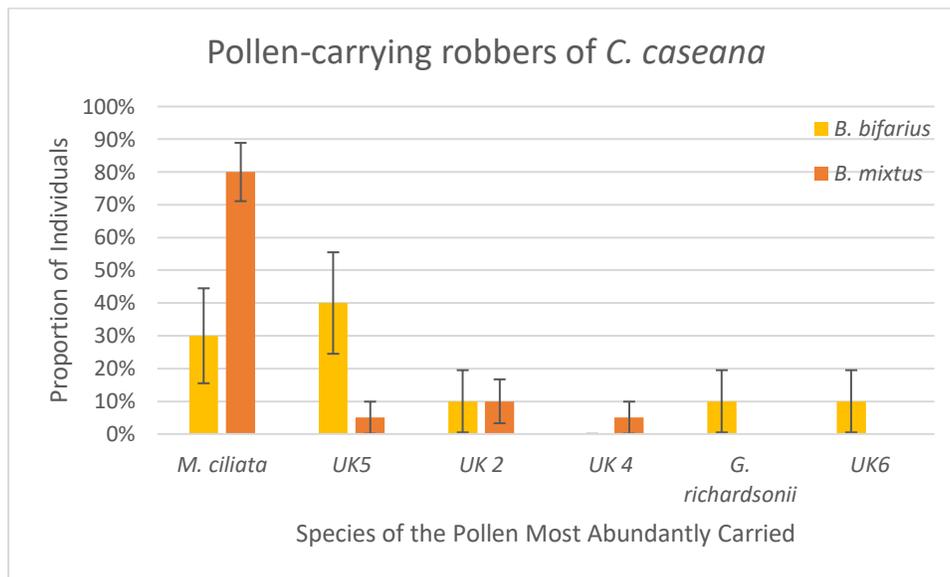


Figure 7: Pollen loads of *C. caseana* robbers: *B. mixtus* robbers (in orange, n = 20) carried loads whose most abundant pollen grains were from one of four plant species. *B. bifarius* robbers (in yellow, n = 10) also carried from those four species plus *Geranium richardsonii* and Unknown #6. Only species of pollen that composed of greater than roughly 50% of the load were included in this analysis. Note that all 30 samples contained one clearly most abundant species. Error bars indicate  $\pm 1$  S.D.

Forty-two percent of *B. bifarius* and 26% of *B. mixtus* robbing *C. caseana* carried pollen. *C. caseana* robbers’ loads were mostly homogenous, with each load having a species that clearly had the most abundant pollens. Four species, *M. ciliata*, Unknown #5, #2, and #4 were found to dominate loads from *B. bifarius* robbers of *C. caseana* (n = 10). Those same four species plus *Geranium richardsonii* and Unknown #6 dominated *B. mixtus* robbers’ loads (n = 20). Of the six species found in *C. caseana* robbers’ loads, two (*M. ciliata* and *G. richardsonii*) are confirmed co-flowering species at KW. Instead of carrying *C. caseana* pollen, most *B. bifarius* caught robbing *C. caseana* carried “Unknown #5”-dominated loads while most *B. mixtus* robbers carried *M. ciliata*-dominated loads.

*Behavior of Individuals Re-observed After Pollen Load Collection*

Of the 90 bees included in the pollen load analyses above, 84 were tagged, yet only nine were re-observed in the days following initial capture. Four were *B. mixtus* initially captured on *M. ciliata*. Five were *B. bifarius* initially captured on *L. vulgaris*.

Table 3: Summary of the foraging behavior of nine individuals as discretely observed at initial capture and then continuously re-observed later. Legitimate foraging is abbreviated to "LF". Nectar-robbing is abbreviated to "NR". If observations of the same individual were more than one hour apart, they were assumed to be of different foraging bouts. "N.D." means no data.

Bee ID	Initial capture				Recapture				
	Tactic	Host	Load?	Load match?	Days after initial	Bout # / Total	Tactic(s) within bout	Host(s) within bout	Load?
B84 <i>B. mixtus</i>	LF	<i>M. ciliata</i>	Y	Y	1	1/1	Pure NR	Constant on <i>C. caseana</i>	N
B88 <i>B. mixtus</i>	LF	<i>M. ciliata</i>	Y	Y	1	1/1	Mixed	Constant on <i>M. ciliata</i>	Y
R40 <i>B. mixtus</i>	LF	<i>M. ciliata</i>	Y	Y	1	1/1	Pure LF	Constant on <i>M. ciliata</i>	Y
Y54 <i>B. mixtus</i>	NR	<i>M. ciliata</i>	Y	Y	1	1/1	Mixed	Constant on <i>M. ciliata</i>	Y
					2	1/1	Pure NR	Switched between <i>M. ciliata</i> and <i>C. caseana</i>	Y
					5	1/4	Mixed	Constant on <i>M. ciliata</i>	Y
						2/4	Mixed	Constant on <i>M. ciliata</i>	Y
						3/4	Mixed	Constant on <i>M. ciliata</i>	Y
						4/4	Pure LF	Constant on <i>M. ciliata</i>	N
6	1/4	Mixed	Constant on <i>M. ciliata</i>	Y					

						2/4	Mixed	Constant on <i>M. ciliata</i>	Y
						3/4	Mixed	Constant on <i>M. ciliata</i>	Y
						4/4	Pure LF	Constant on <i>M. ciliata</i>	N
O27 <i>B. bifarius</i>	LF	<i>L. vulgaris</i>	Y	Y	3	1/1	Mixed	Constant on <i>L. vulgaris</i>	Y
					4	1/2	Pure NR	Constant on <i>L. vulgaris</i>	N
						2/2	Pure LF	Constant on <i>L. vulgaris</i>	Y
O1 <i>B. bifarius</i>	LF	<i>L. vulgaris</i>	Y	Y	0	1/1	Pure LF	Constant on <i>L. vulgaris</i>	Y
					1	1/1	Pure LF	Constant on <i>L. vulgaris</i>	Y
Y63 <i>B. bifarius</i>	NR	<i>L. vulgaris</i>	Y	Y	0	1/1	Pure NR	Constant on <i>L. vulgaris</i>	N. D.
Y52 <i>B. bifarius</i>	NR	<i>L. vulgaris</i>	Y	Y	13	1/1	Pure NR	Constant on <i>L. vulgaris</i>	N
Y29 <i>B. bifarius</i>	LF	<i>L. vulgaris</i>	Y	Y	0	1/2	Pure LF	Constant on <i>L. vulgaris</i>	N
						2/2	Pure LF	Constant on <i>L. vulgaris</i>	N

Six of the nine re-observed individuals only had pure tactic bouts (pure LF, 3 individuals, n = 5 bouts; pure NR, 3 individuals, n = 3 bouts); one only had mixed tactics bouts (n = 1 bout). Individuals Y54 and O27 notably had, in the same day, bouts of mixed tactics interspersed with bouts of pure robbing and legitimate foraging (n = 13 bouts). Y54 was also the only individual in this subset that switched host; it switched between *M. ciliata* and *C. caseana* during a pure robbing bout.

I found that nectar-robbers carried pollen less or as often as legitimate foragers, depending on robber and host species. This suggests that mixed tactic individuals could, in one foraging bout, cheat and collaborate with its plant partner. Both robbers and legitimate foragers carried pollen from the same host species they visited for nectar when that host species could be both robbed for nectar and legitimately foraged for pollen. Visitors were observed switching tactic within a host species and switching tactic between host species. These results suggest that tactic switching is more common than previously thought and that floral constancy is frequently maintained across tactic switches, unless host floral morphology constrains behavior and forces a host switch.

## **Discussion**

Why do bees switch tactic? Why do they switch host? With this system of two focal bumblebee species (*B. bifarius* and *B. mixtus*) on three focal plant species (*L. vulgaris*, *M. ciliata*, and *C. caseana*), I asked three questions to investigate tactic and floral constancy in the context of pollen and nectar foraging. In this Discussion, I will describe the rationale used to infer foraging strategies from the results and summarize the main results that correspond to each question and correlate them with specific foraging strategies. Then I draw conclusions about what new rules may inform floral/tactic constancy, and finally point out new directions for study.

### *Inferring Foraging Strategy from the Results*

Since I rarely was able to observe the behavior of the bees I tagged and sampled for longer than a few floral visits, I could not directly describe their foraging bout strategies. However, from the observations plus the pollen load analysis, I was able to infer some individuals' tactic and/or host constancy. Table 4 summarizes how I interpreted the data as signatures of pure or mixed tactics and hosts.

Table 4: Floral visit observations of the current tactic (columns) are combined with pollen load analysis (rows) to create inferences of what those individuals' strategies were. Since legitimate foraging tends to yield pollen, only pollen carriers can be inferred to have previously legitimately foraged, and either be pure legitimate foragers or mixed tactic individuals. Individuals that lack pollen therefore were inferred to have not previously legitimately foraged, and so to be pure nectar-robbers. Whether the individuals' previous pollen host species matched or mismatched its current host species signaled whether it was constant to one host species or mixed multiple hosts. Unique colors indicate unique strategies, i.e. combinations of tactic and floral constancies. Boxes containing only one color represent signals from the data that could only suggest one foraging strategy; boxes with two colors represent signals that could suggest two different strategies.

	Currently LF	Currently NR
Carrying homogenous loads of matching pollen	Pure LF; constant host	Mixed tactics; constant host
	OR Mixed tactics; constant host	
Carrying homogenous loads of a mismatching pollen	Pure LF; mixed hosts	Mixed tactics; mixed hosts
	OR Mixed tactics; mixed hosts	
Not carrying pollen	Could be any strategy besides NOT pure NR	Pure N; constant hosts
		OR Pure NR; mixed hosts

1) Do nectar-robbers carry pollen as often as do legitimate foragers?

1a) Pure Nectar-robbers of Unknown Floral Constancy

With *B. bifarius*, nectar-robbers proportionally carried pollen much less often than legitimate foragers, as I predicted. This is consistent with descriptions of nectar-robbers as pure floral larcenists that only remove the nectar reward in a way that saves the robber energy but cheats the plant-pollinator mutualism. Pure nectar-robbers (corresponds with the Orange/Purple box in Table 4) would never carry pollen unless it happened to be picked up in the course of robbing – which was not probable in this system. I never saw robbing positions in which the anthers and robbing hole were both contacted, as in Higashi et al (1988). Furthermore, unlike with Higashi et al's *Bombus hypocrita* queens on *Corydalis ambigua* flowers, *B. mixtus* workers' bodies (10-14 mm, Williams et al 2014) are much shorter than *M. ciliata* corollas, making abdomen contact with the anthers while drinking through the robbing hole at the base of the corolla unlikely. Since robbing itself probably did not yield pollen in this system, current nectar-robbers could be separated into pollen-carrying mixed tactic individuals or pure nectar-robbers that did not carry pollen loads.

I hypothesize that pure-robbers are individuals that do not switch tactic because their host is difficult to legitimately visit. This suggests that tactic constancy is context-dependent on current host species. Ninety-one percent of *B. bifarius* robbers of *L. vulgaris* did not carry loads and therefore were likely pure robbers. *L. vulgaris* has complex floral entrance morphology which requires depressing a lip and reaching a relatively long distance from the entrance to the nectaries (spur length: 30 mm, Saner et al 1995; *B. bifarius* tongue length: 5.8 mm, Pyke et al 2012). Those floral traits could deter robbers from switching to legitimately foraging upon it.

### 1b) Mixed Tactic Individuals

With *B. mixtus*, surprisingly a majority of both the robbers and legitimate foragers proportionally carried pollen. This result suggests that while bees that are currently nectar-robbing are cheating their host, it previously cooperated with hosts it legitimately visited. This result is consistent with there being mixed tactic individuals that switch between robbing and legitimately foraging. Assuming the mechanism by which robbers collect pollen is by switching to legitimate foraging, then indeed all pollen-carrying nectar-robbers are tactic switchers, aka mixed tactic individuals.

That I could reject the null hypothesis that legitimate foragers and robbers would carry pollen as often as each other with *B. bifarius* but not with *B. mixtus* suggests there are species differences in both the floral visitors and floral hosts affecting pollen collection.

Additionally, that both species' legitimate foragers frequently carried pollen indicates that legitimate foraging tends to yield pollen. Multiple observations of legitimate visits to *M. ciliata* and *L. vulgaris* in which individuals approached the flowers with their tongues extended and sonicated for pollen further suggest that legitimate foragers can attain both resources in one visit.

### 2) Do pollen-carrying nectar-robbers and legitimate foragers differ in whether their loads contain pollen from the species they are currently visiting?

I could not determine the host history of a current nectar-robber that did not carry pollen. However, pollen-carrying robbers can further be described as visiting one constant host or mixed hosts by examining their load for matching or mismatching pollen.

The nectar-robbers and legitimate foragers of both focal bee species almost always carried pollen from the host species they were visiting (*L. vulgaris* or *M. ciliata*). This went against my prediction that robbers would be less florally constant than legitimate foragers. Not being able to reject the null that robbers and legitimate foragers both tend to carry pollen from the same host species they were visiting for nectar indicates that floral constancy is the norm for both foraging behaviors and across pollen and nectar foraging.

In addition, all the pollen loads analyzed in the Results were essentially homogeneous, with each overwhelmingly dominated by one species' pollen. This homogeneity shows that not only were host species repeatedly visited (legitimately or robbed) during the

span of a foraging bout, but that floral visitors tended to visit *exclusively* one host species for both nectar and pollen.

Pollen-carrying robbers, aka mixed tactic individuals, could then potentially be reliable pollinators of the species they are robbing, in that they tend to carry pollen from one species and visit only that species. There would a low chance of depositing the wrong pollen when the currently robbing switched to legitimately foraging. Robbing flowers tends to reduce plant fitness, but those same robbing individuals may even out that negative effect by pollinating other flowers of the same species during the bout.

### 2a) Legitimate Foragers on a Constant Host Species

From my data, a current legitimate forager could not be distinguished as employing purely legitimate or mixed tactics because previous nectar-robbing would not leave a signal (corresponds with the Pink/Yellow box in Table 4). However, as most legitimate foragers carried pollen, I was able to determine if they were visiting one or multiple host species. From the results of Question 2, 77% of all *B. bifarius* legitimate foragers visited one constant host species (*L. vulgaris*), 2% visited multiple host species, and the remaining 21% have unknown floral constancy because they did not carry pollen. Ninety-two% of all *B. mixtus* legitimate foragers visited *M. ciliata* and the remaining 8% have unknown host constancy because they did not carry pollen.

The high frequencies of host constant legitimate visitors are consistent with my prediction for Question 2 that legitimate foragers would tend to be florally constant. That *B. mixtus* on *M. ciliata* were the most host constant of the legitimate visitors makes sense given that that bee-plant species pair has the smallest difference between floral corolla length and bee proboscis length in this system.

### 2b) Mixed Tactic Individuals on a Constant Host Species

Few observations of heterogeneous pollen loads suggests a low possibility that individuals were legitimately foraging multiple host species. However, multiple hosts could still be visited if one host was legitimately foraged and another robbed. I originally predicted that pollen-carrying nectar-robbers were individuals currently robbing one host species for nectar that had previously legitimately foraged another species whose pollen it carried. With both bee species, this prediction was rejected by data from *M. ciliata* and *L. vulgaris* robbers.

Seventy-five percent of *B. mixtus* robbing *M. ciliata* carried pollen and were likely mixed tactic individuals. This result contrasts strongly with many studies which reported witnessing tactic switching but found high tactic constancy more common (e.g. Stout et al 2000, Ishii & Kadoya 2016).

Furthermore, *B. mixtus* robbers of *M. ciliata* and *B. bifarius* robbers of *L. vulgaris* almost always carried homogenous loads of matching pollen. I hypothesize that the robbers on *L. vulgaris* and *M. ciliata* always carried match pollen because they acquired pollen by switching tactic on the same host species to legitimately forage for pollen (and probably also accessing nectar simultaneously). Mixed tactic individuals maintaining a constant

host as they switched tactic corresponds with the Yellow-only box in Table 4. This preference for host constancy across different tactics could be cognitively more efficient for bees and also means that florally constant nectar-robbers could potentially be reliable pollinators of that host species – not on the robbed flowers, but on the legitimately visited ones. Switching between pollinating and robbing could even potentially cause pollen to be transferred longer distances, which is benefits the plant partner by promoting outcrossing.

Morris (1996) studied *B. mixtus* on a close relative of *M. ciliata*, *M. paniculata*, and also reported frequent tactic switching on *M. paniculata*. Morris attributed the switches between legitimately foraging for pollen and robbing to nectar to how *M. paniculata* flowers offered differential rewards based on age. Younger flowers only produced pollen and were legitimately foraged and sonicated while more mature flowers that had nectar were robbed. The occurrence of young and old flowers in very close proximity, usually even within the same raceme (which I did see in my *M. ciliata* plants), may have also promoted host constant tactic switching.

### 3) Across different robbed species, do nectar-robbers tend to carry pollen from the species they rob?

Whereas *L. vulgaris* and *M. ciliata* robbers always carried their robbing host species' pollen and rejected Hypothesis 2, *C. caseana* showed the opposite pattern and was consistent with my prediction that robbers never carried the robbed host species' pollen. *Corydalis caseana* robbers always visited *C. caseana* for nectar and another host species for nectar.

The difference in pollen load compositions between robbers of different host species rejects Question 3's null that all three plant species would experience similar behavior reinforces the effect of host species traits. This, in addition to the observation that *C. caseana* was never legitimately foraged, always nectar-robbed, by the two focal bee species, makes *C. caseana* a unique context for investigating foraging constancies.

### 3a) Mixed Tactics Individuals on Mixed Host Species

A majority of *C. caseana* robbers of both bee species also lacked pollen loads and were likely pure robbers (corresponds with the Orange/Purple box in Table 4). However, of the pollen-carrying *C. caseana* robbers, all carried homogenous loads of pollen from species other than *C. caseana*, indicating that individuals that robbed *C. caseana* did not interact with its flowers in a way that allowed pollen collection whereas those that robbed *M. ciliata* and *L. vulgaris* did. Why do *C. caseana* robbers have one host for nectar and another for pollen instead of exhibiting host constancy through tactic switches like robbers of *M. ciliata* and *L. vulgaris* do? *L. vulgaris* and *M. ciliata* were observed being legitimately foraged often and successfully whereas *C. caseana* was not. I hypothesize that nectar-robbers of *C. caseana* never carried its pollen because they could not legitimately forage on *C. caseana*. That *C. caseana* apparently could not be legitimately foraged in this system is likely due to a morphological mismatch between *B. bifarius* and *B. mixtus* individuals' short proboscises (*B. bifarius*: 5.8 mm, Pyke et al.

2012; *B. mixtus*: 3.96 mm, Wang, *pers. obs*) and *C. caseana*'s long (26.1 mm, Bronstein, *unpublished data*) corolla. Therefore, a different host had to be selected for the pollen resource.

I hypothesize that pollen-carrying *C. caseana* robbers concurrently switched tactic and host, or were mixed tactic individuals that visited mixed hosts (corresponds with the Green-only box in Table 4). That 80% of pollen-carrying *B. mixtus* robbers of *C. caseana* carried homogenous loads of pollen from *M. ciliata*, an abundant co-flowering species that was frequently seen legitimately foraged suggests that *C. caseana* robbers acquired pollen by switching to legitimately foraging co-flowering species like *M. ciliata* instead.

### Conclusions

Of the six strategies described in Table 1a, I found results consistent with five of them potentially being employed by individuals in this system. Table 1b summarizes the foraging strategies that this study's results were consistent with.

Table 1b: The six different overall strategies an individual bee can theoretically utilize regarding floral host and foraging tactic. Legitimate foraging is abbreviated "LF" and nectar-robbing "NR". One asterisk (\*) indicates strategies the author predicted would be rare while two (\*\*) indicates ones predicted to occur frequently. Bolded are the strategies that actually had signatures in the floral visit observations and pollen load analyses. Greyed out are strategies that were not represented in the data. Note that pure nectar-robbers were indicated by the data, but without any signature for floral constancy.

		Tactical strategy		
		Pure NR	Pure LF	Mixed tactics
Floral Strategy	Constant host	<b>Pure NR on constant host**</b>	<b>Pure LF on constant host**</b>	<b>Mixed tactics on constant host</b>
	Mixed hosts	<b>Pure NR on mixed hosts</b>	Pure LF on mixed hosts	<b>Mixed tactics on mixed hosts *</b>

In this study, I found signals for all three tactical strategies: pure nectar-robbing, pure legitimate foraging, and mixed tactics. I also found signals for both floral strategies: visiting one constant host and visiting mixed hosts.

Tactic switching was found to occur more frequently than I predicted based on the literature. Host switching was rare in legitimate foragers as predicted, but was also rare in *C. caseana* and *M. ciliata* robbers that carried pollen. The finding that robbers do carry pollen, in some cases, as often as legitimate foragers suggests mixed tactic individuals, are at least as frequent as pure legitimate foragers. The not uncommon occurrence of pollen-carrying robbers also suggests mixed tactic individuals are capable of pollinating.

However, host switching occurred with all pollen-carrying nectar-robbers of *C. caseana*. I hypothesize one rule of floral constancy is that a host species is maintained between tactic switches when it is possible for both tactics to be performed on the same host. In

other words, if bees can perform both robbing and legitimate foraging on one host species, it will tend to exclusively visit that host.

I predict that morphological mismatches can constrain foraging strategies by preventing one tactic or another. This was seen with *C. caseana*, where legitimate foraging is suspected to be entirely prevented by floral morphology. Tactic-switchers on a host that can only be robbed are forced to switch host whenever it switches to legitimately foraging.

### Future Directions for Study

Ishii and Kadoya (2016) also observed host switches that corresponded with tactic switches, but interestingly, those host switches did not seem forced by morphological mismatches i.e. the bees were capable of performing both tactics on one species but switched host anyway. Future studies should further investigate how tactic and floral constancy interact with each other. Additionally, it would be interesting to see if the opposite pattern occurs in nature, i.e. a legitimate forager on species A switching to robbing species B because species A cannot be robbed, perhaps due to robbery resistant flower traits (see Irwin et al 2004).

Future studies should also investigate switching rates across different morphologies. For example, in this study, morphology informed whether a host could be legitimately visited and the three species ranged from never experiencing switches from robbing to legitimate foraging (*C. caseana*) to seldom experience this (*L. vulgaris*), to often (*M. ciliata*). These patterns could be explained by looking at corolla lengths and floral entrance dimensions. Though *C. caseana* flowers are shorter than *L. vulgaris* flowers at 26.1 mm from petal to spur tip (Bronstein, *unpublished data*), I observed that their corollas are also narrower, possibly preventing short-tongued bees from pushing as far into the flower as I saw them do with *L. vulgaris*. *M. ciliata* has the shortest corolla (10-17 mm, Pelton 1961) and was probably the most accessible as its visitors almost often carried pollen loads of its pollen.

Raine and Chittka (2007) describe pollen foraging as a complex motor skill that takes significantly more learning investment than nectar foraging and suggest this as a potential reason why bees can be more particular in which species they forage pollen from while being more general with their nectar sources. An interesting new hypothesis to test would be if pure nectar-robbers switch hosts more than pure legitimate foragers because of less discrimination towards potential nectar hosts than pollen hosts. Also, why then do *B. bifarius* and *B. mixtus* nectar-robbers even visit *C. caseana*, if it can only offer nectar and forces host-switching if individuals need to collect pollen? Future studies could explore foraging strategy in the context of the resource quality of different host species (e.g. Francis 2016). Diverse floral morphologies, differential resource needs of a colony, as well as bee species differences should be investigated in future studies to further elucidate the contexts surrounding these foraging strategies.

Unfortunately I did not re-observe enough of the bees I tagged to make longer observations of their overall foraging strategies and directly confirm whether the bolded strategies in Table 1b actually occurred. From Table 3, we see that individuals did in fact exhibit pure robbing on constant and mixed hosts, pure legitimate foraging on constant hosts, and mixed tactics on constant and mixed hosts, but analysis of more bout-long observations is needed.

Longer-period observations would also be pertinent for answering questions of how foraging strategies vary over time (e.g. Russell et al 2017). Individuals Y54 and O27 for example, within a day employed pure robbing, pure legitimate foraging, and mixed tactics. Furthermore, more observations of tactic switches are needed to continue investigating their frequency and determine when they are happening. Do bees sporadically switch throughout a bout or have one long period of one behavior and then make one single switch to the other?

From the phytocentric perspective, whether *B. bifarius* and *B. mixtus* are even pollinating *L. vulgaris* and *M. ciliata* when they legitimately visit would be important for assessing their effects on plant fitness. *Corydalis caseana*'s fitness could also be explored regarding the effects of its pollen never being transferred by these two bee species. Perhaps other species are pollinating despite the high robbery rate as Maloof (2001) found. Yet, though Maloof also studied *C. caseana* at sites near the Rocky Mountain Biological Laboratory, the bee population has likely changed since 2001, with the most common robbing species I saw in 2016 being *B. mixtus*, *B. bifarius*, and *B. flavifrons*, rather than *B. occidentalis*.

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