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Effects of nectar robbing on nectar dynamics and bumblebee foraging strategies in *Linaria vulgaris* (Scrophulariaceae)

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Differences in morphology among bumblebee species sharing a nectar resource may lead to variation in foraging behaviour and efficiency. Less efficient bumblebees might opportunistically switch foraging strategies from legitimate visitation to secondary robbing when hole-biting primary robbers are present. We observed various aspects of pollination and nectar robbing ecology of *Linaria vulgaris* in the Colorado Rocky Mountains, with emphasis on the role of bumblebee proboscis length. Bees can extract nectar from a nectar spur legitimately, by entering the front of the flower, or illegitimately, by biting or reusing holes in the spur. Although *L. vulgaris* flowers are apparently adapted for pollination by long-tongued bees, short-tongued bees visited them legitimately for trace amounts of nectar but switched to secondary robbing in the presence of primary robbers. Longer-tongued bees removed more nectar in less time than did shorter-tongued bees, and were less likely to switch to secondary robbing even when ~100% of flowers had been pierced. As the proportion of robbed flowers in the population increased, the relative number of legitimate visits decreased while the relative number of robbing visits increased. Robbing decreased nectar standing crop and increased the proportion of empty flowers per inflorescence. Despite these potentially detrimental effects of robbers, differences in inflorescence use among robbers and pollinators, and the placement of holes made by primary robbers, may mitigate negative effects of nectar robbing in *L. vulgaris*. We discuss some of the reasons that *L. vulgaris* pollination ecology and growth form might temper the potentially negative effect of nectar robbing.

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Floral adaptations that promote pollen transport by pollinators, which include some of the most striking examples of plant–animal coevolution, are often interpreted as evidence of specialization to a specific pollinator type (Castellanos et al. 2003, 2004). Specialized floral morphology may limit access to nectar and pollen to visitors that effectively transport pollen, by excluding inefficient pollinators. However, specialized flowers are vulnerable to exploitation by parasites of plant–pollinator mutualisms (sensu Mainero and del Rio 1985) that, by removing nectar without pollinating, may have detrimental consequences for plant fitness (Roubik et al. 1985, Irwin and Brody 1998, 1999, 2000, Traveset et al. 1998, Navarro 2001).

Nectar robbers are animals that pierce flowers to obtain nectar, usually without effecting pollination (primary robbing). Other nectar-seeking animals, including corruptible pollinators, can then exploit robber-made holes (secondary robbing). Changes in pollinator behaviour due to nectar robbing may have positive, neutral, or negative effects on plant fitness (Maloof and Inouye 2000, Irwin et al. 2001), although most authors consider

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robbers to be detrimental (Proctor et al. 1996, Yu 2001, Anderson and Midgley 2002, Stanton 2003). Negative effects are typically attributed to pollinator avoidance of robbed plants with reduced nectar rewards (Irwin and Brody 1999, Irwin 2000, Navarro 2001); however, pollinators that switch from legitimate visitation to secondary robbing may be more problematic for plants than pollinator avoidance. For example, bees are unlikely to avoid robbed flowers, as they are not able to discriminate between rewarding and unrewarding flowers without sampling (Maloof and Inouye 2000). Bee-pollinated flowers are therefore likely to receive at least some legitimate visits per bee, provided not all visitors switch to secondary robbing. If bees are numerous, female fitness should not suffer much (Irwin et al. 2001) and male fitness may even increase (Zimmerman and Cook 1985, Richardson 2004, but see Irwin 2003). If avoidance of robbed flowers does not occur, switches to secondary robbing will divert pollinators from serving the plants; this may prove costly to the robbed plants if pollinators in the population are limiting. If avoidance of robbed flowers does occur, secondary robbers will compound its costs by depleting the remaining nectar rewards that could entice less wary pollinators. Despite these potential impacts of nectar robbers on plants, we know of no ecological studies investigating the role of secondary robbers. It is noteworthy that agricultural papers on nectar robbing typically refer not to the problems of pollinator deterrence, but to secondary robbing (Free 1962, 1965, Eaton and Stewart 1969, Poulsen 1973 cited in Goulson 2003, Dedej and Delaplane 2003, 2004). Indeed, Eaton and Stewart (1969, p. 150) were sufficiently alarmed by the rate at which honeybees were abandoning legitimate visitation of *Vaccinium corymbosum* crops to use holes made by *B. occidentalis occidentalis* that they recommended “eliminating this subspecies from areas of highbush blueberry plantings”. Their concerns may have been warranted: Dedej and Delaplane (2004) found that secondary robbing of the related *V. ashei* by honeybees caused significant reductions in seed set and fruit size.

Maloof and Inouye (2000), in the hope of spurring research into finding generalities about nectar robbing, listed four factors that may determine whether its effects are negative, neutral or positive. (1) The identity of the pollinators. Differences among pollinators may cause species to react differentially to the activities of nectar robbers; some may become secondary robbers, others may avoid plants altogether, and others still may not respond at all. A small change in the cost–benefit balance of the interaction – such as the appearance of an easier route to nectar – may cause some visitors to switch from mutualistic pollinators to opportunistic robbers. Therefore, the effects of nectar robbing on plants may depend on how different pollinator species respond to the presence of robbed flowers, on how effective each pollinator is at transporting pollen (Wilson and Thomson 1991, Thomson and Thomson 1992), and on the relative abundances and visitation rates of each of these species (Herrera 1987, Pellmyr and Thompson 1996). For example, if a plant’s most effective pollinator is not deterred from robbed plants and does not become a secondary robber, the fitness effects for the plant will most likely be minimal; on the other hand, if only mediocre or rare pollinators remain, robbed plants will suffer relative to unrobbed neighbours. Even taxonomically similar pollinator species may vary: although some authors have treated bumblebee species as a behaviourally homogeneous group, Goulson et al. (1998) found that species responded differently to floral display size, and cautioned against treating all of them as equivalent despite superficial similarities in foraging behaviour. (2) The amount of nectar that robbers remove is also an important factor in determining the impacts of nectar robbing. Reductions in nectar standing crop can negatively affect plants by discouraging pollinators (Irwin 2000), and increased variability in nectar volume can positively affect plants by promoting outcrossing (Harder and Real 1987, Biernaskie et al. 2002). The effects of nectar robbers on nectar standing crop may also be related to the morphology of the plant’s flowers. In flowers that accumulate nectar at, or close to, the site of nectar production (the nectaries), nectar robbers can easily pierce corollas at that site, and therefore drain all available nectar (e.g. *Ipomopsis aggregata*; Irwin 2000). In flowers whose nectar is presented apart from its production site, as is the case in some spurred flowers (Vogel 1998), primary robbers may face a choice of where to bite holes; they could either pierce flowers near the nectaries to drain nectar as it is produced, or pierce the spurs to obtain nectar accumulation. If primary robbers pierce flowers far from the location of the standing crop, secondary robbers may concentrate on nectar easily accessible from the holes (e.g. the nectaries, or the nectar ducts, Vogel 1998), while legitimate visitors may still obtain nectar from the tip of the spur. Such an effect might reduce the potential negative effects of nectar robbers on nectar standing crop. (3) The plant’s growth form may affect pollinator and robber behaviour in ways that could attenuate or amplify the effects of nectar robbing. Plant with many flowers, rich nectar rewards, or clonal growth may suffer from extensive receipt of self-pollen by pollinators using area-restricted searches (Pyke 1978, Ohashi 2002); nectar robbers, by reducing rewards or by creating increased variability in nectar standing crop, might benefit plants by encouraging pollinators to leave clonal patches. Some plant architectures may also directly influence of nectar robbers and their impacts on plants. The degree of flower congestion on an inflorescence could increase nectar robbers’ handling time, and has been hypothesized to dissuade nectar robbers by making spurs or nectaries difficult to reach (Fogg 1950, Inouye 1983). (4) If alternate nectar resources are abundant, pollinators faced with a nectar-robbed food source can easily switch to other plant species. If such alternatives are scarce, however, they may be forced to remain constant (Irwin et al. 2001), and pollination will not be strongly affected.

In the Colorado Rocky Mountains, we observed a morphologically variable group of bumblebee species foraging on a single, apparently highly specialized, plant species. We paid specific attention to the differences in tongue-length among species and to the role that nectar-robbing bumblebees play in the relationships between a plant, *Linaria vulgaris*, and its pollinators. We used the first three of Maloof and Inouye's (2000) aforementioned factors as guidelines for the following five questions: (1) does the gradual increase in robbing activity in *L. vulgaris* patches over a season affect pollinator and secondary robber assemblages? (2) are shorter-tongued bumblebees most likely to become secondary robbers? (3) does bumblebee foraging efficiency vary among species with different proboscis lengths? (4) how does robbing affect nectar rewards (standing crop) in *L. vulgaris*? and how might these effects affect bumblebee behaviour? and (5) do legitimate and robbing visitors differ in their use of *L. vulgaris* inflorescences?

Methods

Study site and system

We conducted the study between July 24 and August 16, 2003, at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (106°59′15″N; 38°57′30″W; 2900 m). Weather during this period was consistently sunny in the mornings and more or less cloudy in the afternoons; rain was rare and intermittent late in the day, but became increasingly frequent and persistent by the second week of August. In all, we observed plants in ten patches within the town of Gothic; all of these were located in disturbed soils on roadsides or near human housing, and contained between approximately 50 to several thousand individual ramets.

Linaria vulgaris Mill. (Scrophulariaceae) is a long-lived perennial herb introduced to New England in the 1700s, and established in the North American west since at least the early 1900s. It is a noxious weed in pastures and other agricultural lands, due in large part to its aggressive clonal propagation and prolific production of small, winged seeds (Saner et al. 1995). Ramets have several racemose inflorescences with numerous yellow flowers (per inflorescence mean ± SD in this population: 9.45 ± 3.64; n = 155; range = 1–39) that produce nectar at the base of the ovaries, but present it in the end of long spurs (mean ± SD in this population: 13.37 ± 3.04 mm; n = 673). Older flowers are generally found lower on the inflorescence. The vestibular flowers are kept closed, and, as such, limit the availability of nectar rewards to pollinators that are strong enough to pry open the corolla lips (bumblebees and other robust bees). Very small insects, and hummingbirds and hawkmoths whose mouthparts are thin and long enough to fit between the corolla lips can also obtain nectar, although they probably do not pollinate (D. A. Newman, pers. obs.). *Linaria vulgaris* flowers conform to the classic bumblebee syndrome, and authors typically describe them as being adapted to pollination by long-tongued bumblebees, stating that shorter-tongued bees are unable to reach the nectar legitimately (Hill 1909, Proctor et al. 1996, Stout et al. 1998, 2000, Corbet et al. 2001). *Linaria vulgaris* is particularly useful for foraging studies because its nectar spurs are translucent, a feature that allowed us to measure the height of nectar (which correlates strongly with volume; $r_S = 0.98$, $p < 0.01$; Nepi et al. 2002) without removing it or otherwise damaging the plant.

Of nine bumblebee species observed at the RMBL in 2003, five of them were common enough on *L. vulgaris* for inclusion in statistical analyses; of those, only three are included in all experimental and observational studies described below. *Bombus flavifrons* Cresson, a species with an intermediate tongue length (7.3 mm, Pyke 1982; tongue lengths listed here refer only to workers) was the most common. *Bombus bifarius* Cresson, a short-tongued (5.8 mm, Pyke 1982) species and *B. appositus* Cresson, a large long-tongued (10.5 mm, Pyke 1982) species, were also abundant. *Bombus occidentalis* Greene, a large short-tongued (5.7 mm, Pyke 1982) species well known for its ability to rob flowers, was rare early in the season but became more common by the end of July; it does not figure in all studies in this paper due to its rarity in the early summer. *Bombus occidentalis* robs *L. vulgaris* flowers by chewing holes in the spur (Corbet et al. 1981, Stout et al. 1998, 2000, Irwin et al. 2001, Irwin and Maloof 2002). *Bombus californicus* Smith, another large long-tongued species, was only occasionally common, and then only in some sites; like *B. occidentalis*, it does not figure in every study for this reason. These five species are very easy to identify, even in flight, due to marked differences in size and pile colour patterns. Because size variation may be partially responsible for differences in foraging efficiency among species, we measured the radial cell length (Harder 1982) of worker bumblebees of the four species listed above. We measured the radial cell on each bee's right wing with callipers. These bees were either caught wild near the RMBL in 2002 and 2003, or borrowed from the RMBL insect collection.

Study 1. Bumblebee abundances and foraging strategies

On nine sunny days between July 17 and August 14, we haphazardly chose a cluster of five ramets in bloom (i.e. close neighbours), and observed bumblebee activity for five minutes. We repeated this protocol twice a day (once in the mid morning and again in the mid afternoon) at ten sites in the Gothic townsite, except in mid July when only two patches were blooming. During these observation periods, we identified visiting bumblebees to species, and recorded each individual's foraging strategy (legitimate versus robbing).

Study 2. Bumblebee foraging efficiency

Nectar removal and handling time (experimental)
In order to understand why some pollinator species switch to secondary robbing, we compared the foraging efficiency of bumblebee species with different proboscis lengths. We collected inflorescences and kept them in water overnight to allow nectar to accumulate in the spurs. The following day, we cut off flowers until each inflorescence had ten flowers, and individually numbered them with permanent marker. We then measured nectar height in the spurs with a digital calliper. Immediately after this, we put out the inflorescence next to a natural *L. vulgaris* patch, and waited for the first bumblebee visit. We videotaped the visits with a handheld digital video camera in order to measure handling times for individual bees, which we did by watching the video sequences in slow motion (5 × real time). We measured handling time (access time + probing time) from the moment the bumblebee aimed its head downward to open the flower until it pulled out of the flower and groomed its head and thorax (both the starting and ending behaviours are highly stereotypical, and similar across species). After the bee left the inflorescence, we re-measured the height of nectar in the spurs. We conducted this experiment for legitimate visitors, using unrobbed inflorescences, and for robbers using previously robbed inflorescences.

Handling time (observational)
Since we had allowed unusually large amounts of nectar to accumulate in the experiment described above, handling times by bumblebees were artificially long. For a more natural account of handling time differences among species, we also followed wild bumblebees foraging on unmanipulated *L. vulgaris* plants and videotaped them on as many flowers as possible. Later, we viewed the videocassettes and measured handling time as above.

Study 3. Nectar in robbed and unrobbed flowers

Nectar standing crop in robbed and unrobbed flowers
On July 28 and August 2, we randomly collected flowers from *L. vulgaris* in five patches in the townsite of Gothic. We only removed one flower per raceme. We scored each flower as robbed or unrobbed, and measured the height of nectar in the spur. On the morning of August 15, we covered the spurs of 46 haphazardly chosen flowers with the tapered end of disposable micropipette tips, which we stuck on with Minwax™ Polycrylic finish (at this time, we had to actively protect spurs since robbers were biting almost all available flowers). As a sham control, we also glued half-pipette tips onto the spurs of 46 other flowers in a way that would allow robbers to pierce or reuse holes. After six hours, we collected the flowers and measured the nectar height as described above.

Location of bites on robbed flowers
On August 14 and 17, to investigate whether robbers bite holes at specific location on the nectar spur, we excluded bumblebees from several racemes to allow nectar accumulation, measured nectar standing crop and spur length on 100 marked flowers, and placed the inflorescences into natural *L. vulgaris* patches with high bumblebee activity. Four hours later, we collected the marked flowers and measured the location of the robber holes (i.e. the distance between the tip of the spur and the bottom of the hole).

Study 4. Vertical patterns of nectar standing crop and bumblebee behaviour on *L. vulgaris* inflorescences

Bumblebee visitation patterns on inflorescences: location of flower visits on inflorescences
Bumblebee species may visit the vertical inflorescences of *L. vulgaris* differently, with potential consequences to pollen transport and the effects of nectar robbing. On August 12–13, and 15–16, we randomly chose an inflorescence (typically one that had more than 10 flowers) and observed the behaviour of the first bumblebee visitor. We scored the visit as occurring on the bottom, top, or both halves of the inflorescence, and identified the bumblebee species and its foraging strategy.

Bumblebee visitation patterns on inflorescences: effect of flower congestion
Along with the observations above, we scored the flower density in of each inflorescence into three categories: sparse (no overlap between flowers and the spurs of flowers above them), intermediate (some overlap between flowers, but spurs of the upper flowers are

clearly visible), and dense (flowers almost completely hide the spurs of the upper flowers).

Nectar standing crop, nectar accumulation, and flower location on inflorescences

We collected 112 inflorescences between August 3 and 8, and, recording the vertical location of flowers along the inflorescence, measured nectar standing crop and the presence or absence of robber holes. To compare nectar standing crop (which is at least partially determined by the activity of floral visitors) with actual nectar production rates, we also covered patches of inflorescences with metal cages covered with bridal veil (0.5 m in length and width, 1.0 m tall) to prevent bee visitation. Twenty-four hours later, we collected inflorescences and took the same measurements as described above.

Results

Floral visitors

Seven bumblebee species visited *L. vulgaris*. In addition to the five species listed above, we occasionally saw *B. mixtus*, a short-tongued species (all secondarily robbing) and *B. nevadensis*, a long-tongued species (all legitimate except once, by a particularly small worker). In late June 2003, bumblebee numbers were unusually low at the RMBL (N. M. Waser and D. W. Inouye, pers. comm.), but numbers grew rapidly in early July; by late July, bumblebees were so numerous in all *L. vulgaris* patches that we very frequently observed more than one bee per inflorescence. *Anthophora furcata-terminalis* Cresson was an uncommon but regular legitimate visitor throughout the summer. Aside from bumblebees, secondary robbers included ants (*Formica fusca*, *F. lasioides*, *Tapinoma* spp) and unidentified lepidoptera and diptera. Long-tongued bumblebee species (*B. appositus*, *B. californicus* and *B. nevadensis*) only visited legitimately, with a single aforementioned exception. We never saw *B. occidentalis* visiting legitimately.

Bumblebee species collected at Gothic, Colorado, varied significantly in radial cell length (Kruskal–Wallis test for workers only: $H = 42.167$, $df = 3$, $p < 0.0001$, Fig. 1). Larger species, with the exception of *B. occidentalis*, have longer tongues.

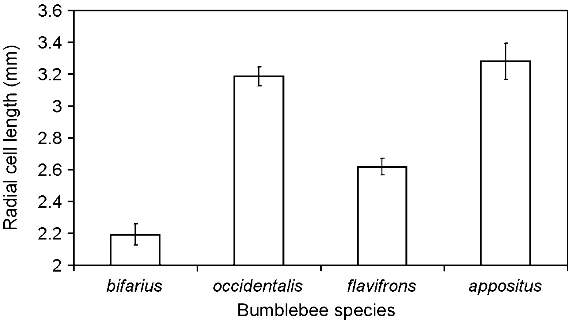

Fig. 1. Radial cell length differences among the four common bumblebees species used in this study. *Bombus bifarius* and *B. occidentalis* have short proboscides, *B. flavifrons* has an intermediate proboscis length, and *B. appositus* has a long proboscis. *Bombus californicus* is excluded due to lack of specimens available for measurement.

Study 1. Bumblebee species abundances and foraging strategies

Before *B. occidentalis* began foraging on *L. vulgaris* around July 24, all flower visits to the plant were legitimate. *Bombus flavifrons* and *B. appositus* made most of these visits, although the short-tongued *B. bifarius* was also quite common (Fig. 2a). Only a few days after we observed the first nectar robbers, some bees had already begun to secondarily rob (Fig. 2b). By the second week of August, secondarily robbing *B. flavifrons* and *B. bifarius* were making almost all of the observed visits, although a small proportion of individuals from both species remained legitimate throughout the study. *Bombus occidentalis*, although active enough to pierce nearly 100% of the flowers at

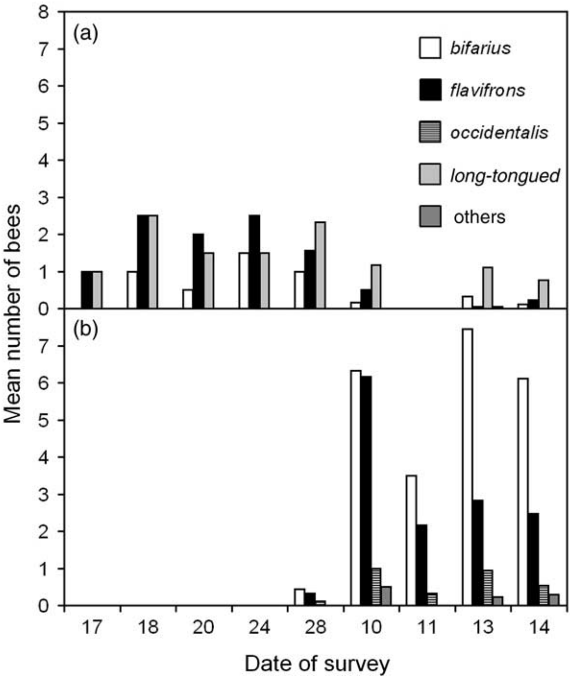

Fig. 2. Mean number of (a) legitimately visiting and (b) primary and secondary robbing bumblebees during five-minute observations of *L. vulgaris* patches. Dates refer to days in July and August 2003; note that this axis is not to scale. *B. appositus* and *B. californicus* are shown together under "long-tongued", although *B. appositus* represents the great majority of observations in this category. The "others" category includes rare bumblebees (*B. mixtus*, *B. nevadensis*) and non-*Bombus* insects.

the RMBL, only made up a small proportion of the total observed visits to *L. vulgaris*. Although all bumblebee populations increased throughout the summer, the absolute number of legitimate visits by all species did not increase significantly ($r_S = 0.330$, $p = 0.368$, $n = 9$), and the proportion of legitimate visits by all species declined significantly ($r_S = -0.905$, $p = 0.0008$, $n = 9$), as did the proportion of visits by long-tongued species ($r_S = -0.867$, $p = 0.002$, $n = 9$; most of these are *B. appositus*).

Study 2. Foraging efficiency of bumblebee species

The long-tongued *B. appositus* was much more efficient than the other species in both handling time and nectar removal (Table 1). *Bombus flavifrons* was intermediately efficient. *Bombus bifarius* workers have such short proboscides that they could very rarely reach the nectar standing crop legitimately; therefore the nectar removal data appear to show zero reward for this species. However, these workers licked the back of spurs along the duct that channels nectar (Vogel 1998), and were still getting a small, if immeasurable, reward. Although some *B. flavifrons* workers could reach up to half of the available standing crop, others only licked the nectar duct. Similarly, all three species of primary and secondary robbers did not drink from the nectar standing crop while robbing, but licked upward along the nectar duct to probe the base of the ovary where the nectaries are located (Fig. 3). Very few robbers visited the inflorescences that we set out for them; this is puzzling, because robbers were much more common than legitimate visitors at the time of the experiment.

Study 3. Effects of robbing on nectar standing crop

Nectar standing crop in robbed and unrobbed flowers

Out of 68 flowers randomly collected on July 28, 38 (56%) were robbed. Unrobbed flowers contained significantly more nectar than robbed flowers (mean ± SE: 1.182 ± 0.303 mm and 0.632 ± 0.222 mm, respectively; Mann–Whitney U test; $Z = 2.379$, $p = 0.017$), and were significantly more likely to contain at least some nectar ($\chi^2 = 15.583$, $df = 1$, $p = 0.017$). Every one of the 135 flowers collected on August 2 was robbed, and therefore no nectar comparison was possible. Out of 46 "sham-protected" flowers on August 15, 45 (98%) were robbed after six hours. In this case, flowers that we had protected from robbers had significantly more nectar than those whose spurs were only partly covered by pipette tips (mean ± SE: 1.13 ± 0.227 mm and 0.319 ± 0.070 mm, respectively; Mann–Whitney U test; $Z = 2.067$, $p = 0.039$).

Location of bites on robbed flowers

In unmanipulated flowers, most of the holes made by *B. occidentalis* were located just below the level of the ovary, and therefore any nectar in the spurs was out of tongue's reach for most visitors; indeed, almost all primary and secondary robbing visits involved bees licking upwards along the back of the spur (in the "nectar duct", Vogel 1998; Fig. 3a). *Bombus flavifrons* workers occasionally licked downwards into the spur, and their relatively long proboscides could probably reach some of the standing crop.

Out of the 100 flowers that we left out for four hours, 98 were robbed. The locations of holes relative to the height of nectar in the spurs suggest that *B. occidentalis* makes a decision of where to bite based on the nectar

Table 1. Differences in foraging behaviours and efficiency among three bumblebee species visiting *Linaria vulgaris*, using legitimate (L) and robbing (R) strategies. Means and standard errors are shown. Analyses are Kruskal–Wallis H tests. Unsuccessful visits occurred when bees attempted to open flowers, but could not. *Bombus occidentalis* and *B. californicus* visited too rarely to be included in analyses. Sample sizes in the experimental study are: *B. bifarius* (L = 5, R = 5), *B. flavifrons* (L = 34, R = 3) and *B. appositus* (L = 22). In the observational study (*), sample sizes are: *B. bifarius* (L = 8, R = 22), *B. flavifrons* (L = 9, R = 13) and *B. appositus* (L = 19).

Variable	Strategy	*bifarius*	*flavifrons*	*appositus*	H	p
Access time (s)*	L	2.94 (0.45)	3.01 (0.30)	2.05 (0.25)	8.324	0.015
	R	1.76 (0.26)	1.47 (0.35)	–	1.593	0.451
Access time (s)	L	9.07 (2.10)	9.28 (1.11)	4.91 (0.61)	12.31	0.002
	R	2.57 (0.26)	4.35 (2.37)	–	0.125	0.724
Flowers visited	L	3.33 (0.49)	6.47 (0.87)	7.81 (1.03)	4.716	0.095
	R	3.50 (0.65)	7.00 (4.51)	–	0	–
Unsuccessful visits	L	1.33 (0.62)	0.73 (0.19)	0.10 (0.07)	9.653	0.080
	R	0.50 (0.29)	0 (0)	–	1.800	0.180
Nectar removal (0.1 mm)	L	0.43 (0.04)	32.80 (8.50)	147.34 (28.35)	18.80	<0.001
	R	3.08 (2.30)	0.24 (0.12)	–	1.559	0.212
Foraging efficiency**	L	0.07 (0.04)	3.62 (0.93)	30.49 (4.84)	23.64	<0.001
	R	1.06 (0.70)	0.06 (0.04)	–	1.559	0.212

*Results from bumblebees visiting natural *L. vulgaris* inflorescences (study 1 – observational). All other results are from the experimental runs with manipulated inflorescences (study 2-experimental). Sample sizes for this experiment are shown in superscript after the standard errors.

**Foraging efficiency = (nectar removal)/(handling time).

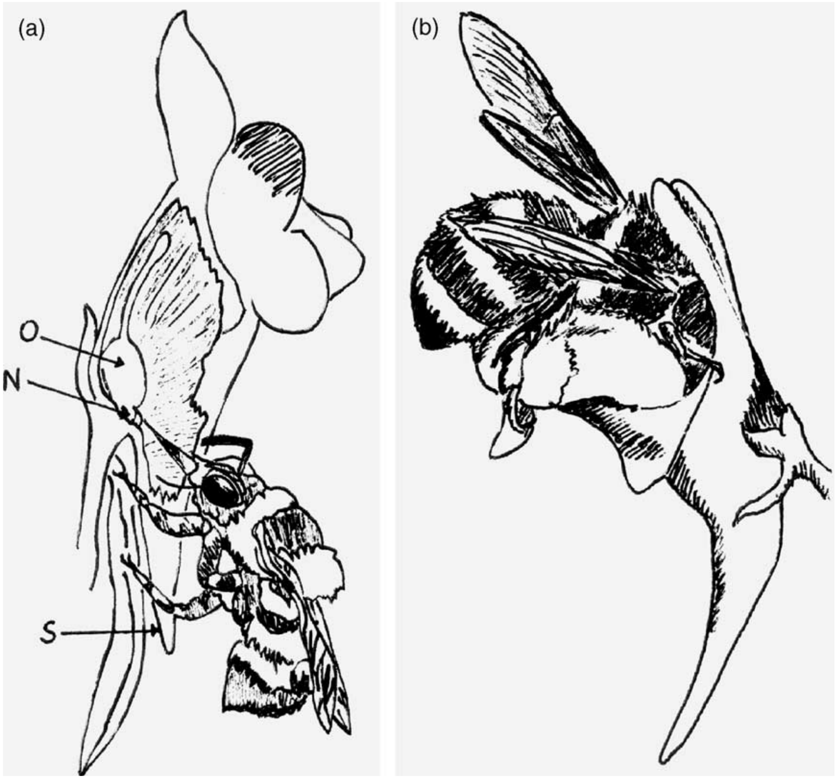

Fig. 3. (a) *Bombus bifarius* worker licking the nectary (N) at the base of a *Linaria vulgaris* ovary (O) (flower is shown in partial cross-section) through a hole made by *B. occidentalis* near the ovary; the nectar standing crop is in the bottom of the nectar spur (S) where secondary robbers cannot reach it. (b) *Bombus flavifrons* probing nectar legitimately from *L. vulgaris.* The bee uses its weight and sometimes, as is illustrated here, its foreleg to hold the flower lips open. Drawings by D. A. Newman adapted from photographs by D. A. Newman.

standing crop. The location of the bite along the spur was negatively correlated with the original level of nectar in the spur ($r_S = -0.467$, $n = 98$, $p < 0.00001$); in flowers with small quantities of nectar, primary robbers bit the upper part of spurs, far from the standing crop. In flowers with greater quantities of nectar, robbers bit holes lower on the spurs, within reach of the standing crop. This result corroborates our observations that robbers drink from the accumulated nectar when standing crop is high, but directly from the nectaries at the base of the ovaries when it is low. Robbers rarely made holes lower than halfway down the spur; only 12.6% of holes were below the middle of the spur, despite the presence of collected nectar in the tip. There was no apparent sidedness to the location of holes; most were either double slits (one on the right and one of the left sides of the spur) or single holes in the centre of the spur.

Study 4. Inflorescence partitioning among bumblebee species, and its effects on nectar dynamics

Bumblebee visitation patterns on inflorescences: location of flower visits on inflorescences

Bumblebee species visited *L. vulgaris* inflorescences differently (Fig. 4). Smaller species (*B. bifarius* and *B. flavifrons*), those most likely to be secondary robbers, visited primarily the bottom half of inflorescences, while the opposite was true for the larger, long-tongued, and exclusively legitimate, species (*B. appositus* and *B. californicus*). Long-tongued bees were more likely than short- and intermediate-tongued bees to visit the top half of the raceme ($\chi^2 = 54.86$, $df = 2$, $p < 0.000001$). Short- and intermediate-tongued bees did not visit inflorescences differently ($\chi^2 = 1.587$, $df = 1$, $p = 0.208$). *Bombus occidentalis* tended to prefer the bottom half

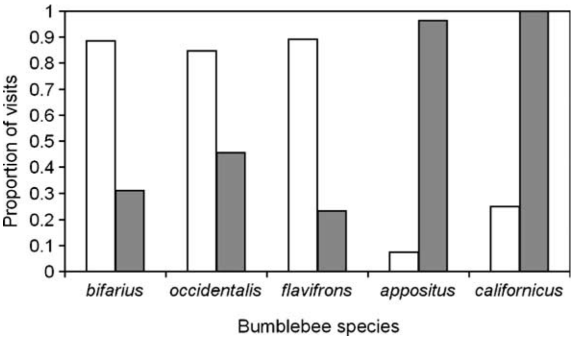

Fig. 4. Proportion of visits by five bumblebee species to the lower (white bars) and upper (grey bars) flowers on *L. vulgaris* inflorescences. Species are arranged from short-tongued on the left to long-tongued on the right. Some proportions exceed 100% because some individuals visited both lower and upper halves of the inflorescences.

of the inflorescence, although less so than the smaller species ($\chi^2 = 3.429$, df = 1, p = 0.064), and most often visited both top and bottom halves. Regardless of species, robbing individuals were more likely to visit the bottom half of inflorescences while the opposite was the case for legitimate visitors ($\chi^2 = 48.86$, df = 1, $p < 0.000001$). Unlike Corbet et al. (1981), we saw no robbers working upside-down on the inflorescences.

Bumblebee visitation patterns on inflorescences: effect of flower congestion

Flower congestion significantly affected inflorescence use by nectar robbers. Robbers only visited upper flowers on dense inflorescences in 5.26% of the observations, compared to 16.27% in intermediate and 25.0% in sparse inflorescences ($\chi^2 = 6.40$, df = 2, p = 0.041). There was no such effect for legitimate visitors ($\chi^2 = 0.220$, df = 2, p = 0.896).

Nectar standing crop, nectar accumulation, and flower location on inflorescences

Empty flowers were frequent and flowers with nectar occurred along the entire length of the inflorescence. However, nectar standing crop was significantly higher in the upper half of the inflorescences, and significantly more flowers in the lower half were empty (Table 2). In addition, significantly more flowers in the lower half of the inflorescences were robbed than in the top half (Table 2). In contrast, in the 24-hour nectar accumulation treatment, there were no differences in either nectar accumulation or in percent empty flowers between the bottom and top halves of inflorescences. Not surprisingly, the significant difference in percent robbed flowers between the lower and upper flowers remained (Table 2).

Discussion

Nectar robbing in *Linaria vulgaris* significantly reduced nectar standing crop and visitation rates by legitimate pollinators. These changes might imply that robbing has negative fitness consequences for the plant (Maloof and Inouye 2000), but two European (Stout et al. 2000, Nepi et al. 2002) and one North American (Irwin and Maloof 2002) studies on the effects of nectar robbing on female fitness on *L. vulgaris* have found no reductions in seed set. This ability to tolerate the potentially damaging effects of nectar robbing may be due to aspects of its growth form and to primary robber behaviour. In this study, we found that inflorescence structure and patterns of flower maturation, as well as the spatial separation of nectar accumulation from the nectaries, might act as 'tolerance traits' that neutralize the impacts of nectar robbing.

Robbed flowers had less nectar than unrobbed flowers under both natural and experimental conditions. This finding is consistent with Stout et al. (2000) for the same plant species in England, although the differences they found were not significant due to high variability in nectar standing crop. We, like Stout et al. (2000), also found that robbed flowers were more often empty than unrobbed flowers. Most flowers in the population were robbed, but it is conceivable that local patches unaffected by robbers might benefit from higher nectar standing crops, and increased legitimate visitation, than those of other plants (Irwin and Brody 1998, 1999, 2000).

Primary robbers might be considered "resource engineers" that make a food source available or easier to obtain to other species. As *B. occidentalis* workers pierced an increasing number of flowers in the population, secondary robbing made up a greater number and proportion of the total visits to *L. vulgaris*. Indeed, even if it is faster and easier than visiting legitimately, secondary robbing will only be worthwhile if individuals

Table 2. Results from Wilcoxon matched pairs tests comparing the lower and upper halves of *Linaria vulgaris* inflorescences in nectar standing crop and nectar accumulation variables. Nectar standing crops were measured immediately after unmanipulated inflorescences were collected. Nectar accumulation was measured after 24 hour pollinator exclusions. Note that since the standing crop and accumulation data were collected from different plants, dates, and patches, standing crop and accumulation values should not be compared quantitatively.

	Variable	Inflorescence location	Mean (SE)	Z-value	n	p-value
Standing crop	nectar height (mm)	bottom half	0.36 (0.05)	7.62	112	<0.00001
		top half	0.93 (0.08)			
	% empty flowers	bottom half	67.99 (2.41)	6.72	112	<0.00001
		top half	45.70 (2.314)			
	% robbed flowers	bottom half	98.32 (0.62)	3.33	112	<0.001
		top half	94.42 (1.31)			
Accumulation	nectar height	bottom half	0.576 (0.064)	0.69	31	0.491
		top half	0.506 (0.053)			
	% empty flowers	bottom half	59.87 (15.79)	0.26	31	0.795
		top half	60.87 (16.82)			
	% robbed flowers	bottom half	100.0 (0.0)	2.95	31	0.003
		top half	92.009 (2.218)			

do not have to waste much time seeking flowers with holes (Inouye 1983). Secondarily robbing bumblebees appear to find holes in nectar spurs while crawling from flower to flower on racemes; following the discovery, there is a period during which individuals alternate between visiting legitimately and illegally (D. A. Newman, pers. obs.). Provided there are enough holes in flowers, secondary robbing seems to become a fixed strategy for most individuals. In a flight cage experiment, short-tongued *B. rufocinctus* workers trained to visit *L. vulgaris* legitimately quickly (within one or two foraging trips) switched to secondary robbing, but then resisted switching back to legitimate visitation when we removed robbed plants. Instead, individuals flew around inflorescences for several minutes, presumably to look for holes, before returning to the colony, and only switched back to legitimate visitation after more than 24 hours (D. A. Newman, pers. obs.). Not far from the RMBL, *B. bifarius* and *B. flavifrons* workers only began to secondarily rob *Penstemon strictus* when the frequency of robbed flowers approached 100% (K. Ohashi, pers. comm.).

Bumblebee species used *L. vulgaris* inflorescences differently. Secondary robbers preferentially used the lower half of inflorescences while legitimate visitors used the top half. This is likely due to the increased probability that older flowers, which are located lower on the inflorescences, will have been pierced by *B. occidentalis* (Corbet et al. 1981), and perhaps because lower flowers (whose spurs are exposed) are easier to rob when inflorescences are congested. While almost all of the flowers in the population we studied were robbed, flowers in the top half of inflorescences were more likely to be unrobbed, and had more nectar than flowers on the bottom half. Young flowers, whose corollas were not yet fully developed, had more nectar on average than mature flowers, although the difference was not significant, and were less often robbed than their mature counterparts ($\chi^2 = 18.331$, df = 1, $p < 0.0001$). *Bombus appositus* and occasionally *B. flavifrons* preferred these younger flowers, spending considerable amounts of time trying, often unsuccessfully, to open them. The partitioning of flower use among bumblebees using different foraging strategies may reduce or neutralize potential negative effects of nectar robbing. *Linaria vulgaris* flowers begin anthesis before they open (Corbet et al. 1981), and most anthers in the open flowers we observed were already empty (D. A. Newman, pers. obs.). Therefore, if legitimate pollinators are visiting mostly young flowers on the upper end of inflorescences, they are likely importing enough outcross pollen to guarantee full seed set, and exporting all of the pollen produced by individual flowers, even before primary robbers have attacked all of the flowers on the plant, or before secondary robbers have the time to deplete nectar rewards. Although not a defensive trait, the *L. vulgaris* inflorescence arrangement, in combination with its patterns of flower development and anthesis, might act as a tolerance mechanism that reduces or eliminates any detrimental effect of nectar robbers. *Linaria vulgaris* appears to keep its older (lower) flowers long after they are useful for reproduction. It is likely that such a pattern of flower longevity might benefit the plant by increasing attractiveness to pollinators, as Ishii and Sakai (2001) showed in *Narthecium asiaticum*. This characteristic has the additional benefit of keeping most robbing visits away from the younger flowers.

Our observations of wild bees also suggested that the degree of flower congestion along an inflorescence (mean ± SD in this population $= 3.00 \pm 0.869$ flowers per cm; range = 1.05 to 5.94) might also reduce the impact of secondary robbing by making the spurs difficult to reach; although the robust *B. occidentalis* can pry flowers apart to bite the spurs, the smaller *B. bifarius* and *B. flavifrons* appeared to put considerable effort into reaching them, and often left inflorescences after several unsuccessful attempts. The disproportionate preference by secondary robbers for lower flowers in dense inflorescences supports this observation. Although the notion that congested inflorescences might act as protection from nectar robbers is not new (Fogg 1950, Inouye 1983), these are to our knowledge the first reported observations and results supporting the possibility that such protection might occur in the field. Variation in flower congestion among plants within and among patches may make some plants less vulnerable to primary or secondary robbing.

Due to the location of the holes in most spurs (Fig. 3), most short-tongued bees (*B. bifarius*, *B. occidentalis* and even *B. flavifrons*) did not reach the nectar standing crop even when they robbed; instead, they usually probed upwards along the back of the nectar duct to the nectaries. The location of holes far from the site of nectar collection allowed any accumulation (i.e. in the morning, or after a day with low bumblebee activity) to be effectively “reserved” for legitimate long-tongued visitors. When visitation was low or artificially prevented, and nectar was allowed to accumulate, primary robbers made their holes lower on the spurs, and were able to drain flowers completely. *Bombus occidentalis* workers probably find it difficult to bite holes near the tapered ends of nectar spurs. Therefore, it appears that the abundance of legitimate visitors can influence the robbers’ choice of where to make holes in the flower. If legitimate visitors are common, and are able to keep nectar standing crops low, robbers appear to prefer making holes closer to the nectaries; therefore any residual nectar accumulation is protected from secondary robbers and more legitimate visits are likely. As mentioned above, reductions in nectar standing crop due to robbing are expected to affect plants negatively (Maloof and Inouye 2000). However, we found that as long as nectar standing crop was low, *B. occidentalis* made holes closer to the nectaries, and therefore left nectar in the spur where only long-tongued pollinators could reach it. This behaviour by hole-biting bees, in plants with separate nectar production and nectar storage sites, may reduce the likelihood that a flower will be completely empty unless it has just been visited by a legitimate visitor; it is likely that long-tongued bees will continue to visit flowers that contain some nectar. Although primary and secondary robbers might severely or completely stem the flow of nectar into *L. vulgaris*' spurs on a daily basis, resulting in a higher percentage of empty flowers following nectar depletion by a long-tongued visitor, continuous nectar production would replenish a standing crop in each flower overnight, thereby increasing its odds of successful pollen deposition and removal.

Bumblebee species varied in foraging efficiency on *L. vulgaris* flowers. The larger long-tongued species could open flowers more rapidly, and removed a much greater volume of nectar than their shorter-tongued counterparts. Shorter-tongued bees removed only trace amounts of nectar by visiting flowers legitimately, and often could not reach the standing crop. Pollinating bumblebee species also differed in their preference for secondary robbing; shorter-tongued species, less efficient legitimate visitors than longer-tongued species, were more likely to exploit the holes made by *B. occidentalis*. Bees with longer tongues can reach more of the available nectar, so that their absolute reward is greater; in addition, manoeuvring a long proboscis into a small hole may make secondary robbing difficult or impossible for long-tongued species (Ranta and Lundberg 1980, Plowright and Plowright 1997). Furthermore, since longer-tongued bees are also generally larger (Heinrich 1976, Harder 1983), obtaining nectar legitimately is easier for these species, probably because their weight aids in opening the flower. A plausible consequence of this advantage is a more stereotypical visitation technique relative to smaller species, which could result in more precise pollen transfer from anthers to the stigmas of other flowers.

Nectar robbers may radically alter the relationship between *L. vulgaris* and its visitors because they provide a new route to the nectar. Shorter-tongued bees will thus find their access to the nectar made easier. Short-tongued bees most likely benefit, since nectar is easier to obtain in the presence of holes. Long-tongued bees probably suffer from increased competition with a larger community of nectar foragers due to robbing (Mainero and del Rio 1985, Irwin and Brody 1998). In the presence of holes, it is in the best interest of short-tongued bumblebees to switch to secondary robbing, provided the frequency of holes is high enough to make the strategy sustainable. The reason that some *B. bifarius* visited *L. vulgaris* legitimately despite the presence of holes is most likely that they were collecting pollen (Macior 1967), either exclusively or in addition to nectar. *Bombus flavifrons* observed preference for secondary robbing is puzzling in light of our foraging efficiency measurements (Table 1). However, despite the apparent trade off between handling time and reward that bumblebees, especially *B. flavifrons*, face when they secondarily rob instead of visiting legitimately, cheating probably has other benefits that we did not measure. An unmeasured energetic cost incurred by *B. flavifrons* visiting *L. vulgaris* legitimately probably accounts for the species' preference for secondary robbing. Indeed, it is commonly assumed that bees expend much less energy by robbing than by opening closed flowers (Macior 1966, Inouye 1983), and this seems apparent based on our observations of smaller bees struggling to enter *L. vulgaris* flowers.

The nectar robbing literature concentrates on the effects of nectar-parasitism on plant fitness. However, results have proved so variable among systems that conclusions about the phenomenon elude generalization. In *L. vulgaris*, nectar robbing is apparently not detrimental (Stout et al. 2000, Irwin and Maloof 2002, Nepi et al. 2002), despite reductions in nectar standing crop and in legitimate pollinator visitation. Most of the reduction in legitimate visitation in this study appeared to result from pollinators switching to secondary robbing. In a year or area with a small long-tongued bumblebee population, it is likely that nectar robbing would have more severe effects, since most pollinators visiting *L. vulgaris* would be short-tongued and therefore prone to switch to robbing.

Our findings point towards some of the plant traits that may mitigate the effects of nectar robbing. Plants with racemose inflorescences whose flowers mature along the vertical axis, and whose female and male functions are easily fulfilled (*L. vulgaris* has sticky pollen that is very effectively picked up in large quantities by bumblebees), may not suffer from the pollen limitation associated with nectar robbing, as do some other species (e.g. *Ipomopsis aggregata*; Irwin and Brody 1998, 1999, 2000). Spatial separation of nectaries from the site of nectar accumulation, found in several plant families (e.g. Scrophulariaceae, Violaceae, Solanaceae, Alliaceae, among others; Vogel 1998), might also help plants tolerate nectar robbing if it prevents robbers from completely draining the flowers they attack. Although it may be impossible to find generalizations about the impacts of nectar robbers on plants, identifying traits such as these may help determine in what plant species to expect negative or neutral effects of nectar robbing.

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