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Nectar robbing, forager efficiency and seed set: Bumblebees foraging on the self incompatible plant *Linaria vulgaris* (Scrophulariaceae)

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Abstract — In southern England, *Linaria vulgaris* (common yellow toadflax) suffers from high rates of nectar robbery by bumblebees. In a wild population of *L. vulgaris* we found that 96 % of open flowers were robbed. Five species of bumblebee were observed foraging on these flowers, although short-tongued species (*Bombus lapidarius, B. lucorum* and *B. terrestris*) robbed nectar whilst longer-tongued ones behaved as legitimate pollinators (*B. hortorum* and *B. pascuorum*). Nectar rewards were highly variable; on average there was less nectar in robbed than in unrobbed flowers, but this difference was not statistically significant. The proportion of flowers containing no nectar was significantly higher for robbed flowers compared with unrobbed flowers. Secondary robbers and legitimate pollinators had similar handling times on flowers and, assuming they select flowers at random to forage on, received approximately the same nectar profit per minute, largely because most flowers had been robbed. There was no significant difference in the number of seeds in pods of robbed flowers and in pods of flowers that were artificially protected against robbing. However, more of the robbed flowers set at least some seed than the unrobbed flowers, possibly as a consequence of the experimental manipulation. We suggest that nectar robbing has little effect on plant fecundity because legitimate foragers are present in the population, and that seed predation and seed abortion after fertilization may be more important factors in limiting seed production in this species. © 2000 Éditions scientifiques et médicales Elsevier SAS

***Bombus* spp. / pollination / nectar rewards / corolla perforation / secondary robbers / foraging behaviour / common toadflax**

1. INTRODUCTION

Plants which offer rewards to their pollinators have often evolved specific adaptations to ensure that only pollinating animals can receive this food. In particular, many have evolved a floral structure which attempts to limit access to visitors which will effectively transport pollen [7, 14, 15, 25, 32]. Nevertheless flowers are often exploited by animals that collect the rewards (usually nectar) without contacting the plant's reproductive structures. Hummingbirds, ants, wasps and bees have all been reported to obtain nectar from flowers in this way [13, 27, 28, 30, 31].

Three foraging strategies enable foragers to collect nectar rewards without effecting pollination. First, foragers can obtain nectar from polypetalous flowers by pushing in between the petals at the base of the flower corollas and by-passing the reproductive structures of the flower ('base foragers'). Honeybees (*Apis mellifera* L., Hymenoptera, Apidae) and bumblebees (*Bombus* spp. Latreille, Hymenoptera, Apidae) sometimes forage at the base of flowers as part of their mixed foraging strategies [12]. Second, a mismatch of morphologies may allow foragers to collect rewards without contacting the androecium and/or the gynoecium ('nectar thieves'). For example, common alpine ants of Colorado (*Formica neorubfibarbus gelida* Wheeler, Hymenoptera, Formicidae) take nectar from flowers which are adapted for bumblebee visitation [13]. Finally, some animals make holes in sympetalous flower corollas to allow direct access to the nectaries ('nectar robbers') [16]. Nectar robbers are either primary robbers (individuals which actually make holes in the flower corolla by piercing or biting) or secondary robbers (individuals which use the holes made by primary nectar robbers). If flowers have previously been robbed, primary nectar robbers may re-use holes and act as secondary robbers.

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Bumblebees are common nectar robbers of many flower species in both Europe and North America [17]. In southern England *Bombus terrestris* (L.) and *B. lucorum* (L.) are common primary robbers whilst *B. lapidarius* (L.), *B. pratorum* (L.) and *B. pascuorum* (Scopoli) sometimes secondarily rob [11]. All of these robbing species have relatively short tongue lengths, with the exception of *B. pascuorum* which has an intermediate tongue length, and are thus unable to reach nectar in flowers with a deep corolla by foraging legitimately. The species with the longest tongue in southern England, *B. hortorum* (L.), is rarely seen to rob nectar from flowers [4].

The impact of nectar robbing on plant fecundity has been assessed in various tropical and temperate plant species. Some plants may actually benefit from the activity of nectar robbers since legitimate foragers are forced to make more long-distance flights, hence increasing genetic variability through outcrossing [33]. Conversely, nectar robbers may have a detrimental effect on seed set in the plants they visit [10]. Robbers reduce the amount of reward available to pollinators which may result in decreased visitation rates by pollinators [22] and a reduction in seed set [18, 28, 29]. Robbers can also damage floral tissues and thus prevent seed production [13]. However, nectar robbing may have little influence on plant fecundity if nectar robbers also collect pollen and in doing so effect pollination [20, 23, 31] or if other pollinators are present [1, 24].

It is difficult to generalize on the effects nectar robbers have on plants in different systems. Many factors, including the breeding biology of the plant, the foraging strategy of the robber and the abundance and efficiency of the pollinator, affect the impact that nectar robbing has on the plant-pollinator system. In this study, we quantify the frequency with which flowers are robbed, and the effects of bumblebee nectar robbers on the self-sterile perennial herb *Linaria vulgaris* Mill. (Scrophulariaceae) (common yellow toadflax). *L. vulgaris* produces medium sized (15–25 mm) zygomorphic flowers which, to human vision, have a yellow corolla, with a bright orange projecting palette on the lower lip which completely closes the tube [5]. Each flower has a long spur (15–20 mm) in which large amounts of sucrose-rich nectar collects [2]. Hence, only long-tongued bumblebees can collect the nectar if they enter the flower through the top of the corolla tube, but short-tongued bumblebees can rob the nectar through holes bitten into the spur of the flowers. Since *L. vulgaris* flowers are nototribic (pollen is brushed onto the dorsal side of the pollinator as it enters the flower and probes for nectar [21]), nectar robbers do not collect or deposit pollen. Also, robbers deplete the amount of nectar available to legitimate foragers, perhaps forcing them to change their foraging behaviour. Legitimate foragers are defined in this case as visitors which enter the flower in such a way that pollen is deposited and collected.

We investigated the following hypotheses: a) that bumblebee species with long tongues visit flowers in the legitimate manner, while short-tongued species are restricted to nectar robbing; b) that foraging methods differ in their efficiency; c) that flowers which have not been robbed contain more nectar than flowers which have been robbed; d) that robbing is costly to the plant, rendering flowers less attractive to legitimate foragers and so leading to a reduction in seed set.

2. MATERIALS AND METHODS

L. vulgaris plants were studied in a wild flower meadow near Broughton Down, Stockbridge, Hampshire, UK. An area of approximately 100 × 400 m contained 308 naturally occurring *L. vulgaris* plants.

2.1. Proportion of flowers robbed

One hundred and fifty inflorescences were randomly selected on three different days (27 July, 6 and 14 August, fifty inflorescences per day). For all flowers on these inflorescences we recorded whether they were open or closed (buds), and whether they had been robbed or not. Small holes in the flower corolla indicated that flowers had previously been robbed, and although flowers often had more than one hole in the spur only the presence or absence of holes was noted. We tested for differences between dates in the proportions of flowers which were robbed using a Chi-squared test.

2.2. Nectar rewards

Nectar was sampled from forty robbed and twenty unrobbed flowers on 28 July and from thirty-six robbed and five unrobbed flowers on 14 August. All flowers were from different plants. Nectar was only sampled from open flowers, in order to exclude age effects. Nectar samples were taken at noon on both days which were warm (25 °C) and sunny. Nectar was extracted using a drawn-out microcapillary tube and was blotted onto filter paper [9]. The area of the blot was measured and compared with a calibration curve constructed using known volumes of sucrose solution (volume (μL) = area (mm)/15.02, $R^2 = 0.98$). Mean nectar volumes per robbed flower were compared for the two sampling dates using a *t*-test. Similarly, mean nectar volumes in unrobbed flowers were also compared for the two sampling dates. As the mean nectar volume per flower was not significantly different on each date for either robbed ($t_{74} = 1.24$, $P = 0.22$) or unrobbed ($t_{23} = 0.13$, $P = 0.89$) flowers, the data for the two dates were pooled. Mean nectar rewards were then compared for robbed and unrobbed flowers using a *t*-test. Separate analyses were performed rather than a two-factor ANOVA because sample sizes were not balanced among treatments. The number of flowers containing no nectar was compared for robbed and unrobbed flowers using a Chi-squared test with Yate's correction.

2.3. Bumblebee visits

On 7 d between 27 July and 21 August 1998, between 11.00 and 15.00 hours, we observed ninety individual bumblebee foraging bouts (34 *B. terrestris*, 25 *B. pascuorum*, sixteen *B. lapidarius*, thirteen *B. lucorum* and two *B. hortorum*) on *L. vulgaris*. Bees were selected opportunistically, so the numbers of bees of each species closely represents the relative abundance of each species at the time of the investigation. It is almost impossible to reliably distinguish between *B. terrestris* and *B. lucorum* workers in the field with certainty, but the majority can be discerned by the colour of the hairs on the tip of the abdomen. It is possible that some individuals identified as *B. terrestris* may actually have been *B. lucorum* and vice versa.

Individual bumblebees were followed for fifty *L. vulgaris* flower visits or until they were lost (the minimum foraging bout recorded consisted of three flower visits). It was noted for each flower visit whether bees visited the flowers legally, were primary robbers, were secondarily robbing or were doing both (i.e. robbing and legally visiting the same flower). The time taken by each individual to visit all flowers was also noted. Individual bees were not marked (to minimize the effects we had on the bees' behaviour) and so it is possible that the same individuals were observed more than once. Observations were alternated between species and were taken at a range of sites within the study area to minimize the likelihood of reobservation.

For each individual bee, the number of flowers visited using each foraging method (primary robbing, secondary robbing, legal visits or both) was examined as a proportion of the total number of flowers visited by that individual bee. Since data were proportional, they were analysed with binomial errors in GLIM according to bee species. As the ratio of residual deviance to the residual degrees of freedom was less than 1.5, the test statistics given are χ^2 values [6]. The two *B. hortorum* individuals were not included in the analysis.

2.4. Expected profit per unit time

Individual bees that only employed one method of foraging (53 bees) were used to measure the average number of flowers visited per minute. Only legitimate visits made by *B. pascuorum* ($n = 16$) and secondary robbing visits made by *B. lapidarius* ($n = 15$), *B. lucorum* ($n = 10$) and *B. terrestris* ($n = 12$) were considered. The total number of flowers visited per individual was divided by the total amount of time taken to visit them (including travel time). Robbers occasionally landed on unrobbed flowers; these were not counted as visits since the bees were unable to feed. Average numbers of flowers visited per minute for each species were compared using single-factor ANOVA. The expected profit per randomly selected flower was calculated for secondary nectar robbers and legal visitors. Expected profits for secondary nectar robbers are equal to the average nectar reward in robbed flowers, whilst the expected profits for legal visitors are calculated as given below:

$$E = (P_R \times N_R) + (P_U \times N_U)$$

where E is the expected profits, P_R and P_U the probability of encountering a robbed or an unrobbed flower respectively and N_R and N_U the average nectar content of robbed and unrobbed flowers, respectively. The expected profit per minute was then calculated for each individual bee and differences among species analysed using single-factor ANOVA. These calculations make the assumption that all foragers remove all of the nectar in the flower. They must be treated with caution since nectar rewards were only measured at a specific time of day.

2.5. Seed set

On 7 August the spurs of fifty randomly selected flowers which had not been robbed (often buds which had not yet opened) on eleven plants (an average of 4.5 flowers per plant) were protected with the cut-off ends of Gilsson Pipette tips so that bees could not get to the floral tissue of the spur to bite through it to rob nectar. Casual observations showed that these barriers remained on the flowers for the duration of the time the flowers were open and did not deter pollinating bees from making legal visits to the flowers they were on. All flowers to which pipette tips were attached were tagged, as were fifty robbed flowers selected at random on the same plants. On 1 September the seed pods were collected. A further fifty seed pods from untagged flowers (which were almost all robbed) were also collected at random from the same plants, as a control for the effect of tagging. In total, approximately four seed pods for each treatment (protected, robbed and control) were taken from each plant. Numbers varied due to the original availability of unrobbed flowers and the loss of tagged flowers. The number of seeds in all pods collected was counted.

Seed set data were transformed [$x' = \log_{10}(x + 1)$] to stabilize variances (Cochran's $C_{4,30} = 0.106$, n.s.) and were analysed using a two-way ANOVA, with 'individual plant' and 'treatment' as factors. The design was balanced so that there were four replicates for each treatment from each plant. This was done by replacing missing data with means and randomly removing excess data where necessary. One plant had only enough flowers for two replicates per treatment and was excluded entirely from the analysis.

It was noted whether seed pods contained larvae or adult insect seed predators. In some pods the ovaries had not developed and they produced no seeds. The proportion of undeveloped pods was analysed for robbed, protected and randomly picked flower pods using binomial errors in GLIM according to 'individual plant' and 'treatment'. Again, the ratio of residual deviance to the residual degrees of freedom was less than 1.5 and the test statistics given are χ^2 values [6]. All plants were included in this analysis.

3. RESULTS

3.1. Proportion of flowers robbed

Nearly all the open flowers examined showed evidence of having been robbed (96 % of open flowers had holes in the corolla). Furthermore, 54 % of buds had already been robbed. The number of open flowers which were robbed was significantly different on the three sampling dates ($\chi^2_2 = 22.8$, $P = 0.000$), the proportion of robbed, open flowers increased through the season (*table I*). Similarly, the number of closed flowers which were robbed was significantly different on the three dates ($\chi^2_2 = 9.05$, $P = 0.011$), although in this case numbers increased then decreased again (*table I*).

3.2. Nectar rewards

The average nectar content of open, robbed flowers was less than half that of open, unrobbed flowers (average nectar volume per flower for robbed flowers was 0.26 µL ± 0.16 SE and for unrobbed flowers was 0.58 µL ± 0.17 SE), but this difference was not significant ($t_{68} = 1.4$, $P = 0.08$). Robbed flowers were more likely to be empty than those which had not been robbed: 56.6 % of robbed flowers were empty, while only 8.0 % of unrobbed flowers were empty ($\chi^2_1 = 16.1$, $P = 0.000$).

3.3. Bee visits

Bumblebees were the only foragers observed visiting *L. vulgaris* to collect nectar. Hoverflies (Diptera, Syrphidae) often approached *L. vulgaris* flowers, but were not able to get inside the closed flower corolla. Bumblebee species differed significantly in their feeding techniques. There were significant differences in which species were primary robbers ($\chi^2_4 = 105.6$, $P = 0.000$), secondary robbers ($\chi^2_4 = 184.5$, $P = 0.000$), legal visitors ($\chi^2_4 = 259.5$, $P = 0.000$) or performed both robbing and legal visits to the same flower ($\chi^2_4 = 39.6$, $P = 0.000$). *B. terrestris* and *B. lucorum* were the only species observed primary robbing, whilst all species apart from *B. hortorum* were secondary robbers. *B. pascuorum* and *B. hortorum* were the only species to visit flowers legally. *B. pascuorum* was the only species to both rob and legally visit the same flower (*figure 1*).

3.4. Expected profits

On average, *B. terrestris* individuals visited the greatest number of flowers per minute and had the greatest expected nectar profit per minute (*table II*). However, there was no statistically significant difference among the bumblebee species in the number of flowers visited per minute ($F_{3,49} = 0.84$, $P = 0.48$). The expected rewards for secondary nectar robbers was 0.256 µL nectar per flower and for legal visitors (visiting both robbed and unrobbed flowers) was 0.269 µL. Bee species did not differ significantly in their expected profit per minute ($F_{3,49} = 0.70$, $P = 0.55$).

Table I. The number of flowers with perforated corollas on the three sampling dates. Open and closed flowers were examined on fifty inflorescences on each date.

Date	Open flowers				Closed flowers			
	Perforated	Unperforated	% Perforated	*n*	Perforated	Unperforated	% Perforated	*n*
27-07-98	154	16	90.6	170	27	39	40.9	66
06-08-98	176	2	98.9	178	58	31	65.1	89
14-08-98	225	3	98.7	228	34	30	53.1	64

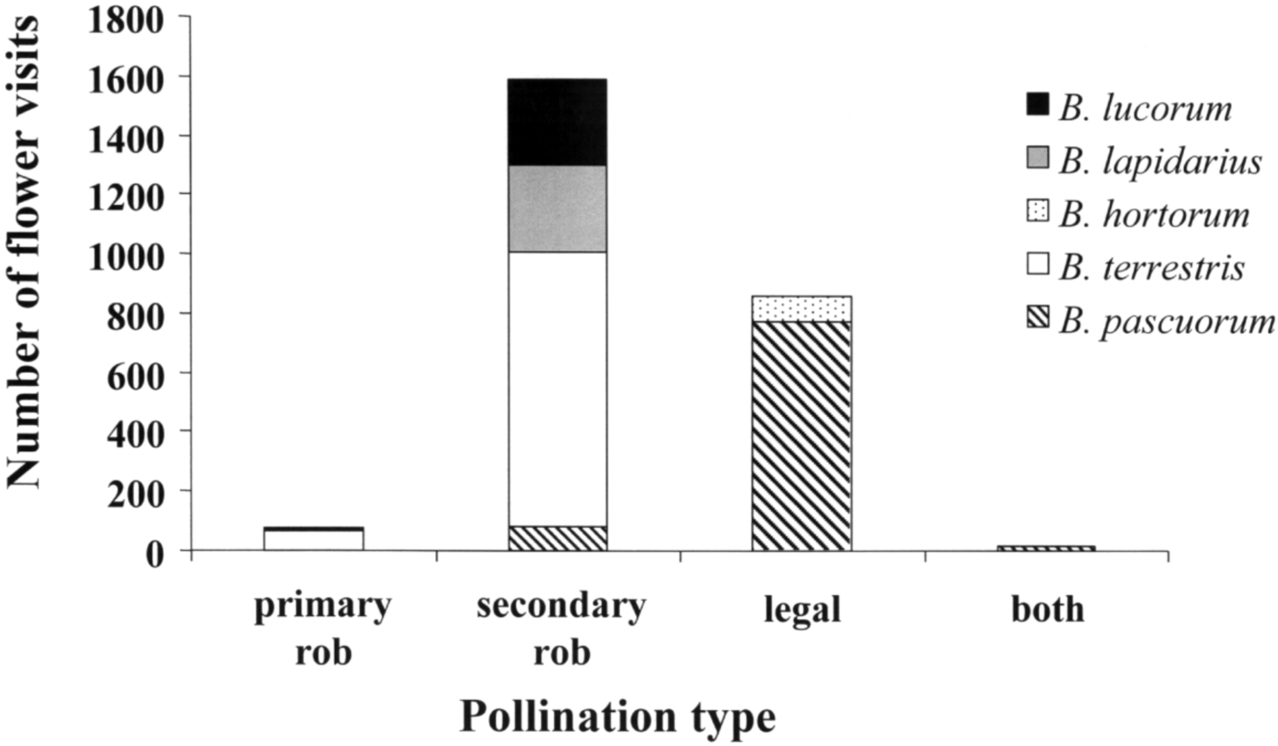

Figure 1. The total number of *L. vulgaris* flowers visited by bumblebees of all species according to foraging method. 'Both' refers to individuals which robbed and legally entered the same flower.

3.5. Seed set

There were no significant differences in the number of seeds set among the protected (unrobbed), tagged (robbed) and randomly picked (control) flowers ($F_{2,18} = 0.013$, $P = 0.99$). This indicates that robbing did not adversely affect seed set, nor did tagging flowers. Furthermore, seed set was not significantly different among plants ($F_{9,78} = 1.8$, $P = 0.08$) and the interaction term was also non-significant ($F_{18,78} = 0.623$, $P = 0.87$). Overall, 36.4 % of all pods failed to produce seeds (the ovaries had failed to enlarge). There was a significant difference in the proportion of pods that produced no seed according to whether the flower was robbed, protected or randomly selected ($\chi^2_2 = 7.41$, $P = 0.02$). Fifty-two percent of protected flowers contained no seeds, compared with

Table II. Nectar rewards per minute for foragers employing legal nectar visits and secondary nectar robbers. Expected reward per flower for legal visitors was calculated as the probability of finding a robbed flower multiplied by the average reward per robbed flower plus the probability of finding an unrobbed flower multiplied by the average reward per unrobbed flower. Expected reward per flower for secondary nectar robbers was just the average reward per robbed flower.

	Number of individuals	Total number of flower visits	Method of foraging	Average flowers per minute (± SE)	Expected reward per flower, μL (± SE)	Expected reward per minute, μL (± SE)
B. pascuorum	16	455	legal	12.2 (1.01)	0.269 (0.16)	3.27 (0.27)
B. terrestris	12	242	secondary robbing	14.0 (1.41)	0.256 (0.16)	3.59 (0.36)
B. lucorum	10	191	secondary robbing	11.3 (1.53)	0.256 (0.16)	2.90 (0.39)
B. lapidarius	15	294	secondary robbing	13.2 (0.99)	0.256 (0.16)	3.37 (0.25)

30.6 % of robbed and 28.0 % of randomly picked pods. There was no difference among plants in the proportion of pods that failed to develop (χ^2_{10} = 15.43, P = 0.12), nor was there a significant interaction between individual plant and treatment (χ^2_{20} = 19.79, P = 0.47).

Of the developed pods, 17.9 % contained insect seed predators, 10 % larvae and 7.9 % adults. Adults were mostly *Meligethes* sp. (Coleoptera, Nitidulidae).

4. DISCUSSION

In accordance with other studies (for example [19, 26, 30]), we found that short-tongued bumblebee species (*B. terrestris*, *B. lucorum* and *B. lapidarius*) performed only robbing visits, whilst the long-tongued species (*B. hortorum*) visited flowers in the legitimate way. *B. pascuorum*, with an intermediate tongue length, mostly visited *L. vulgaris* flowers in the legitimate way, but some individuals also secondarily robbed flowers. *B. pascuorum* was far more abundant than *B. hortorum*, and is presumably the main pollinator of *L. vulgaris*.

We found that bumblebee foragers were more likely to find a nectar reward in unrobbed *L. vulgaris* flowers than in robbed ones, since robbed flowers were more frequently empty. On average, the volume of nectar found in unrobbed flowers was twice that in robbed flowers, but variability between flowers was such that this difference was not significant. However, seed set was not reduced in robbed flowers. We suggest that this may be due to a number of factors. First, the proportion of robbed flowers in the population of *L. vulgaris* examined was very high, so that it would probably not be a viable strategy for pollinators to search for unrobbed flowers. Casual behavioural observations suggested that foraging *B. pascuorum* individuals were not discriminating between robbed and unrobbed flowers. Individuals foraging in the legitimate way headed straight for the orange lip of the flowers without investigating the spur. Bees also visited flowers in which the spurs had been protected, apparently unconcerned by the plastic barrier on the spur. If legitimate foragers do not discriminate against robbed flowers, this would account for the similarity in seed set in mature fruits of robbed and unrobbed flowers. Second, both robbers and pollinators were abundant. It has been previously shown that one pollinating visit by a bumblebee per *L. vulgaris* flower is sufficient to fertilize all the ovules in that flower (this study was carried out in the USA but it is probable that the pollination requirements are the same in the UK) [2]. Since *B. pascuorum* was abundant in the study site and flowers remain open for 4 d [2], it is likely that most flowers will receive at least one legitimate visit, even if they receive many robbing visits also.

The rate at which flowers were handled and the expected nectar profit per minute was similar for secondary nectar robbers and legitimate foragers, suggesting that both strategies are equally efficient. However, our calculations of profit considered only nectar foragers, and are based on nectar levels at 12.00 hours. Bees foraging at different times or which collected pollen as well as nectar may receive different profits. *B. pascuorum* may have been collecting both pollen and nectar from flowers as some individuals robbed and legitimately visited the same flowers. None of *B. lapidarius*, *B. lucorum* or *B. terrestris* collected pollen during the observation periods, although they may have collected pollen from *L. vulgaris* at a different time of day or earlier in the season [26]. If this were the case then these nectar robbers could also perform a pollinating role. Pollen loads or larval provisions [3] would need to be examined to investigate this.

The number of seeds found in almost all pods examined was low and the ovaries of over a third of all pods failed to enlarge suggesting that they were not fertilized or were aborted after fertilization. This is consistent with the results of Arnold [2] who found that the ovaries of 48 % of *L. vulgaris* flowers which had been pollinated failed to enlarge and that seed set per pod was low. This suggests that, for at least some plants, seed set may be resource limited rather than limited by pollination. A higher proportion of the ovaries of the protected flowers failed to enlarge than of the robbed or randomly picked flowers. This is possibly because the extra weight of the pipette tip on the flower corolla may have caused it to fall off prematurely, decreasing fertilization rates and increasing post-fertilization abortion.

The effect nectar robbers have on this plant species seems to be minimal, at least in the population studied, perhaps because pollination is not limited. Legitimate pollinators are abundant and individual flowers can therefore be both robbed and pollinated. Nectar robbing may even have a positive impact on the pollination of *L. vulgaris* if the reduction in rewards per flower due to nectar robbing causes pollinators to visit more flowers per foraging bout [8]. Intuitively, nectar robbing is a process that we would expect to be costly to the plant. In some systems clear negative effects have been reported (for example [18]), but more often no adverse effects have been found [1, 20, 23, 24, 31].

We do not as yet fully understand the factors that determine the costs (or benefits) of nectar robbery to plants.

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