Nectar robbing in bellflower (*Sesamum radiatum*) benefited pollinators but unaffected maternal function of plant reproduction

Sangeetha Varma & Palatty Allesh Sinu

Nectar robbing – foraging nectar illegitimately – has negative, neutral, or positive effects on maternal function of plant reproduction and/or on pollinators. It has been suggested that nectar robbing has a non-negative effect on maternal function of plant reproduction in autogamous and mixed breeding plants; however, this hypothesis requires deeper understanding with more studies. We investigated the impact of natural nectar robbing on maternal function of plant reproduction and visitation characteristics of pollinators in *Sesamum radiatum*, an autogamous plant. Pollinators were observed on unrobbed open flowers and robbed open flowers. In robbed flowers, pollinators' visit type and foraging time were examined. The seed sets of these flower types were examined. *Xylocopa latipes* was both a primary robber and a legitimate pollinator, *X. bryorum* was an exclusive primary robber, and *Megachile disjuncta* was a cosmopolitan pollinator. In robbed flowers, most of the pollinators foraged mostly as secondary nectar robbers. The foraging time shortened considerably when pollinators robbed nectar – a positive effect on pollinators' foraging efficiency. Robbing did not negatively affect seed set – a neutral effect on the plant's reproduction. Our study agrees that nectar robbing might have a non-negative effect on reproduction in autogamous and mixed breeding plants.

Plant-pollinator interaction is an example of mutualism. In this interaction, both the plant and the pollinator are benefited from the visits of pollinators on the flowers. However, many plant-pollinator mutualisms are disrupted by cheaters – visitors that exploit but leave the flowers unrewarded. Nectar robbers are often costly and ubiquitous disruptor of plant-pollinator mutualisms. Nectar-robbing is an adaptive trait evolved in some pollinators, which increases their foraging efficiency over legitimate pollinators. It has been predicted that facultative exploiters, such as floral nectar foragers, might exploit rather than collaborate with the robbed flowers in order to improve their foraging efficiency.

In plant-pollinator-robber interactions, although robbers are always benefited, plants and pollinators may be affected positively or negatively; or remain unaffected. Like any other species interactions, the net effect of nectar robbing on each partner species and on the plant-pollinator mutualism depends on the context. The breeding mechanism of plants might predict the net effect of nectar robbing on plants' maternal function of plant reproduction.

Nectar robbing in plants can affect male or female reproductive functions. Nectar robbing has a negative effect on female reproductive function in both self-compatible and self-incompatible species which have not developed autogamy as a reproductive strategy. Nectar robbing in plants that set seeds through selfing may have a positive or neutral effect on the maternal function of the plant reproduction. *Zhang et al.* studied the effect of nectar robbing in three sympatric plant species having three different mating strategies (selfing, facultative outcrossing, and obligate outcrossing) and found that the female reproductive function of selfing species was not affected, the facultative outcrossing species was benefited, and the obligate outcrossing species was negatively affected. Similarly, Burkle et al. suggested that nectar robbing has negative effect on female reproductive function of pollen-limited self-incompatible plants. However, testing this hypothesis requires deeper understanding with more case studies.

Present address: Department of Animal Science, Central University of Kerala, Periya, Kasaragod, 671316, Kerala, India. Sangeetha Varma and Palatty Allesh Sinu contributed equally. Correspondence and requests for materials should be addressed to S.V. (email: 1sangeethavarma@gmail.com)
Nectar robbing may also indirectly affect plant reproduction by affecting the visitation characteristics of pollinators\textsuperscript{15,16}. As the nectar-robbed flowers are manipulated, some pollinators may find such flowers less attractive and avoid or reduce their legitimate visitation rate\textsuperscript{17-20}. Some pollinators may also reduce the time they spent on the robbed flowers during their legitimate visits\textsuperscript{13,21}. Usually, the nectar – a major commodity that attracts legitimate pollinators to the flowers – is manipulated in robbed flowers; and the nectar in robbed flowers may be consumed or evaporated quickly, making the nectar viscous and the flowers less attractive\textsuperscript{22}. However, some plants overcome this loss by altering the nectar replenishment pattern in robbed flowers and ensure the visits of legitimate pollinators\textsuperscript{23}.

Another consequence of nectar robbing is that some legitimate pollinators bypass the flower opening and access nectar as secondary nectar robbers\textsuperscript{4,11,17,24}. The robbed flowers may also open themselves to a new suite of ephemeral visitors if the robbers are not guarding the robbed flowers\textsuperscript{24}. Studies also suggest that robbing through the holes made by primary robbers is more economical for the pollinators than using flower opening for nectar efficient nectar foraging\textsuperscript{4,23}. True pollinators may improve pollen delivery and cross pollination\textsuperscript{25}. However, nectar robbers may not help in plant reproduction directly\textsuperscript{26}. Also, since these outcomes are likely to be predicted by the reproductive strategies of plants\textsuperscript{12,14}, drawing a general conclusion in this regard needs more consistently harmonious results. Nectar robbing, therefore, has mixed or different outcomes for plants and pollinators.

In the present study, we examined the effect of nectar robbing by two species of carpenter bee – \textit{Xylocopa latipes} and \textit{X. bryorum} – on female reproductive function and pollinators of \textit{Sesamum radiatum} (Pedaliaceae). Unlike many previous studies, the effect of nectar robbing on pollinators in this study was examined on naturally-robbed flowers. Since bees mark the visited flowers, effect of nectar robbing on pollinators’ visits and behaviour can be understood only if the observations are made on naturally-robbed flowers\textsuperscript{4}. \textit{S. radiatum} is an annual herb that attains a maximum height of about 1.5 metres on both sandy and laterite rocky soils. It produces deep pink bell-shaped tubular hermaphrodite flowers on leaf axils (Fig. 1), which is open only for a day. The corolla tube is made up of five fused petals; one petal has an extended lip, which is used by the legitimate insect pollinators to land and enter the flower from front. The androecium has four didynamous anther filaments (two 1.7-cm long and two 1.1-cm long), which are attached on the inner wall of the corolla tube opposite to the extended lip. The anthers dehisce longitudinally. The gynoecium with a style
per plant (F6,239 in terms of visits/flower of visits and the number of flowers to calculate visitation rate. Visitation rate of a species in a given site, expressed every visits. Because we used different numbers of flowers across sites for the observation, we used the number the selected plants. We recorded visitor species, number of visits, and mode of visit (robbing or legitimate) for flowers varied between three and twenty-six and 20 and 169, respectively. We recorded visitors to all flowers of allowed the observer to record the visits on a convenient number of flowers. The numbers of observed plants and observation hours. All the observations on robbed and unrobbed flowers were completed within two hours from.

Although Sesamum spp including the domesticated S. indicum are self-pollinated\(^2\), the reproductive strategy of S. radiatum was unknown before our study. We observed carpenter bees, honey bees, solitary bees, wasps, and butterflies foraging both the nectar and pollen from S. radiatum flowers (Table 1). X. latipes and X. bryorum were the dominant primary robbing visitors of S. radiatum. Megachile disjuncta was the cosmopolitan pollinator of the flowers.

Effect of nectar robbing on pollinators. Surveys of nectar robbing in ten sites (151.6 ± 27.98 flowers/site) revealed a mean robbing rate of 61.91 ± 13.11% (±SE; range = 0–97.87%; median = 82.74%) of flowers per site. Nectar robbing rate in seven sites was consistently higher (85.71 ± 5.09%) than the other three sites (4.4 ± 3.86%; F\(_{1,481} = 1476, p < 0.0005\)). The heavily robbed sites (N = 7) were also different on the proportion of robbed flowers per plant (F\(_{6,239} = 7.38, p < 0.0005\)). In each site we watched flowers soon after anthesis (approx. 0800 h) on clear sunny days for one hour (normally between 0800 h–0900 h) during the peak flowering period. The observer stood at a convenient spot that allowed the observer to record the visits on a convenient number of flowers. The numbers of observed plants and flowers varied between three and twenty-six and 20 and 169, respectively. We recorded visitors to all flowers of the selected plants. We recorded visitor species, number of visits, and mode of visit (robbing or legitimate) for every visits. Because we used different numbers of flowers across sites for the observation, we used the number of visits and the number of flowers to calculate visitation rate. Visitation rate of a species in a given site, expressed in terms of visits/flower \(^{-1}\), is therefore calculated by dividing the total number of visits made by that species on the focal flowers of that site by the number of focal flowers watched in that site. We used the same method to find out legitimate and nectar robbing visitation rates. For some visits of pollinators and robbers, we also recorded the time spent/visit.

Although the frequency of robbed flowers in three sites was very low, the effects of nectar robbing on pollinators and plant reproduction were studied in robbed and unrobbed flowers of all the ten sites. Like other visitors, the primary nectar robbers also made their robbing visits soon after anthesis. Therefore, we caged flower buds the previous evening using paper bags to limit the visitors in flowers before our arrival. At around 0800h, we opened the bags and allowed visitors. At the beginning of our observations all flowers were unrobbed. As soon as we saw a robbing visit in a flower, we labelled that flower as primary nectar robbed flower and observed for one hour from then. The flowers that had no robbing visits for one hour of observation were considered as unrobbed open pollinated flowers. These flowers were revisited before senescing to ensure that they were not robbed after our observation hours. All the observations on robbed and unrobbed flowers were completed within two hours from.

| Visitor species          | Robbed flower | Unrobbed flower |
|--------------------------|---------------|-----------------|
|                          | Family        | Legitimate      | Secondary Robber | Legitimate    |
| Apis mellifera           | Apidae        | ✓               | ✓               |              |
| Apis dorsata             | Apidae        | ✓               | ✓               |              |
| Ceratina hieroglyhica    | Apidae        | —               | —               | ✓             |
| Ceratina smaragdula      | Apidae        | —               | ✓               | ✓             |
| Xylocopa acauculennisis  | Apidae        | —               | ✓               |              |
| Xylocopa bryorum*        | Apidae        | —               | ✓               |              |
| Xylocopa latipes*        | Apidae        | ✓               | ✓               | ✓             |
| Nomia curvipes           | Halictidae    | —               | —               | ✓             |
| Nomia iridesens          | Halictidae    | —               | ✓               | ✓             |
| Lastroloppum sp           | Halictidae    | —               | ✓               | ✓             |
| Megachile disjuncta      | Megachilidae  | ✓               | ✓               | ✓             |
| Megachile fulvousvesta   | Megachilidae  | —               | ✓               | ✓             |
| Megachile sp             | Megachilidae  | ✓               | ✓               | ✓             |
| Choetostoma sp           | Megachilidae  | —               | ✓               | ✓             |
| Campsomeriella collaris  | Scoliidae     | —               | —               | ✓             |
| Anterhynchium abdominale | Vespidae      | —               | —               | ✓             |
| Hesperidae sp1           | Hesperidae    | —               | —               | ✓             |
| Catopilia pomona         | Pieridae      | —               | —               | ✓             |
| Delius eucharis          | Pieridae      | ✓               | ✓               | —             |
| Graphium agamemnon       | Papilionidae  | —               | —               | ✓             |
| Hawkmoth                 | Sphingidae    | —               | —               | ✓             |

Table 1. Flower visitors and their functions in robbed and unrobbed flowers of Sesamum radiatum. *Primary nectar robber.
Effect of nectar robbing on maternal function of plant reproduction. We had two types of flowers for studying the impact of nectar robbing on seed set: robbed open flowers and unrobbed open flowers; the robbed open flowers had robbing visit first and subsequent legitimate and secondary robbing visits and the unrobbed open flowers had only legitimate visits. We studied a third category of flowers – unrobbed caged flowers – which shuts off for all visitors; this is used to investigate the impact of caging on seed set in S. radiatum. We harvested fruits on the 10th day of tagging flowers, opened the fruit capsules, and counted the number of seeds. To assess the impact of nectar robbing on maternal function of plant reproduction, we used seed set per capsule as the response variable. Although we collected data on fruit set, we did not use it as many fruits despite had developed normal capsules had no seeds in them. However, there were no signs of seed predation on fruit capsules. Assuming that the number of available fruit capsules on plants may have a negative feedback on subsequent fruit setting, we recorded the number of fruit capsules present on plants on the day of tagging flowers and used it as a random factor in the model. We used linear mixed effect model (function lmer in package lme4) to study the effects of robbing on the mean seed set per plant with number of available fruit capsules nested within plants within sites within location.

Results
Effect of nectar robbing on pollinators. The flowers of S. radiatum attracted 22 visitors (fifteen bees including the two primary robber species, five Lepidoptera including one hawk moth and four butterfly species, and two wasp species). Among the two species of primary nectar robbers – Xylocopa latipes and X. bryorum – the former was both a pollinator and a nectar robber, but the latter was an exclusive nectar robber. Both the species made only one hole at the nectary/ovary level of the corolla tube of pendent S. radiatum flowers. Among the remaining 20 floral visitors, Megachile disjuncta was a cosmopolitan dominant pollinator of S. radiatum.

Although the proportion of robbed flowers of seven heavily robbed sites was different, the visitation rate of pollinators on robbed and unrobbed flowers of those sites was not different (F₆,₁₇ = 0.385, p = 0.87); but, that on robbed flowers of those seven sites was different (F₆,₄ = 4.37, p = 0.03). Robbing had no effect on richness (robbed flowers = 13; unrobbed flower = 16; Chi-square = 0.03, d.f. = 1, p = 0.8) and visitation rate (slope ± SE = −0.20 ± 0.19; t = −1.04, df = 179, p = 0.29) of overall floral visitors in robbed flowers (Fig. 2). The species richness of legitimate visitors of robbed and unrobbed flowers were not different (robbed flowers = 10; unrobbed flower = 15; Chi-square = 1.00, d.f. = 1, p = 0.31). The richness of legitimate visitors and secondary nectar robbers of robbed flowers were also not different (legitimate visitors = 10; secondary nectar robbers = 13; Chi-square = 0.39, d.f. = 1, p = 0.53). However, when we examined the robbing and legitimate visitation rates on robbed flowers, we found that the robbing visits of overall visitors (slope ± SE = 0.53 ± 0.19; t = 2.73, df = 143, p = 0.007), pollinators (slope ± SE = 0.31 ± 0.07; t = 4.00, df = 95, p = 0.0001), and M. disjuncta (slope ± SE = 0.24 ± 0.08; t = 3.05, df = 56, p = 0.003) had increased over their legitimate visits. X. latipes – the primary robber cum pollinator – also had made more number of robbing visits than the legitimate visits (slope ± SE = 0.61 ± 0.19; t = 3.29, df = 15, p = 0.004) (Fig. 3).

The foraging time of overall pollinators (slope ± SE = −12.61 ± 1.00, t = −12.55, df = 127, p < 0.00005), M. disjuncta (slope ± SE = −13.8 ± 1.32, t = −10.4, df = 81, p < 0.00005), and X. latipes (slope ± SE = −6.05 ± 0.55, df = 23, t = −11.03, p < 0.00005) decreased drastically when they robbed nectar as secondary nectar robbers (Fig. 4).

Effect of nectar-robbing on maternal function of plant reproduction. Like the proportion of rolled flowers differed significantly between the seven heavily-robbed sites, the seed set of those sites also differed significantly (F₆,₅₁ = 4.98, p = 0.0004). The robbing had no significant effect on seed set (slope ± SE = 8.27 ± 4.74; t = 1.74, df = 27, p = 0.09). The caging of flowers had a significant negative effect on seed set (slope ± SE = −7.51 ± 2.71; t = −2.77, df = 157, p = 0.006). The results suggest that pollinator visits improve seed set in S. radiatum, but robbing does not affect seed set (Fig. 5).
Discussion

The present study on naturally-occurring plant-robber interaction in Sesamum radiatum – the wild relative of oilseed, Sesamum indicum – in tropical India suggests that robbing has no significant effect on maternal function.

Figure 2. Nectar robbing had no effect on visitation rate of overall flower visitors of Sesamum radiatum (N_{obs} = 199).

Figure 3. Nectar robbing had a negative effect on legitimate visits of (A) overall visitors (N_{obs} = 144), (B) pollinators (N_{obs} = 97), (C) Megachile disjuncta – a cosmopolitan pollinator of Sesamum radiatum (N_{obs} = 59), and (D) Xylocopa latipes – a primary nectar robber cum pollinator of Sesamum radiatum (N_{obs} = 39).
of plant reproduction despite having some impact on the visitation characteristics of pollinators. Studies have reported that nectar robbing has positive, negative, and neutral effects on the maternal function of plant reproduction (see a review and references therein). Our results also agree with the previous studies that show nectar robbing has mostly either neutral or positive effect on maternal function of plant reproduction in autogamous and facultative outcrossing species.

Identified mechanisms of nectar robbing which have negative effects on maternal function of plant reproduction include damaging ovary and other reproductive structures of flowers while probing for flowers at nectary level, aggressively interacting with the pollinators, and/or making the robbed flowers unattractive to pollinators. The robbed flowers will be unattractive to some pollinators when the nectar profile of flowers is affected or when the flower morphology is considerably mutilated for a pollinator to visit (Varma et al. (under review)). In our study the robber seemed not to have an aggressive interaction with the pollinators. The pollinators maintained both the legitimate and robbing visits on robbed flowers. The flower was also not mutilated badly; therefore the legitimate visits were also maintained on robbed flowers.

There are multiple mechanisms that suggest that nectar robbing has non-negative effects on the maternal function of plant reproduction in autogamous and facultative outcrossing plants. One hypothesis suggests that the pollinators do not distinguish between robbed and unrobbed flowers, and hence maintain their legitimate visits on robbed flowers and pollinate the flowers. The second hypothesis is that the pollinators do distinguish robbed flowers from unrobbed flowers, and that they visit robbed flowers as secondary nectar robbers; however, during their robbing visits they load the stigma with pollen. Our result that nectar robbing has no negative effect on plant reproduction in S. radiatum might have been partly due to the second mechanism explained here.

Mating system in plants also predicts the direction of the effect of nectar robbing on plants’ maternal reproductive function. It is predicted that self-incompatible plants experience negatively in terms of fruit set or seed set and self-compatible plants have a non-negative effect on maternal function of plant reproduction. In an Andean self-compatible tree, Oreocallis grandiflora, nectar robbing, despite caused a drop in the frequency of pollinators on robbed flowers, had no effect on seed set or seed mass. In an alpine self-compatible plant, Salvia przewalskii, because the nectar resecretion allowed legitimate visits of pollinating bumblebee on robbed flowers, the fruit set and seed set of robbed flowers were not affected. In congruence with these studies, we also found
that nectar robbing had not significantly affected seed set. The stigma of *S. radiatum* flower opens at the level of two longest anther filaments. Therefore subtle vibrations on flowers can transfer pollen grains to stigma. Since *S. radiatum* is benefited from autogamous pollination, robbing visits might have allowed the anthers to liberate pollen grains and facilitate self-pollination in robbed flowers. The seed set data of caged flowers also suggests that the plant is benefited from the visits of legitimate pollinators. The seed set of robbed open flowers was not different from that of unrobbed open flowers. The robbing had no effect on the visitation rate of overall pollinators on robbed flowers. Both the pollinators and the primary robber – *X. latipes* – maintained some legitimate visits in robbed flowers. Additionally, the species richness of legitimate visitors of robbed flowers was not considerably affected by nectar robbing. These visitors might have facilitated both the self and cross-pollination in the robbed flowers.

Nectar robbing in *S. radiatum* had a positive effect on pollinators’ foraging efficiency. The pollinator richness did not differ significantly between robbed and unrobbed flowers; however, the foraging behaviour of pollinators is changed by nectar robbing. It seems nectar robbing had improved the nectar foraging efficiency of pollinators, holding the predictions of foraging theory. It has been predicted that facultative exploiters, which often lack traits required for primary robbing, may choose secondary robbing strategy if not controlled, because this can improve their nectar foraging efficiency. Lichtenberg et al. found that *Bombus mixtus* visiting *Corydalis caseana* more frequently as a robber than as legitimate pollinator. Ye et al. found that the robbing visits of *Bombus friseanus* were considerably shorter than its legitimate visits in an Alpine plant, *Salvia przewalskii*. Both the studies suggest that exploitation yields these bees higher net benefits than collaborating. In our study, pollinators in general and *M. disjuncta* – a cosmopolitan pollinator of *S. radiatum* – in particular became exploiters than collaborators in robbed flowers. The nectar foraging time was considerably low when pollinators robbed nectar as secondary nectar robbers. In addition to this, at least six species of bees (*Ceratina hieroglyphica*, *C. maragdula*, *Chelostoma sp.*, *Nomiia iridicen*, *Xylocopa acutipennis*, and *Lasioglossum sp.*) foraged robbed flowers exclusively as secondary nectar robber, holding the predictions of mutualism and foraging theories. As juxtaposed with the previous results, *Apis dorsata* selectively visited only unrobbed flowers of *S. radiatum*; it made 2.82 (±0.16) visits/flower. *A. dorsata* therefore might have distinguished unrobbed flowers from the robbed flowers; however, no visits on robbed flowers prevented us statistical testing separately.

Cases where nectar robbing had no net negative effect on visitation rate of pollinators have a sustained nectar replenishment pattern in robbed flowers. Although we did not examine the nectar dynamics of robbed and unrobbed flowers in the present study, the sustained visits of pollinators, despite as robbers, on robbed flowers suggest that nectar robbing in *S. radiatum* is unlikely to have a negative effect on nectar replenishment pattern or on quality of nectar in robbed flowers. However, future studies may shed some light on this. We observed flowers for one continuous hour from the time of anthesis to record the visits of pollinators and robbers in unrobbed flowers. Although we started our observation from 0800 h, it continued till noon as the one hour observation on robbed flowers had started from the time when they were robbed. Therefore, it is likely that we recorded most of the flower visitors and captured their temporal foraging behaviour in the flowers of *S. radiatum* in this study.

Studies examining the effect of nectar robbing on pollinators’ foraging efficiency in naturally-robbed flowers are rare. Artificially robbed flowers – creating a hole and removing nectar manually using a syringe – although useful for studying the effect of nectar robbing on various aspects of pollinators, has limitations as well. Bees may scent-mark the visited flowers which can cause changes in the behaviour of conspecific and heterospecific pollinators. It is also applicable in robber–pollinator interactions. The studies that make observations on naturally-robbed flowers can only allow for the likely role of scent marking of robbers and discern the effect of nectar robbing on pollinators’ foraging behaviour. All robbed flowers that we monitored in the present study were done by carpenter bees.

In brief, nectar robbing in *S. radiatum* had a positive effect on pollinators’ foraging efficiency. However, nectar robbing had not affected seed set in the plant. This might be due to the fact that the sustained legitimate visits and the secondary nectar robbing visits of both the pollinators and *X. latipes* – the robber species – in robbed flowers might have facilitated both the self- and cross-pollination. *Sesamum* spp despite are autogamous, cross-pollination contributes to a small proportion of overall pollination. Studies examining the effect of nectar robbing on plants in tropical environments are relatively very rare (but see, González-Gómez and Valdivia). It is not clear whether the natural plant-robber interaction is rare in tropics or less studied. However, plant-pollinator network is complex in tropics, where robbers can destabilise the pollination system of a species or a community. Our study might give an insightful understanding of nectar robbing in tropical plants and may prompt researchers to find more such interesting cases in old-world tropics.

References

1. Bronstein, J. L. The exploitation of mutualisms. *Ecol. Lett.* 4, 277–87 (2001).
2. Maloof, J. E. & Inouye, D. W. Are nectar robbers cheaters or mutualists? *Ecology* 81, 2651–2661 (2000).
3. Maloof, J. E. The effects of a bumble bee nectar robber on plant reproductive success and Pollinator behavior. *Am. J. Bot.* 88, 1960–1965 (2001).
4. Irwin, R. E., Bronstein, J. L., Manson, J. S. & Richardson, L. Nectar Robbbing: Ecological and Evolutionary Perspectives. *Annu. R. Ecol. Evol. S.* 41, 271–292 (2010).
5. Jones, E. I. et al. Cheaters must prosper: reconciling theoretical and empirical perspectives on cheating in mutualism. *Ecol. Lett.* 18, 1270–1284 (2015).
6. Sachs, J. L. The exploitation of mutualisms: Mutualism (ed. Bronstein, J. L.) 93–106 (Oxford Univ. Press, 2015).
7. Lichtenberg, E. M., Irwin, R. E. & Bronstein, J. L. Costs and benefits of alternative food handling tactics help explain facultative exploitation of pollination mutualisms. *Ecology* 99, 1815–1824 (2018).
8. Zhang, C. et al. Selective seed abortion induced by nectar robbing in the selfing plant *Comastoma pulmonarium*. *New phytol.* 192, 249–255 (2011).
9. Higashi, S., Ohara, M., Arai, H. & Matsuo, K. Robber-like pollinators: overwintered queen bumblebees foraging on *Corydalis ambigua*. *Ecol. Entomol.* 13, 411–418 (1988).
10. Navarro, L. Pollination ecology of Anthyllis vulneraria subsp. vulgaris (Fabaceae): nectar robbing as pollinators. Am. J. Bot. 87, 980–985 (2000).
11. Richardson, S. C. Are nectar-robbing mutualists or antagonists? Oecologia 139, 246–254 (2004).
12. Burkle, L. A., Irwin, R. E. & Newman, D. A. Predicting the effect of nectar robbing on plant reproduction: Implications of pollen limitation and plant mating system. Am. J. Bot. 94, 1935–1943 (2007).
13. Bronstein, J. L. Mutualisms In Evolutionary Ecology: Perspectives and synthesis (ed. Fox, C., Fairbairn, D. & Roff, D.) 315–330 (Oxford Univ. Press, 2001).
14. Zhang, Y., Yu, Q., Zhao, J. & Guo, Y. Differential effects of nectar robbing by the same bumble-bee species on three sympatric Corydalis species with varied mating systems. Ann. Bot. 104, 33–39 (2009).
15. Newman, D. A. & Thomson, J. D. Effects of nectar robbing on plant fitness and bumblebee foraging strategies in Linaria vulgaris (Scrophulariaceae). Oikos 110, 309–320 (2005).
16. Richman, S. K., Irwin, R. E., Nelson, C. J. & Bronstein, J. L. Facilitated exploitation of pollination mutualisms: fitness consequences for plants. J. Ecol. 105, 188–196 (2017).
17. Irwin, R. E. & Brody, A. K. Nectar robbing in Ipomopsis aggregata: effects on pollinator behavior and plant fitness. Oecologia 116, 519–527 (1998).
18. Irwin, R. E. Humming bird avoidance of nectar-robbed plants: spatial location or visual cues. Oikos 91, 499–506 (2000).
19. Irwin, R. E. The impact of nectar robbers on estimates of pollen flow: conceptual predictions and empirical outcomes. Ecology 84, 485–95 (2003).
20. Zhang, Y. W., Zhao, J. M. & Inouye, D. W. Nectar thieves influence reproductive fitness by altering behaviour of nectar robbers and legitimate pollinators in Corydalis ambigua (Fumariaceae). J. Ecol. 102, 229–237 (2014).
21. Zimmerman, M. & Cook, S. Pollinator foraging, experimental nectar-robbing, and plant fitness in Impatiens capensis. Am. Midl. Nat. 113, 84–91 (1985).
22. Kim, W., Gilet, T. & Bush, J. W. M. Optimal concentrations in nectar feeding. Proc. Natl A Sci 108, 16618–16621 (2011).
23. Ye, Z., Jin, X., Wang, Q., Yang, C. & Inouye, D. W. Nectar replenishment maintains the neutral effect of nectar robbing on female reproductive success of Salvia przewalskii (Lamiaceae), a plant pollinated and robbed by bumble bees. Ann. Bot. 119, 1053–1059 (2017).
24. Hazlehurst, J. A. & Karubian, J. N. Nectar robbing impacts pollinator behavior but not plant reproduction. Oikos 2, 1–9 (2016).
25. Loveless, M. D. & Hamrick, J. L. Ecological determinants of genetic structure in plant populations. Annu Rev Ecol Systemat 15, 65–95 (1984).
26. Gracia-Meneses, P. M. & Ramsay, P. M. Pollinator responses to within-patch spatial context determines reproductive output of a giant roastee plant. Basic Appl Ecol 13, 516–523 (2012).
27. Langham, D. R. Phenology of sesame: New crops and new uses (ed. Janick, J. & Whieky, A.) 144–148 (ASHS Press, 2011).
28. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. Nature 403, 853–858 (2000).
29. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48 (2015).
30. Marcelis, L. F. M. & Hofman-Eijer, L. R. B. Effects of seed number on competition and dominance among fruits in Capsicum annuum L. Ann. Bot. 79, 687–693 (1997).
31. Traveset, A., Willson, M. F. & Sabag, C. Effect of nectar-robbing birds on fruit set of Fuchsia magellanica in Tierra Del Fuego: a disrupted mutualism. Funct Ecol 12, 459–464 (1998).
32. Roubik, D. W. The ecological impact of nectar robbing bees and pollinating humming birds on a tropical shrub. Ecology 63, 354–360 (1982).
33. Lasso, E. & Naranjo, M. E. Effects of pollinators and nectar robbers on nectar production and pollen deposition in Hamelia patens (Rubiaceae). Biotropica 35, 57–66 (2003).
34. Arizmendi, M. C., Dominguez, C. A. & Dirzo, R. The role of an avian nectar robbing and of hummingbird pollinators in the reproduction of two plant species. Funct. Ecol. 10, 119–127 (1996).
35. Sampson, B. J., Danka, R. G. & Stringer, S. J. Nectar Robbery by Bees Xylocopa virginica and Apis mellifera Contributes to the Pollination of Rabbiteye Blueberry. J. Econom. Entomol. 97, 735–740 (2004).
36. Irwin, R. E., Howell, P. & Galen, C. Quantifying direct vs. indirect effects of nectar robbers on male and female components of plant fitness. J. Ecol. 103, 1487–1497 (2015).
37. Wilms, J. & Eltz, T. Foraging scent marking of bumblebees: footprint cues rather than pheromone signals. Naturwissenschaften. 95, 149–153 (2007).
38. Pearce, R. F., Giuggioli, L. & Rands, S. R. Bumblebees can discriminate between scent marks deposited by conspecifics. Sci. Rep 7, 43872, https://doi.org/10.1038/srep43872 (2017).
39. González-Gómez, P. L. & Valdivia, C. E. Direct and Indirect Effects of Nectar Robbing on the Pollinating Behavior of Patagonagigas (Trochilidae). Biotropica 37, 693–696 (2005).
40. Wang, Y., Wua, H. & Sun, S. Persistence of pollination mutualisms in plant – pollinators – robber systems. Theor Popul Biol 81, 243–250 (2012).
41. Singh, V. K., Mohanty, D., Barman, C. & Tandon, R. Plant – Pollinator – Robber Interaction In Mutualistic Interactions between flowering plants and animals (eds Sinu, P. A. & Shivanna, K. R.). 34–49 (Manapal University Press, 2016).

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Author Contributions
S.V. and P.A.S. conceived the study; S.V. wrote the first draft of the manuscript; P.A.S. reviewed and edited the manuscript; P.A.S. did the analysis; S.V. performed field work.

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