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Author(s): Rebecca E. Irwin and Alison K. Brody

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CONSEQUENCES OF NECTAR ROBBING FOR REALIZED MALE FUNCTION IN A HUMMINGBIRD-POLLINATED PLANT

REBECCA E. IRWIN¹ AND ALISON K. BRODY

Biology Department, Marsh Life Science Building, University of Vermont, Burlington, Vermont 05405 USA and The Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, Colorado 81224 USA

Abstract. The effects of nectar robbers on plants and their mutualistic pollinators are poorly understood due, in part, to the paucity of studies examining male reproductive success in nectar-robbed plants. Here we measured the effects of a nectar-robbing bumblebee, *Bombus occidentalis*, on realized male reproductive success (seeds sired) in a hummingbird-pollinated plant, *Ipomopsis aggregata*. To determine the effects of nectar robbing on paternity, we used a series of experimental populations of plants containing a known allozyme marker. In each population, we experimentally controlled the levels of nectar robbing on each *I. aggregata* plant by cutting a hole in the corolla with dissecting scissors and removing nectar with a micro-capillary tube. We measured hummingbird-pollinator foraging behavior and fruit and seed production (maternal function) for each plant. We then genotyped seeds for the allozyme marker to determine the number of seeds sired by plants with known levels of robbing. Heavy nectar robbing (> 80% of flowers robbed) significantly reduced the number of seeds sired, as well as the number of seeds produced due to pollinator avoidance of heavily robbed plants. Total plant reproduction, both male and female contributions, were reduced by 50% due to high levels of robbing. To date, no other studies have measured the effects of nectar robbing on realized male function (number of seeds sired). Ours is the first study to demonstrate that robbing can simultaneously decrease realized male reproductive success as well as female reproductive success, and that the effects are incurred indirectly through pollinator avoidance of robbed plants.

Key words: *Bombus occidentalis*; hummingbird-pollinator behavior; *Ipomopsis aggregata*; male function; nectar robbing; effect on plant reproductive success; Rocky Mountain Biological Laboratory (Colorado, USA); siring success.

INTRODUCTION

Plants that offer food rewards to entice pollinators may also attract non-pollinating floral visitors, among them nectar robbers. Robbers typically obtain nectar without pollinating, by piercing flowers and avoiding contact with the sexual parts of plants (Inouye 1980, 1983). The effects of nectar robbers on plants and their mutualistic pollinators have been debated over the past three decades, and range from positive to neutral to negative. Nectar robbers may increase the receipt of outcrossed pollen if robbing causes pollinators to increase movement among plants (Heinrich and Raven 1972, Zimmerman and Cook 1985) or if “robber-like pollinators” incidentally pollinate flowers they rob (Waser 1979, Higashi et al. 1988, Arizmendi et al. 1996). However, robbers may reduce plant reproductive

success if robbers damage floral reproductive structures (McDade and Kinsman 1980, Traveset et al. 1998), if pollinators avoid robbed plants (Irwin and Brody 1998), or if robbers aggressively deter pollinators from foraging (Roubik 1982).

Most studies have considered the effects of nectar robbers only on maternal plant function (see references above and Barrows 1976, Kendall and Smith 1976, Rust 1979, Newton and Hill 1983, Roubik et al. 1985, Reddy et al. 1992, Olesen 1996, Goulson et al. 1998). However, hermaphroditic plants gain fitness through both female function (seeds produced) and male function (seeds sired). Because seed production is often resource limited, pollinator visitation may affect seeds sired more than seeds produced (e.g., Bateman 1948, Bell 1985, Stanton et al. 1986, 1991, Young and Stanton 1990); therefore, nectar robbers that reduce pollinator visitation in a resource-limited plant may influence male reproductive success more strongly than female reproductive success. Thus, to accurately assess the effects of nectar robbing, studies must include the effects of robbing on both male and female function.

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¹ Present address: Section of Evolution and Ecology, 2320 Storer Hall, One Shields Avenue, University of California, Davis, California 95616 USA. E-mail: reirwin@ucdavis.edu

To date, no studies that we know of have measured the effects of nectar robbers on realized male plant function (seeds sired), although the effects of robbers on estimates of male function (pollen removal and donation) have been examined in several species. Nectar-robbing ants had no consistent effect on pollinia removal in milkweed (Wyatt 1980), and nectar-robbing bumblebees had a positive effect on pollen removal in bluebells because robbers also acted as pollinators (Morris 1996). Although pollinia removal is a reliable estimate of male function in milkweed (Broyles and Wyatt 1990), in general, pollen removal often does not translate into the number of seeds sired (for a review see Stanton et al. [1992]). In scarlet gilia, *Ipomopsis aggregata*, nectar-robbing bumblebees decreased pollen donation, as estimated by the use of fluorescent dyes, by 80% because hummingbird pollinators avoided robbed plants and flowers (Irwin and Brody 1998, 1999). In comparison to pollen removal, pollen grain (or dye) donation is often a more accurate estimate of the number of seeds sired by plants (e.g., Waser and Price 1982, but see Thomson et al. 1986). However, it is still not known how an observed reduction in pollen donation translates into a reduction in the number of seeds sired. The relationship between estimates of male function (pollen removal and donation) and realized male function (seeds sired) is a missing link in assessing the outcome of nectar robbing on plant reproductive success.

The objective of this study was to investigate the effect of nectar robbing on male reproductive success of the hummingbird-pollinated plant *Ipomopsis aggregata*. We used a series of experimental populations of *I. aggregata* containing individuals of known genetic identity for the enzyme 6-phosphogluconate dehydrogenase (6-PGD). We artificially imposed high (80% of flowers robbed) and low (10% of flowers robbed) robbing levels on *I. aggregata* and measured hummingbird-visitation rates and fruit and seed production. We then genotyped seeds for the 6-PGD marker to determine the number of seeds sired by plants with high and low robbing levels.

METHODS

Study system

We conducted this study using the montane, perennial herb *Ipomopsis aggregata* (Polemoniaceae), near the Rocky Mountain Biological Laboratory (RMBL), elevation 2800 m, in the Elk Mountains of central Colorado. Around the RMBL, *I. aggregata* is a long-lived monocarp where it grows as a vegetative rosette for 2–7 yr or longer, flowers once, and dies (Waser and Price 1989). Thus, it is possible to measure the lifetime reproductive success of individuals in one flowering sea-

son. In the year of flowering, plants produce a single stalk with numerous red, trumpet-shaped flowers. Plants bloom for 4–8 wk (mid-June to mid-August) and produce an average of 84 ± 66 flowers (mean \pm 1 SD) over their lifetime (Campbell 1989). The flowers are hermaphroditic, protandrous, and last for 3–5 d. Nectaries are located at the base of flowers, and nectar is produced at a rate of 1–5 μ L of nectar per flower per day, with a concentration of 20–25% sucrose equivalents (Pleasants 1983).

Ipomopsis aggregata is self-incompatible and does not reproduce vegetatively. Therefore, all seeds are a result of inter-plant pollen transfer. *I. aggregata* is pollinated primarily by Broad-tailed Hummingbirds (*Selasphorus platycercus*) and Rufous Hummingbirds (*S. rufus*) around the RMBL (Waser 1978). Lifetime seed production in natural populations of *I. aggregata* is limited by both pollen (Hainsworth et al. 1985, Campbell 1991, Campbell and Halama 1993) and resources (Campbell and Halama 1993). In addition, excessive geitonogamy in *I. aggregata* can reduce fruit and seed production (de Jong et al. 1992).

Ipomopsis aggregata is robbed by the bumblebee *Bombus occidentalis*. The bees use their sharp, toothed mandibles to chew a hole through the side of the corolla near the basal nectaries, insert their proboscis into the hole, and extract all available nectar. While robbing, the bees neither pollinate the plant nor damage the plant's reproductive or nectar-producing structures (Pleasants 1983, Irwin and Brody 1998). Robbers have no significant direct effect on *I. aggregata* seed production. Hand-pollinated robbed and unrobbed flowers produce similar numbers of seeds (R. E. Irwin, unpublished data). Robbing rates on *I. aggregata* range from 0% to 100% of available flowers per plant over the blooming season, with a seasonal mean of 51.3% of available flowers robbed (Irwin and Brody 1998). Mean robbing per plant shows a bimodal distribution with peaks at low (0–20% of open flowers robbed) and high (80–100% of open flowers robbed) robbing levels (Irwin and Brody 1998). Nectar robbers are usually non-random in their foraging behavior; some plants consistently have most of their flowers robbed while others are virtually ignored (R. E. Irwin and A. K. Brody, unpublished data). Individual flowers are robbed multiple times; however, nectar robbing has no effect on subsequent nectar production (R. E. Irwin, unpublished data).

Effects of nectar robbing on plant reproductive success

In May 1998, we identified 64 plants that were homozygous at the 6-phosphogluconate dehydrogenase locus (6-PGD) using starch gel electrophoresis (Soltis et al. 1983). The plants were growing in four natural

populations 25 km south of the RMBL. We identified 32 individuals homozygous for a slow-migrating allele ("SS") and 32 homozygous for a fast-migrating allele ("FF") that were similar on the basis of plant height, architecture, and phenology. We potted the plants individually in flower pots and transported them back to the RMBL. We placed the plants in a greenhouse for 4 d and watered and fertilized them daily to allow them to recover from transplant shock.

We then randomly assigned the 64 plants to four arrays (16 plants per array) with eight homozygous SS and FF plants per array. We assigned all individuals of the same genotype in a given array to one of two artificially imposed robbing treatments—either light nectar robbing (10% of all flowers robbed) or heavy nectar robbing (80% of all flowers robbed). Genotype assignments to the two robbing treatments were reversed among arrays to control for any spurious genotype \times treatment interactions. The light and heavy robbing levels in this experiment simulate low and high robbing levels commonly found in natural populations of *I. aggregata* (see *Study system*, above, and Irwin and Brody 1998). Because this experiment was conducted in mid-May, nectar-robbing bees were not yet active; therefore, artificial-robbing treatments were maintained without extraneous natural robbing.

We artificially robbed flowers by cutting a hole, ~ 1 mm in diameter, in the side of flowers in male phase using dissecting scissors. All available nectar was removed from each flower using a 10- μ L microcapillary tube inserted into the hole. Because individual flowers are robbed multiple times by *B. occidentalis*, nectar was removed each day that a flower was in bloom. As a control, we also handled flowers in the undamaged treatment, but we did not make a hole in them. Naturally and artificially robbed flowers do not differ in pollen donation or receipt, fruit or seed production, or seed mass (Irwin and Brody 1998, 1999). In addition, neither artificial robbing nor natural robbing damages floral reproductive structures (Irwin and Brody 1998). Therefore, our artificial robbing technique adequately mimics natural robbing by *B. occidentalis*.

On 10 successive days, we robbed plants according to their assigned robbing treatments. We marked the calyces of robbed flowers with a small black dot using a permanent, felt-tipped marker to distinguish robbed from unrobbed flowers when mature fruits were collected. All unrobbed flowers were marked with a contrasting color to control for unforeseen effects that our marks might have caused, and to distinguish those flowers present during the experiment from flowers produced in the greenhouse after the experiment ended. We placed the four arrays in the field in open meadows around the RMBL. Each array was separated from all

others by > 3 km. In each array, the plants were arranged in a square grid so that all plants were 1 m apart from their nearest neighbors. Members of each array were randomly assigned to a position within the grid for the duration of the experiment. Because plant position does not change throughout the season in naturally growing plants, we did not re-randomize the position of plants within arrays each day. No other *I. aggregata* were in bloom in mid-May when the experiment was conducted at the RMBL, but hummingbirds were actively foraging. Therefore, the experimental arrays did not receive extraneous pollen from non-study plants.

We placed the plants in the field for 2 h each day between 0800 and 1700 and recorded all hummingbird visits to the plants. Using hand-held tape recorders, we recorded the species and sex of each bird visitor and the identity of the plants visited in each hummingbird-foraging bout. We placed plants in the field for only 2 h each day because hummingbird-visitation rates during this period were extremely high as no other *I. aggregata* were in bloom. Our arrays experienced an average of 12 bouts/h, whereas similar arrays during the blooming season of *I. aggregata* receive an average of 1 bout/h (a 12-fold difference in the number of bouts; R. E. Irwin, *unpublished data*). Therefore, leaving the arrays out for only 2 h per day ensured that hummingbird visitation to the plants would be similar in magnitude to that which plants would experience during the normal blooming season of *I. aggregata*.

After each 2-h observation period, we returned the plants to the greenhouse to allow them to replenish nectar over the next 24 h. The average standing crop of nectar in a flower was ~ 1.5 μ L before daily robbing treatments, which approximates the average standing crop of nectar in flowers in natural populations (Pleasants 1983).

We ran the experiment for 10 d, after which all plants were left in the greenhouse and watered and fertilized daily. Once seeds matured, we collected all fruits from flowers in bloom during the observation period. To determine the female reproductive success of plants in the low- and high-robbing treatments, we recorded the number of marked flowers that did not produce fruits and counted the number of seeds in each seed-bearing fruit.

To determine the number of seeds sired by the low- and high-robbing treatments (male reproductive success), we randomly chose 25% of the fruits produced by each plant (for a total of 1588 seeds and an average of 28% of the seeds produced per plant) and genotyped their seeds at the 6-PGD locus using starch gel electrophoresis (Soltis et al. 1983). Since all plants in each array were homozygous and self-incompatible, all homozygous offspring were sired by fathers from the

TABLE 1. Male reproductive success. Results of ANCOVA examining the effects of nectar-robbing treatment, array, and the mean number of open flowers on the number of seeds sired by plants with low and high robbing.

Source of variation	ss	df	F	P
Robbing treatment	7.306	1	21.701	<0.0001
Array	3.432	3	3.399	0.0203
Treatment \times array	0.715	3	0.708	0.5492
No. open flowers	0.001	1	0.001	0.9798
Error	37.708	112		

same robbing treatment as the maternal parent. Conversely, all heterozygous offspring were sired by fathers from the robbing treatment different from their maternal parent.

Statistical analysis

We used ANCOVAs to analyze the effect of nectar-robbing treatment on (1) realized male reproductive success (mean number of seeds sired per fruit in each robbing treatment for each maternal plant, natural-log transformed), (2) female reproductive success (percent fruit set: number of expanded fruits/total number of flowers, arcsine square-root transformed; and mean seed set per successful fruit, natural-log transformed), and (3) mean hummingbird-visitation rate per plant. We used the mean number of open flowers per plant per day as a covariate to adjust for among-plant differences in inflorescence size. An assumption in ANCOVAs is that the slope of the covariate (mean number of open flowers per day) by the independent variable (robbing treatment) be the same for all levels of the independent variable; therefore, we first tested for homogeneity of slopes (Sokal and Rohlf 1981). We found no significant robbing treatment \times covariate interaction terms ($P > 0.05$ in all cases). We then ran ANCOVA analyses with nectar-robbing treatment (10% and 80%) as a fixed effect, array as a random effect, and the mean number of open flowers as a covariate. All statistical analyses were carried out using the GLM procedure in SAS (SAS Institute 1985a, b).

RESULTS

Plants in the high-robbing treatment sired significantly fewer seeds than plants in the low-robbing treatment (Table 1). High robbing reduced seeds sired by 56% (Fig. 1a). Arrays differed in the number of seeds sired by each robbing treatment; however, the interaction term robbing treatment \times array was not significant, indicating that plants with high robbing sired fewer seeds than plants with low robbing in all arrays (Table 1).

In addition, plants with high robbing were less successful as females than plants with low-robbing, as measured by percentage fruit set and seed set per fruit

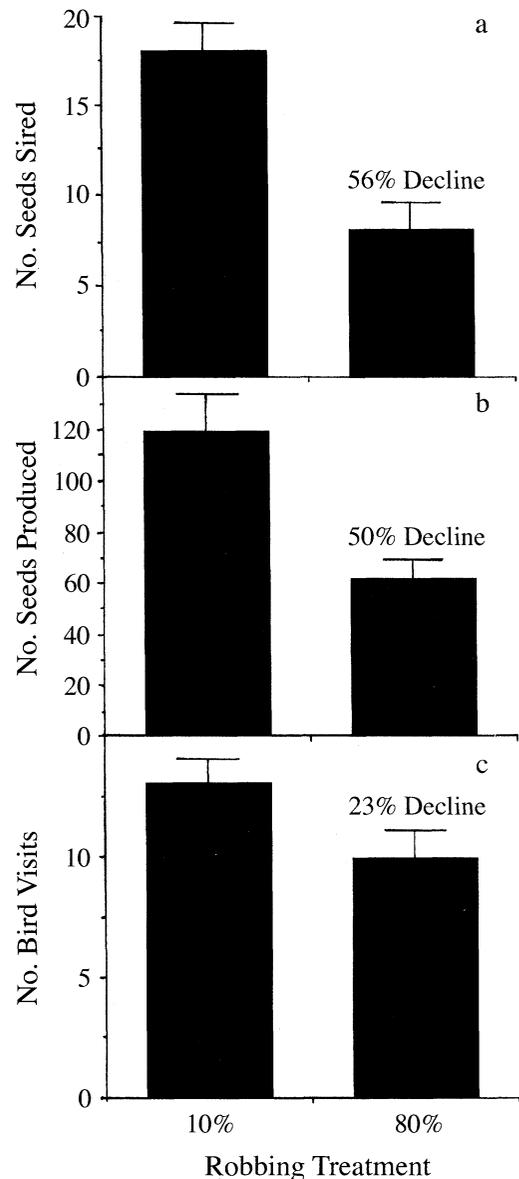


FIG. 1. Effects of two levels of nectar robbing on (a) number of seeds sired, (b) number of seeds produced, and (c) mean number of pollinator visits. Histogram bars show means; error bars indicate $+ 1$ SE. There were 32 plants in each robbing treatment. Over the 40 h of observation at the four experimental arrays, we recorded 155 hummingbird foraging bouts by at least 12 male Broad-tailed Hummingbirds and 776 visits to individual *Ipomopsis aggregata* plants.

(Table 2a and b). Robbing decreased percentage fruit set by 36% and seed set per fruit by 24%. Therefore, robbing decreased total seed production per plant by 50% (Fig. 1b). The four arrays differed significantly in percentage fruit set and seed set per fruit (Table 2a and b); however, the interaction term robbing treatment \times

TABLE 2. Female reproductive success. ANCOVAs examining the effects of nectar-robbing treatment, array, and the mean number of open flowers on (a) percentage fruit set and (b) seed set per fruit.

Source of variation	ss	df	F	P
a) Percentage fruit set				
Robbing treatment	0.161	1	8.353	0.0055
Array	0.329	3	5.687	0.0018
Treatment \times array	0.031	3	0.532	0.6620
No. open flowers	0.081	1	4.203	0.0451
Error	1.059	55		
b) Seeds/fruit				
Robbing treatment	1.497	1	7.307	0.0092
Array	5.107	3	8.308	0.0001
Treatment \times array	0.307	3	0.499	0.6847
No. open flowers	0.609	1	2.973	0.0904
Error	11.065	55		

array was not significant for either fruit set or seed set, indicating that the direction of response to robbing treatments was the same in the four arrays (Table 2a and b).

The mechanism behind reductions in both male function and female function in nectar-robbled plants was changes in hummingbird-pollinator behavior. Pollinator visitation to plants in the study was significantly biased against plants with high robbing ($F_{1,55} = 17.34$, $P = 0.0001$). Plants with high robbing received 23% fewer visits than plants with low robbing (Fig. 1c). Arrays differed in the mean number of visits plants received ($F_{3,55} = 27.88$, $P < 0.0001$); however, plants with high robbing received fewer visits across all arrays (robbing treatment \times array, $P > 0.05$), and the number of open flowers did not affect the number of visits plants received ($P > 0.05$). In addition, plant genotype at the 6-PGD locus had no effect on hummingbird visitation, seeds sired, or fruits or seeds produced ($P > 0.05$ in all cases).

DISCUSSION

Our study demonstrates that nectar robbing decreases both male reproductive success and female reproductive success in *Ipomopsis aggregata*. *I. aggregata* with heavy robbing experienced a 56% reduction in seeds sired and a 50% reduction in seeds produced. Decreasing the number of hummingbird-pollinator visits to *I. aggregata* plants and flowers decreases both the amount of pollen removed from anthers and the amount of pollen deposited on stigmas (Mitchell and Waser 1992). Therefore, reductions in male and female function in plants with heavy robbing are due to the deterrence of hummingbird pollinators from foraging on robbed plants (this study and Irwin and Brody 1998). This work corroborates previous findings that hummingbird visitation is lower in plants with high rob-

bing, which results in a significant reduction in female plant function (Irwin and Brody 1998). The results we present here demonstrating the effects of robbing on realized male plant function provide a critical link that has been missing from studies examining the effects of robbers on plant reproductive success.

One caveat about the interpretation of the results of this study is that we used an experimental approach that relied on small, artificial populations of plants. Because no other *I. aggregata* were in bloom, small experimental populations may have exaggerated the degree of geitonogamy and hetero-specific pollen transfer that plants would normally receive. However, these factors probably affected plants with low robbing more than plants with high robbing because plants with high robbing were often ignored by hummingbirds. Increasing the number of hummingbird visits to *I. aggregata* increases the amount of pollen deposited on stigmas (Mitchell and Waser 1992). Thus, plants with high robbing probably experienced pollen limitation due to pollinator avoidance of robbed plants, while plants with low robbing probably experienced the highest degree of geitonogamy resulting in self-pollination and the highest deposition of hetero-specific pollen transfer. Therefore, we biased ourselves against finding significant differences between our robbing treatments in seeds sired and produced. Here, the benefits of multiple-plant and multiple-flower visitation outweighed the potential disadvantages of geitonogamy and hetero-specific pollen transfer in plants with low robbing. Nonetheless, it would be valuable to repeat this study in natural populations of *I. aggregata* where amounts of compatible *I. aggregata* pollen on hummingbirds would likely be greater.

Nectar robbing in this study reduced both male function and female function similarly. Other studies, including those involving *I. aggregata* (Campbell 1989), have also found that selective agents (i.e., pollinators) affect male and female function similarly (e.g., O'Connell and Johnston 1998). The most likely explanation for the similarity of male and female function in this study is that plants were not resource limited. Resource limitation often affects female function, whereas pollen limitation often affects male function (e.g., Bateman 1948, Stanton et al. 1986). Because plants were watered and fertilized daily, resource limitation probably did not affect female function. Therefore, similar reductions in both pollen donation and receipt to plants with heavy robbing resulted in similar reductions in seeds sired and seeds produced. However, in nature there could be interactions between resource limitation and pollen limitation in such a way that a reduction in pollinator visitation would not lower fruit and seed set if female function was strongly resource limited. Therefore, the effects of nectar robbing might

be reduced when seed production from some or all of the flowers on a plant is resource limited.

Yet, we were surprised that heavy nectar robbing did not decrease male function more. In previous studies, we found that heavy artificial robbing in *I. aggregata* (80% of flowers robbed) decreased an indirect estimate of male function, pollen (dye) donation, by 80% (Irwin and Brody 1999), but in the present study, robbing decreased realized male function by only 50%. Two mechanisms may explain the discrepancy between these results. First, indirect estimates of male function (such as pollen removal and donation) often overestimate the number of seeds sired by plants (e.g., Broyles and Wyatt 1990, Ashman 1998). The relationship between estimates of male function and realized male function may be uncoupled by pre-pollination processes, such as pollen wastage and loss of pollen viability (Thomson and Thomson 1989), and by post-pollination processes, such as pollen-tube competition, incompatibility, and selective fruit abortion (Mulcahy 1979, Mulcahy et al. 1983, Marshall 1988, 1990). Therefore, an association between estimates of male function and realized male function may not indicate a one-to-one relationship (Broyles and Wyatt 1990, Ashman 1998) and such comparisons should be made with caution. Clearly, more studies are needed to evaluate the strength of the association between estimates of paternity and realized paternity.

Second, the effects of robbing on male reproductive success may differ due to variation in pollinator abundance and/or pollinator foraging behavior (e.g., Waser and Real 1979, Mitchell and Waser 1992, Campbell and Halama 1993, Mitchell 1993, Brody and Mitchell 1997). Pollinator limitation and changes in pollinator behavior often strongly influence male reproductive success (e.g., Bateman 1948, Stanton et al. 1986). Therefore, male reproductive success may vary among years and sites depending on the pollinator assemblage present.

Nectar robbing reduced total plant reproductive success (seeds sired and seeds produced) by ~50%. Nectar robbing occurs in over 150 flowering species across 40 plant families (Barrows 1980, Inouye 1983). However, our knowledge of the outcome of multiple-species interactions involving nectar robbers, plants, and pollinators remains poorly understood. The lack of studies on the cumulative effects of robbing on both male and female function may have underestimated the importance of nectar robbers to plant ecology and evolution. Our results provide new insight that nectar robbing can decrease realized male reproductive success as well as female reproductive success due to pollinator avoidance of nectar-robbed plants.

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