

# THE EFFECTS OF A BUMBLE BEE NECTAR ROBBER ON PLANT REPRODUCTIVE SUCCESS AND POLLINATOR BEHAVIOR<sup>1</sup>

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Interactions between a plant species (*Corydalis caseana*), a bumble bee nectar robber (*Bombus occidentalis*), and a bumble bee pollinator (*B. appositus*) were studied. There were no significant differences between naturally robbed and unrobbed flowers in fruit set or mean seed set per fruit. Plots of *C. caseana* plants were subjected to treatments of robbing and no robbing using commercially available colonies of *B. occidentalis*. Robbers did not pollinate the flowers. Pollinator behavior was observed to determine (1) the number of bees attracted to each plot, (2) the number of inflorescences visited in a plot, (3) the number of flowers visited on each inflorescence, and (4) the distance flown between inflorescences. There were no significant differences in the number of inflorescences visited per bee or the number of flowers visited per inflorescence per bee when robbed and unrobbed treatments were compared. Of the parameters measured, only distance flown between inflorescences differed in the robbed and the unrobbed treatments. Bees flew significantly further between inflorescences in the robbed plots than in the unrobbed plots. The results indicate that the nectar robbers have no negative effect on fruit set or seed set in *C. caseana* and that they may cause increased pollen flow distances by changing the behavior of the pollinator.

**Key words:** *Bombus*; community ecology; *Corydalis*; flight distances; nectar robbing; outcrossing; robbers.

There has been a recent increase of interest in nectar robbers, i.e., flower visitors such as birds or insects that remove nectar through a hole that has been pierced or bitten in the corolla. The focus of current research is whether or not nectar robbers have adverse effects on the flowers they rob. For >100 yr it was generally assumed that robbers were cheaters in the plant–pollinator mutualism and most likely had some detrimental effect on the plants they robbed (see Maloof and Inouye, 2000). However, researchers who closely examined the effects of nectar robbers often found that the robbers were behaving as pollinators by moving pollen onto the stigma as a result of their movements during pollen or nectar gathering (Koeman-Kwak, 1973; Waser, 1979; Higashi et al., 1988; Guitán, Guitán, and Navarro, 1993; Guitán, Sánchez, and Guitán, 1994; Navarro, 2000). A new terminology has developed to describe animals that behave in this way: robberlike pollinators (Higashi et al., 1988). These robberlike pollinators often have positive effects on the reproductive success of the plants they visit.

In addition to enhancing reproductive success directly through pollination, robbers may also influence reproductive success indirectly by causing changes in the behavior of the legitimate pollinators either through scent marking, changes in nectar volume, or both. Reduced nectar volume has been shown to cause bumble bees to increase interplant flight distances (Heinrich, 1983; Zimmerman and Cook, 1985) and to visit fewer flowers on the same inflorescence (Pyke, 1982;

Heinrich, 1983; Hodges, 1985; Johnson and Nilsson, 1999). Both of these behaviors can reduce geitonogamy (the fertilization of flowers by pollen from other flowers on the same plant), increase pollen flow distances, and thereby increase outcrossing rates (see de Jong, Waser, and Klinkhamer, 1993; Barrett and Harder, 1996). Higher rates of outcrossing often lead to increased seed set and improved survival rates of seedlings (e.g., Charlesworth and Charlesworth, 1987; Fenster, 1991).

It seems likely then that robbers, by reducing nectar volume, might change pollinator behavior and consequently affect pollen transfer. Holsinger (1996) states that “identifying the factors that affect the patterns of pollen transfer should probably be the overriding goal of future empirical research in pollination and mating system biology.” But to date, only two studies have attempted to measure the effects of robbers on pollinator foraging behavior (Zimmerman and Cook, 1985; Irwin and Brody, 1998). Zimmerman and Cook (1985) artificially robbed flowers of *Impatiens capensis* by making a hole in the spur of the corolla and removing nectar with a syringe. The authors concluded that “the presence of nectar-robbers in the system does not alter the general pollination behavior, but it does induce foragers to fly longer distances thus further promoting outcrossing.” Irwin and Brody (1998) artificially robbed experimental arrays of *Ipomopsis aggregata*. They found that the legitimate pollinator, a hummingbird, visited fewer plants and fewer flowers per plant in the heavily robbed arrays, thus decreasing fruit set and seed set and having a negative effect on plant fitness.

In both of these studies, the flowers were “artificially” robbed, meaning that humans mimicked the actions of real nectar robbers by cutting holes in the flowers and extracting nectar. Evidence is accumulating, however, that bumble bees (one of the most prevalent nectar robbers, and the robbers in both of these systems) may scent-mark flowers while foraging and detect the scent-markings of previous visitors (see Goul-

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son, Hawson, and Stout, 1998). In a number of instances these scent markings have been shown to change the behavior of foraging bumble bees (Schmitt and Bertsch, 1990; Goulson, Hawson, and Stout, 1998; Williams, 1998). In one study the bumble bees were apparently able to discern scents created by human fingerprints on floral surfaces (Marden, 1984). Therefore, if we wish to examine the effect of bumble bee nectar robbers on legitimate pollinators, we should consider the possibility that scent marking plays a role in this interaction and design our experiments accordingly.

In this study I have examined the interactions among a plant species (*Corydalis caseana* subsp. *brandegei*), its nectar robber (a bumble bee, *Bombus occidentalis*), and its pollinator (a bumble bee, *Bombus appositus*). Specifically I have addressed the following questions: (1) At what age are the flowers generally robbed? (2) Is there a difference in fruit set or seed set between the robbed and the unrobbed flowers? (3) Do robbers pollinate the flowers they visit? (4) How much nectar is removed by the robbers? (5) Do robbers change the behavior of the legitimate pollinators by changing the number of bees attracted, the number of inflorescences visited per bee, the number of flowers visited per inflorescence, or the flight distances between inflorescences?

To allow for the possibility that scent marking plays some role in the effect of nectar robbers, all robbing in this study was done by *Bombus occidentalis*, the natural robber of the plant species. This study represents the first time the effect of nectar robbers on the behavior of the legitimate pollinator has been tested experimentally using real nectar robbers.

## MATERIALS AND METHODS

**The study site and the plant**—My study site was located in Washington Gulch (38°56' N, 107°01' W) at an altitude of 2940 m near the Rocky Mountain Biological Laboratory in Gothic, Colorado. *Corydalis caseana* subsp. *brandegei* (hereafter referred to as *C. caseana*) is a tall (1–2 m), perennial, herbaceous plant that typically grows in subalpine meadows near a source of fresh water such as a stream or snowmelt basin. Where the plant occurs, it is locally abundant, forming large, almost monospecific patches. However, the distribution of *C. caseana* is so patchy and disjunct that it is considered a rare species (Colorado Natural Heritage Program, 1996). Young plants have only a single stem, but older plants (>7 yr) have numerous stems (2–25) arising from a single large root. Each mature stem is topped by a terminal racemose inflorescence bearing up to 70 flowers; stems also have numerous side inflorescences with 5–40 flowers each. It was sometimes difficult, without digging up the plants, to determine if stems in close proximity were from the same, or different, individuals. For that reason, the behavioral studies were done at the level of the inflorescence.

The flower (Fig. 1) has a long nectar spur (12–16 mm; Ownbey, 1947), and only long-tongued visitors, such as *Bombus appositus*, can reach the nectar through the front. Short-tongued, nectar-robbing bumble bees bite holes in the spur-shaped petal to reach the nectar. In the absence of visitors, nectar, with an average sugar concentration of 35%, accumulates in the flowers at a rate of ~1  $\mu$ L per day. Flowers remain in good condition for ~4 d before they begin to wilt. *Corydalis caseana* is self-compatible, yet it is dependent upon insect visitors for pollination. When compared with open-pollinated and outcross-pollinated flowers, self-pollinated flowers produced fewer fruits, fewer seeds per fruit, and smaller seeds, suggesting lower fitness due to inbreeding depression. (For additional information on the distribution and reproductive biology of *C. caseana* see Maloof, 2000b.)

**Effect on fruit and seed set**—To determine the age at which flowers were robbed and the effects of robbing on fruit and seed set, 101 flowers were followed from bud stage until they were either in fruit or had fallen off the plant. The flowers were on eight inflorescences on eight different plants. Each

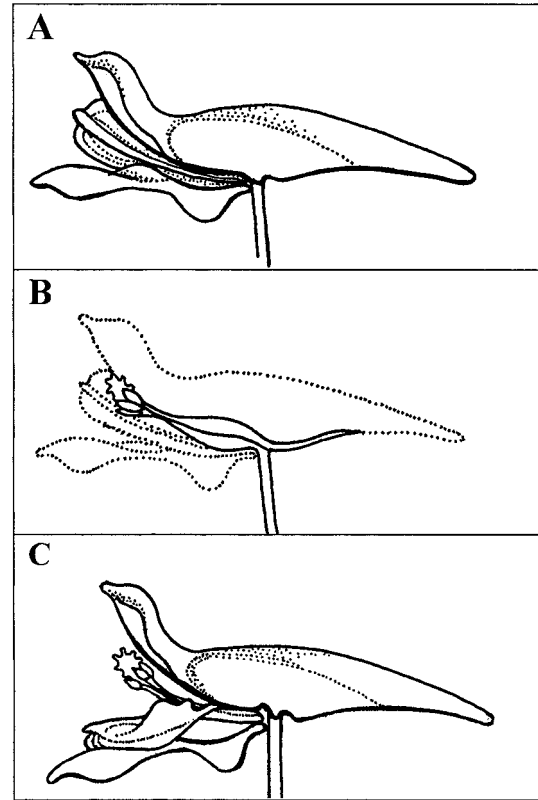


Fig. 1. Flower structure of *Corydalis caseana*. (A) Outer view of an open flower. (B) Cut-away view showing location of the reproductive organs within the inner petals. The nectary is projecting to the right of the pedicel, inside the nectar spur. (C) View of flower from the outside showing the inner petals and the reproductive organs exposed as they would be during a visit from a pollinator. Actual length of flower is 2 cm. (Drawn by Heather O'Connor, reproduced with permission; Maloof, 2000a.)

inflorescence had between 10 and 20 flower buds. By following all flowers on an inflorescence, instead of widely scattered individual flowers, fruit set and seed set could be measured on a per inflorescence basis and flowers with the same genetic and environmental conditions could be compared. Every bud or flower was observed in 1996 on 25, 26, 27, 28, 29, and 30 June and on 1, 2, 3, 5, 7, 9, 11, 12, 15, and 17 July. During visits the condition of each flower was described according to the following categories: (1) closed (bud stage); (2) open, without holes from nectar robbers; (3) open, with holes from nectar robbers; (4) flower with brown spots or wilted; (5) flower fell off, no fruit forming; and (6) fruit forming. Fruits were collected and brought to the laboratory where seeds in each fruit were counted. In this way, the complete history of 101 flowers was recorded.

**Pollination study**—The aim of this study was to determine if *B. occidentalis* robbers pollinate *C. caseana*. Monospecific patches of *C. caseana* plants were temporarily enclosed in tents 3.9 m wide  $\times$  2.7 m deep  $\times$  2 m high. The walls of the tents were made of fine mesh and the roofs were made of opaque polyethylene. The tents prevented legitimate pollinators from gaining access to the experimental plants and kept robbers contained inside with the plants during the experimental treatments. Commercially raised colonies of *Bombus occidentalis* robbers were used in these studies (suppliers: 1997, Bees West, Freedom, California, USA; 1998, Koppert Biological Systems, Romulus, Michigan, USA). Each colony contained ~80 bees. Commercially supplied pollen pellets were freely administered to the colonies, but no supplemental nectar was available to them during the course of the experiments. Prior to the initiation of the experiments, the bees were allowed to forage freely in enclosures for a few hours a day. This "training period" gave the

bees an opportunity to learn how to collect nectar from *C. caseana* by robbing. None of the bees foraged legitimately or collected pollen from the flowers. After 1 wk, all foraging workers were robbing nectar from flowers. Thus, the foraging behavior of the commercial bees was the same as the behavior of the naturally occurring *B. occidentalis*.

After foraging, whether for training or experimental purposes, the bees were returned to the colony box by adjusting the nest entrance so that returning bees could enter but not leave and by capturing any remaining foragers in plastic vials and returning them to the nest.

For this experiment, eight inflorescences in each tent (experimental and control) were protected with netting while the flowers were still in bud. When the inflorescences were in peak bloom, the netting was removed and the pedicels of all open flowers on the test inflorescences were marked with permanent ink. (Pilot studies showed that fruits and seeds developed normally when the pedicels were marked in this way.) Immediately after marking, the colony of robbers was allowed to forage for 4 h inside the experimental tent. No robbers were released into the control tent. After 4 h the bees were removed from the experimental tent and the open and robbed flowers on each inflorescence were counted. The inflorescences were rebagged and checked for fruit set after 16 d.

The experiment was repeated four times (17, 19, 21, and 23 July) in a crossover design that alternated the experimental (with robbers) treatment and the control (without robbers) treatment. Previous research had shown that *C. caseana* would not set fruit if all visitors were excluded (Maloof, 2000a); therefore, fruit set in the experimental inflorescences would indicate pollination by the robbers.

**Nectar removal**—To determine how much nectar a robber removes from a filled flower, a tent protected plants from visitors for 4 d. On the fifth day (16 July 1997) the robbers were allowed to forage in the tent. When a flower was robbed, it was collected, along with an adjacent (same-age) unvisited flower from the same inflorescence. The nectar volume in both flowers was measured immediately by using a 10- $\mu$ L microcapillary tube to extract the nectar and a digital micrometer (Mitutoyo, Utsunomiya-shi, Japan) to measure the filled length of the tube. Length measurements were converted to volume.

**Effect on pollinator behavior**—To determine if *B. occidentalis* robbers changed the behavior of *B. appositus* (the legitimate pollinator) a pair of tents was erected a minimum of 5 m apart over a naturally occurring *C. caseana* patch. I attempted to match the densities of the inflorescences in both tents. Tents were left in place for 3–4 d. On the morning of the experiment, a colony of *B. occidentalis* was allowed to forage freely in one of the tents. All foragers collected nectar by robbing. After 4 h, the colony was removed from the tent. Immediately following the removal of the robber, the footprints of the tents were outlined using plastic tagging tape and the tents were removed. To avoid disturbing any possible scent marks, flowers were not handled. Three researchers were stationed by each outlined patch. Both patches were observed simultaneously by the three-person teams. When a *B. appositus* (pollinator) bee entered the patch it was identified and its movements were followed. Observers noted the number of flowers visited on an inflorescence and the distance flown to the next inflorescence. Distances were estimated visually to the nearest cm with the assistance of a meter rule. Bees were followed until they flew out of the patch. If the distance of the final flight, which took the bee out of the patch, could be determined, that flight distance was recorded as well. It was rare for visitors besides *B. appositus* to enter the patch, but if they did, they were brushed out. The experiment could not be conducted as a blind test, because robbing holes in the flowers were evident to the observers. After 1 h, the observers exchanged patches in order to eliminate any bias in estimation and continued observations for a second hour. This process was repeated on 20, 23, and 27 July 1998 with the tents in a new location for each trial.

**Data analysis**—To eliminate differences in fruit set or seed set that could be caused by genetic and/or environmental factors, the fate of robbed and unrobbed flowers on the same inflorescence were compared by paired *t* test.

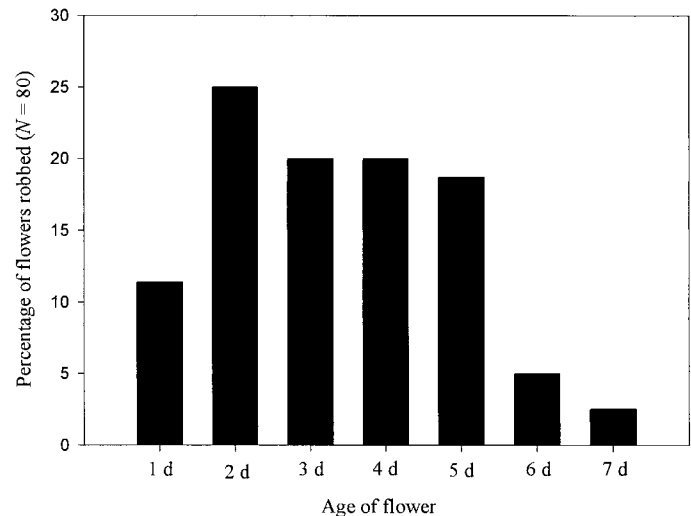


Fig. 2. Age of flower when first robbed.

Nectar volumes from robbed and unrobbed flowers on the same inflorescence were also compared by paired *t* test.

To determine if there was any relationship between the initial nectar volume and the amount of nectar removed, the volumes removed from the robbed flowers (determined by subtracting the nectar volume remaining in the robbed flower from the nectar volume in its unrobbed counterpart) were compared with the nectar volumes in unrobbed flowers by linear regression.

Pollinator behavior was analyzed on a per bee basis. Because marking the bees could interfere with their normal behavior, I did not mark them. Consequently, it is possible that a bee could have left the plot and then reentered at a later time without being recognized as a previous visitor. The number of inflorescences visited per bee, the number of flowers visited per inflorescence per bee, and the distance flown between inflorescences were compared for the two treatments (robbed and unrobbed; treatment = fixed, date = random) by the General Linear Method procedure in SPSS 8.0 (Norusis, 1998).

## RESULTS

**Effect on fruit and seed set**—Eighty percent of the censused flowers ( $N = 101$ ) were robbed at least once during their lifetime. The initial robbing hole occurred most frequently the day after the flowers opened (day 2), but robbing also occurred on newly opened flowers and older flowers (Fig. 2).

Per inflorescence, 62% of the robbed flowers formed fruits and 54% of the unrobbed flowers formed fruits (Fig. 3). The difference in fruit set was not significant (paired *t* test,  $N = 8$ ,  $P = 0.536$ ). Mean seed set per flower per inflorescence was 3.6 seeds per fruit for the robbed flowers and 3.3 seeds per fruit for the unrobbed flowers (Fig. 3). This difference was also not significant (paired *t* test,  $N = 8$ ,  $P = 0.847$ ).

**Pollination study**—The overall proportion of flowers robbed in experimental inflorescences, after 4 h exposure to the robbers, was 59% ( $N = 32$ ). None of the flowers protected from all visitors (control) set fruit. Likewise, none of the flowers exposed only to robbers (experimental) set fruit; therefore, the robbers are not pollinating *C. caseana*. Breeding experiments being conducted in the tent at the same time had normal rates of fruit set; consequently, the lack of fruit set in this experiment was not an artifact of tent effects.

**Nectar removal**—As expected, robbers reduced the availability of nectar in *C. caseana* ( $P < 0.0005$ ; Fig. 4). The

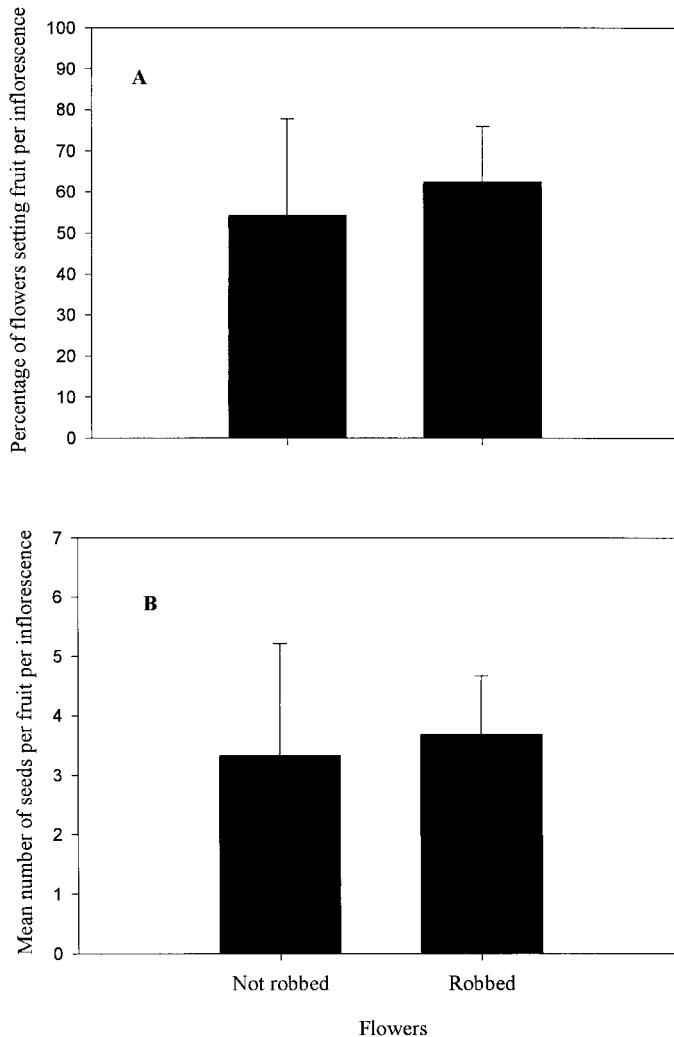


Fig. 3. Effects of robbing (A) on fruit set and (B) on seed set. Bars = +2 SE. Differences are not significant ( $t$  test).

unrobbed flowers contained a mean ( $\pm 2$  SE) nectar volume of  $4.8 \mu\text{L}$  ( $\pm 1.74$ ,  $N = 28$ ), and the robbed flowers contained a mean nectar volume of  $1.0 \mu\text{L}$  ( $\pm 0.74$ ,  $N = 28$ ). It is important to note, however, that these observations were made on flowers previously protected from visitors. The natural standing crop nectar values were lower (e.g.,  $0.60 \pm 0.73 \mu\text{L}$ , mean  $\pm$  SD; Maloof, 2000b), and it has not been determined exactly how robbers influence nectar volume or variation in the flowers under open field conditions. In the previously protected flowers of this experiment, not all the nectar was drained by the robbers. In the 28 pairs of flowers tested (assuming that the robbed flowers began with a nectar level similar to the unrobbed flowers) the robbers removed an average of 79.7% of the available nectar, leaving behind a mean of  $1 \mu\text{L}$  of nectar. There was a significant relationship between the amount of nectar in the unrobbed flowers and the amount of nectar presumably removed from the robbed flowers ( $F_{1,27} = 134.8$ ,  $P < 0.0005$ ,  $r^2 = 0.838$ ; nectar removed =  $0.37 + 0.72$  original nectar in flower). In other words, the robbers did not remove a fixed volume of nectar; the more nectar that was contained in a flower, the more nectar they removed, though

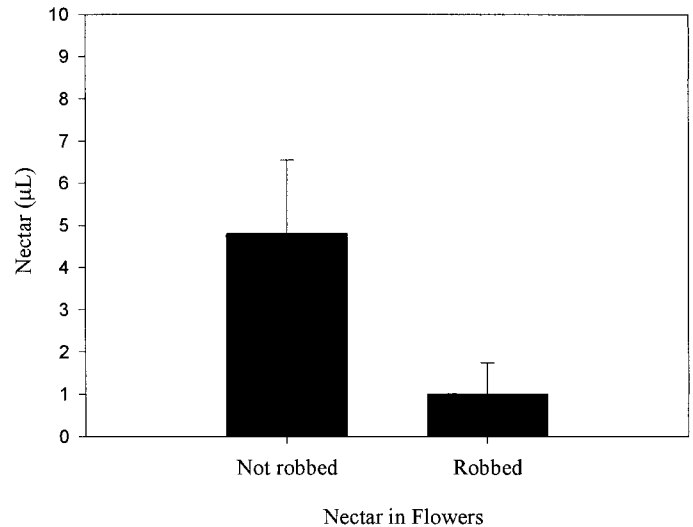


Fig. 4. Comparison of nectar volume in flowers that were not robbed and flowers that were robbed. Bars represent +2 SE. Differences are significant ( $t$  test,  $P < 0.0005$ ).

still leaving behind an average of 20% of the original nectar volume.

**Effect on pollinator behavior**—During this study, a total of 75 *B. appositus* were observed visiting 785 inflorescences and 3453 flowers. Thirty-five *B. appositus* were observed on the plants in the unrobbed plots and 40 bees were observed on the plants in the robbed plots (mean per date  $\pm 2$  SE;  $11.7 \pm 10.4$  observations vs.  $13.3 \pm 6.7$  observations; Fig. 5). There were no significant differences in the number of inflorescences visited per bee ( $10.0 \pm 2.6$  vs.  $10.9 \pm 2.9$ ;  $F_{1,71}$ ;  $P = 0.784$ ) or the number of flowers visited per inflorescence per bee ( $4.1 \pm 0.7$  vs.  $4.7 \pm 0.8$ ;  $F_{1,71}$ ;  $P = 0.094$ ) when unrobbed and robbed treatments were compared.

Of the four parameters I measured, only distance flown between inflorescences differed in the robbed and the unrobbed treatment (Fig. 5). Bees flew significantly further between inflorescences in the robbed treatment (mean  $\pm 2$  SE,  $32 \pm 5.6$  cm;  $N = 40$ ) than they did in the unrobbed treatment ( $21 \pm 2.2$  cm,  $N = 35$ ; GLM,  $F_{1,71} = 5.57$ ,  $P = 0.021$ ).

## DISCUSSION

Eighty percent of the flowers of the rare *C. caseana* plants in this location are naturally robbed, so it is important to determine what effects robbers have—positive, negative, or neutral. Here I have examined the effects of a nectar robber on a plant species and on the plant's primary pollinator.

The natural place to look for effects is in fruit set and seed set. Darwin (1872) assumed that robbers had negative fitness effects, but in a recent survey (Maloof and Inouye, 2000) robbers were equally as likely to have positive or neutral effects, as they were to have negative effects. In this study I have found that the robber has no discernable negative effect on fruit set or seed set.

In other studies, where robbers had positive effects on reproductive success (Koeman-Kwak, 1973; Waser, 1979; Higashi et al., 1988; Guitián, Sánchez, and Guitán, 1994; Navarro, 2000), the robbers were pollinating in the process of nectar robbing. In this study, I have determined that the rob-



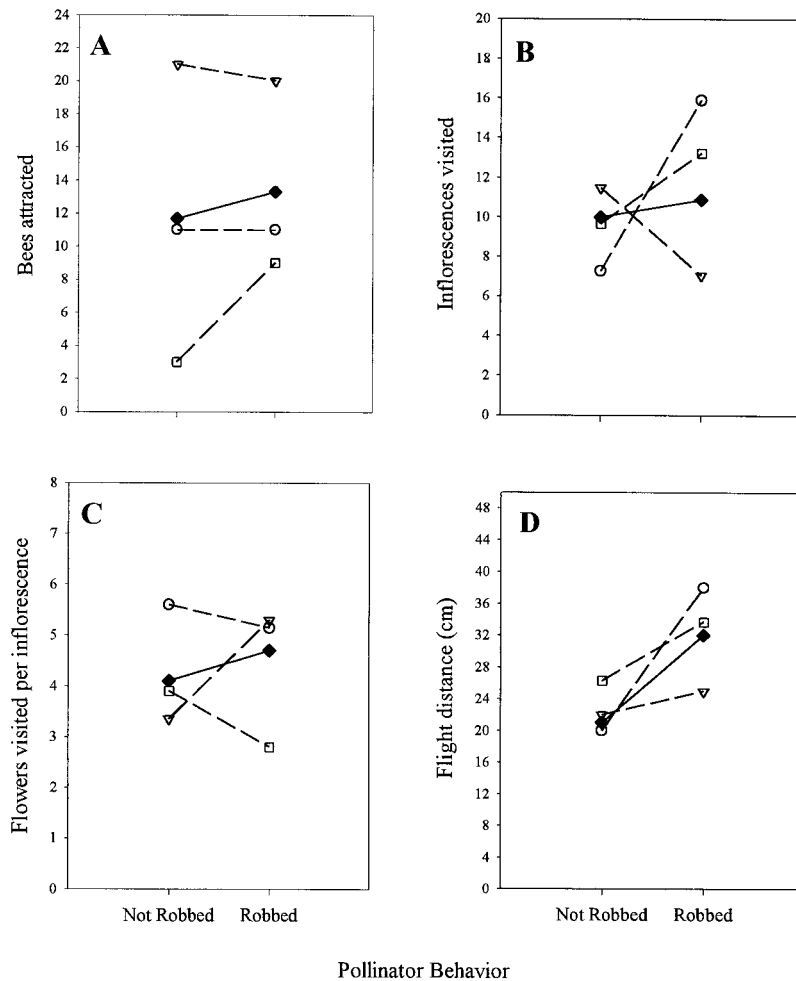


Fig. 5. Effects of robbing on pollinator behavior. Open symbols represent repetitions of the experiment:  $\circ$  = 7/20/98;  $\nabla$  = 7/23/98;  $\square$  = 7/27/98. The closed symbol ( $\blacklozenge$ ) represents the mean of the means for all bees over all trials. (A) Total bees attracted. (B) Mean number of inflorescences visited per bee in each plot (no significant difference). (C) Mean number of flowers visited per bee per inflorescence (no significant difference). (D) Mean flight distance per bee (differences are significant, GLM;  $N = 75$ ,  $P = 0.021$ ).

bers do not pollinate *C. caseana*. This result was somewhat surprising because earlier experiments showed that *C. caseana* is self-compatible, with no spatial or temporal separation of male and female function (Malooof, 2000a). I suspected that the activity of the robbers would result in fertilization, as in *Corydalis ambigua* (Higashi et al., 1988), but experiments proved that this was not so. To my knowledge this is the first study in which a controlled experiment showed that the robbers were not pollinating. More studies of this type would greatly aid our understanding of robbers.

Although the robbers removed a substantial proportion of the nectar from the previously protected flowers, it is noteworthy that in most cases some nectar was left in the flowers. Additional studies should be done comparing nectar volumes and variance for naturally occurring (unprotected) robbed and unrobbed flowers. In a study on *Impatiens capensis* the standing crop of nectar in robbed flowers was lower than the standing crop of nectar in unrobbed flowers, because robbers could reach more of the nectar (H. Young, Middlebury College, personal communication).

*Corydalis caseana* requires a pollinator visit for reproduction (Malooof, 2000a), and the consistently high rate of fruit

set in my study plots between 1996 and 1999 (>80%), despite robbing rates of 39–87% (Malooof, 2000b, and unpublished data), indicates that nectar removal by robbers may not be consequential enough to cause the legitimate pollinators to switch their foraging to another species. Also, complex flowers, such as *C. caseana*, take longer for pollinators to learn how to handle and bees are more likely to be constant to complex flowers once they have learned to handle them (Lavery, 1994). Similarly, Stout, Allen, and Goulson (2000) found that despite nectar robbing levels of 96%, the pollinator bumble bees continued visiting the complex flowered species they studied, *Linaria vulgaris*.

The tent studies showed that pollinating bumble bees did not avoid the experimental robbed plots by comparing pollinator visitation to these plots to visitation within the experimental unrobbed plots. This indicates that the bees either cannot tell from a distance which flowers are robbed or that they do not discriminate between robbed and unrobbed flowers. Stout, Allen, and Goulson (2000) also observed no discrimination by bumble bee pollinators between robbed and unrobbed flowers. In both their study and this study, there was no difference in seed set between robbed and unrobbed flow-

ers, most likely because of equal pollinator visitation to robbed and unrobbed flowers. Similarly, Rust (1979) and Hodges (1995) found that manipulating the nectar volume did not change the number of pollinators arriving at plants. Hummingbird pollinators, however, may avoid robbed flowers (Irwin and Brody, 1998). Measuring avoidance, or its contrary, attraction, is important because if pollinators avoid robbed flowers, then robbers would have negative fitness effects on plants, albeit indirectly.

Once the pollinators (*B. appositus*) are in the experimentally robbed plot, one would expect them to visit fewer flowers on an inflorescence and fewer inflorescences before moving out. Although these are the responses produced by lowered nectar levels in other studies (see Kadmon and Shmida, 1992; Johnson and Nilsson, 1999), the pollinators in this study did not show those behaviors: they visited similar numbers of flowers per inflorescence and a similar number of inflorescences before they left the experimental robbed plot. The one difference I did detect between the robbed plots and the unrobbed plots was that *B. appositus* tended to fly longer distances between foraging bouts in the robbed plots. A pollinator flying longer distances between visits to the same plant species when total visit numbers are not reduced might have positive effects on the fitness of the plant through increased pollen flow distances. In previous studies on *C. caseana*, outcross-pollinated flowers produced more fruits and more seeds than self-pollinated flowers (Malooof, 2000a). In plants with numerous stems and numerous inflorescences, such as *C. caseana*, longer flight distances could minimize the possibility of geitonogamy and the resulting effects of inbreeding.

Both the bumble bee nectar robber and the bumble bee pollinator are necessary for the indirect positive fitness effect of increased outcross pollination due to longer flight distances. Flowers visited by both robbing and nonrobbing bumble bees are not uncommon. Willis and Burkill (1903) mention this combination of visitors on *Arctostaphylos uva-ursi*, *Erica cinerea*, *Vicia sepium*, and *Oxytropis campestris*. A number of species in the vicinity of the Rocky Mountain Biological Laboratory are also visited by both robbing bumble bees and nonrobbing bumble bees: *Delphinium nuttallianum*, *D. barbeyi*, *Aconitum columbianum*, *Mertensia ciliata*, *Lathyrus leucanthus* (D. Inouye, University of Maryland, personal communication) and *Linaria vulgaris* (personal observation). Further research is needed to determine if longer flight distances by the pollinators, such as those found in this study, are a typical result of these three-species interactions.

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