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ARE NECTAR ROBBERS CHEATERS OR MUTUALISTS?

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Abstract. Nectar robbers are birds, insects, or other flower visitors that remove nectar from flowers through a hole pierced or bitten in the corolla. This paper is a review of the effects of nectar robbers on pollinators, pollination, and fitness of the plants they rob. Charles Darwin assumed that nectar robbers had a negative impact on the plants that they visit, but research done in the last 50 years indicates that they often have a beneficial or neutral effect. Several studies document that robbers frequently pollinate the plants that they visit. Robbers may also have an indirect effect on the behavior of the legitimate pollinators, and in some circumstances, the change in pollinator behavior could result in improved fitness through increased pollen flow and outcrossing. The effects of nectar robbers are complex and depend, in part, on the identity of the robber, the identity of the legitimate pollinator, how much nectar the robbers remove, and the variety of floral resources available in the environment.

Key words: Bombus *spp. bumble bee; cheater; foraging; hummingbird; indirect effects; mutualism; nectar robbing; plant fitness; pollination.*

INTRODUCTION

Nectar robbers are birds, insects, or other flower visitors, that remove nectar from flowers through a hole pierced or bitten in the corolla. The last comprehensive review on nectar robbing was by Inouye in 1983. Since then, new studies have appeared that broaden our view of the phenomenon. The goals of this paper are to review the recent literature on nectar robbing and to attempt an expanded understanding of the ecological and evolutionary roles that robbers play. Understanding the effects of nectar robbers on the plants they visit and on other flower visitors is especially important when one considers the high rates of robbing that a plant population may experience (Table 1) and the high percentage of all flower visits that nectar robbers make to some species (Table 2).

The plant–pollinator relationship is considered a mutualism because the plant benefits from the pollinator's transport of male gametes (but see Thomson and Thomson 1992), whereas the pollinator benefits from a reward (nectar, pollen, oil, fragrance, etc.). Mutualisms are thought to be especially susceptible to cheaters, species that can obtain the reward produced for the mutualist without providing service in return (Boucher et al. 1982, Thompson 1982, Bronstein 1994). Nectar robbers are frequently described as cheaters in the plant–pollinator mutualism (Darwin 1841, Thompson 1982, Bronstein 1994, Richardson 1995), because it is assumed that they obtain a reward (nectar) without providing a service (pollination). In this paper, however, we will explore the legitimacy of that assumption.

In the 18 studies we found that measured the effect of nectar robbers on seed set, the incidences of negative effects, neutral effects, and positive effects were equal (Table 3). For example, Morris (1996) found that, ''despite the expectation that nectar larceny should be detrimental to plant fitness . . . there were no significant differences . . . in the percent of flowers initiating fruits, the number of nutlets initiated per successful flower, or the mass of seeds produced by robbed and unrobbed flowers.''

Why does the expectation that nectar robbers are universally detrimental cheaters persist, in the presence of evidence to the contrary? Perhaps it has to do with the difficulty of changing attitudes that have been held for so long. Charles Darwin (1872) himself wrote that, ''all plants must suffer in some degree when bees obtain their nectar in a felonious manner by biting holes through the corolla.''

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TABLE 1. Percentage of flowers robbed on plants of various species, as reported in the literature.

Robber species	Flower species	Flowers robbed (%)	Reference
Flower-piercer birds			
Diglossa baritula	*Erythrina leptorhiza*	91–100	Hernandez and Toledo (1979)
Diglossa baritula	*Salvia mexicana*	92	Arizmendi et al. (1996)
Diglossa baritula	*Fuchsia microphylla*	37	Arizmendi et al. (1996)
Diglossa baritula	*Penstemon kunthii*	50–80	Lyon and Chadek (1971)
Hummingbirds			
Eupherusa exima	*Razisea spicata*	98	D. Boose, *unpublished report*
Carpenter bees			
Xylocopa violacea	*Petrocoptis grandiflora*	44.6	Guitian et al. (1994)
Bumble bees			
Bombus occidentalis	*Corydalis caseana*	40–80	Maloof (2000)
Bombus occidentalis	*Ipomopsis aggregata*	32.9	Irwin and Brody (1999)
Bombus terrestris	*Vicia faba*	62	Newton and Hill (1983)
Bombus terrestris	*Corydalis cava*	83.9	Olesen (1996)
Bombus hypocrita sapporensis	*Corydalis ambigua*	71–98	Higashi et al. (1988)
Trigona bees			
Trigona fulviventris	*Lantana camara*	34	Barrows (1976)
Ants			
Polyrachis spp.	*Aerangis verdickii*	62–67	Koopowitz and Marchant (1998)
Multiple species	*Quassia amara*	83	Roubik et al. (1985)
	Lonicera etrusca	99	Guitian et al. (1993)
	Justicia aurea	81.1	Willmer and Corbet (1981)
	Justicia aurea	>90	McDade and Kinsman (1980)
	Aphelandra golfodulcensis	>90	McDade and Kinsman (1980)

We propose here a reexamination of the attitude held by Darwin, and many others, about nectar robbers. When the existing literature on robbers is examined as a whole, it appears that robbers, at least bumble bee nectar robbers, are as likely to be beneficial to the flowers they visit as they are to be detrimental. In this paper, we discuss six questions that help to predict whether the presence of robbers will have negative or positive fitness consequences for the plant: (1) Are the robbers pollinating? (2) What type of organism is the robber? (3) Does the robber change the behavior of the legitimate pollinator? (4) What is the identity of the legitimate pollinator(s)? (5) How much nectar is left by the robber? (6) What other resources are available to the pollinator?

Nectar theft (sensu Inouye 1983), characterized by a morphological mismatch between flower and visitor, and not by damage to corollas, will not be addressed in this paper.

ARE THE ROBBERS POLLINATING?

Inouye (1980) wrote that robbers ''generally are not pollinators,'' but in most cases, it is merely assumed that the robbers are not pollinating; no controlled studies have been done to explore this assumption. In fact, many studies that have examined robbers more closely have suggested that they often do pollinate. In some cases, this conclusion was made through observation and inference (the robbers appear to be pollinating, e.g., Guitian et al. 1993, 1994). In other cases, observations coupled with field experiments enable us to say conclusively that the robbers are pollinators. Palmer-Jones et al. (1966) caged red clover (*Trifolium pratense*). In cages containing long-tongued bumble bees, 60–79% of the flowers set fruit; in cages containing only short-tongued nectar robbers (*Bombus terrestris*), 10–27% of the flowers set fruit; and in cages that excluded pollinators, 0–0.2% of the flowers set fruit. Although the

TABLE 2. Percentage of all flower visits to eight plant species that are from nectar robbers.

Plant species	Visits from robbers (%)	Reference
Erythrina leptorhiza	89	Hernandez and Toledo (1979)
Quassia amara	52–98	Roubik et al. (1985)
Anthyllis vulneria	45	Navarro (2000)
Mertensia ciliata	50	Geber (1982)
Salvia mexicana	17	Arizmendi et al. (1996)
Fuchsia microphylla	11	Arizmendi et al. (1996)
Fuchsia magellanica	80	Traveset et al. (1998)
Aphelandra golfodulcensis	50	McDade and Kinsman (1980)

TABLE 3. The effect of nectar robbers on seed set of 18 plant species.

Effect on seed set	Robber(s)	Reference
Negative	birds (*Phrygilus*)	Traveset et al. (1998)
Negative	tropical bees (*Trigona*)	Roubik et al. (1985)
Negative	tropical bees (*Trigona*)	Roubik (1989)
Negative	tropical bees (*Trigona*)	Roubik (1982)
Negative	wasps (*Rynchium* and *Ropalidia*)	Reddy et al. (1992)
Negative	bumble bees (*Bombus*)	Irwin and Brody (1999)
Neutral	birds (*Diglossa*)	Arizmendi et al. (1996)
Neutral	carpenter bees (*Xylocopa*)	Guitian et al. (1993)
Neutral	bumble bees (*Bombus*)	Bilinski (1970)
Neutral	bumble bees (*Bombus*)	Newton and Hill (1983)
Neutral	bumble bees (*Bombus*)	Zimmerman and Cook (1985)
Neutral	bumble bees (*Bombus*)	Morris (1996)
Positive	carpenter bees (*Xylocopa*)	Waser (1979)
Positive	carpenter bees (*Xylocopa*)	Guitian et al. (1994)
Positive	bumble bees (*Bombus*)	Hawkins (1961)
Positive	bumble bees (*Bombus*)	Koeman-Kwak (1973)
Positive	bumble bees (*Bombus*)	Higashi et al. (1988)
Positive	bumble bees (*Bombus*)	Navarro (2000)

long-tongued bees were more effective as pollinators, it is also clear that the robbers were pollinating. Similar results were found by Kendall and Smith (1976), who studied fruit set in the bean, *Phaseolus coccineus*. Previously unvisited flowers were observed for visitors and subsequent fruit set. Of the flowers visited by the legitimate pollinators (long-tongued bumble bees and short-tongued honey bees), 18–31% set fruit, of flowers visited only by the robbing bees (*Bombus terrestris* and *B. lucorum*) 6.5% set fruit, whereas only 2.8% of unvisited flowers set fruit.

Waser (1979) observed carpenter bees (*Xylocopa* sp.) contacting the reproductive parts of self-incompatible desert shrubs, *Fouquieria splendens*, while robbing them of nectar. The bees that he collected carried pollen from the species they were robbing. When he excluded hummingbirds, the presumed primary pollinators, but allowed the carpenter bees to access the plants, the flowers set seed. In addition, he found a strong positive relationship between seed set and carpenter bee abundance. Scott (1989), studying the same species, found that 80% of the flowers formed fruits and 54–77% of the ovules formed seeds when a flower was visited at least twice by nectar-robbing carpenter bees. He concluded that carpenter bees are the major pollinators of *F. splendens* in Big Bend National Park, Texas, USA.

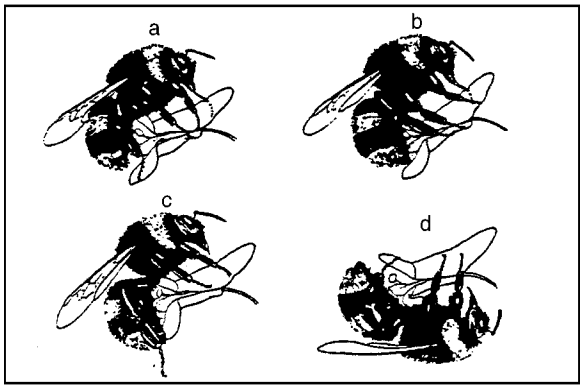

FIG. 1. *Bombus hypocrita sapporensis* on *Corydalis ambigua* flowers (from Higashi et al. 1988; used with permission from Blackwell Science Publishers). The anthers and stigma are exposed while the queens are nectar robbing (a,b) or walking around on the flower (c,d). This may result in pollination.

Higashi et al. (1988) studied the behavior of bumble bee queens (*Bombus hypocrita sapporensis*) that robbed nectar from *Corydalis ambigua* flowers. Breeding studies suggested that the plant was self-incompatible; therefore, it was not surprising that the four plants that were not visited by insects did not produce any seeds. However, 59.7% of the *C. ambigua* plants that were visited *only* by nectar robbers set seed, prompting the researchers to conclude that ''robbers contributed directly to pollination.'' Pollination probably took place when the large queens positioned themselves to rob the flower (Fig. 1). The authors suggest that these bumble bees are not real ''robbers,'' but should be called ''robber-like pollinators.''

Birds may also act as ''robber-like pollinators.'' In one example, a flower-piercer, *Diglossa* sp., pollinated *Tristerix longebracteatus* flowers while robbing them of nectar (Graves 1982). In the population that Graves studied, ''virtually every open flower was basally pierced by *Diglossa* or hummingbirds,'' yet the fruit set was 87.5%. He concluded that ''*Diglossa* appears to be a principal pollinator of *T. longebracteatus* in northern Peru.''

These examples document cases in which the robber pollinates in the process of collecting nectar. However, pollination by robbers is not always concurrent with nectar collection. Angiosperms have a broad range of reproductive strategies, and the morphology and phenology of the flower will influence the behavior of the

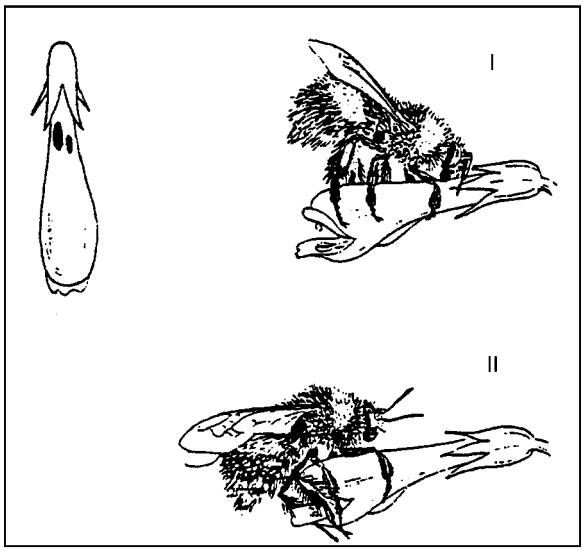

FIG. 2. Holes in *Melampyrum pratense* flower from nectar robbing (from Meidell 1944; used with permission). (I) *Bombus lucorum* nectar robbing, and (II) pollen gathering.

robber. For example, many short-lived flowers offer both pollen and nectar during their entire life span (e.g., *Hibiscus moscheutos;* Spira 1989). Some longer lived flowers offer both nectar and pollen on the first day, and negligible rewards after that (e.g., *Lantana camara;* Barrows 1976). Other flowers stagger their reward presentation, offering first pollen and later nectar, or vice versa (e.g., *Mertensia paniculata;* Morris 1996). Because of the differences in reward presentation, visitors may be differentially attracted to flowers in a particular stage of development, and visitors may ''handle'' flowers differently depending on the reward that they are seeking. This could result in a bumble bee robbing nectar by biting a hole through the corolla, but then subsequently pollinating while attempting to collect pollen.

An example of this bimodal foraging behavior (see Fig. 2) is given by Meidell (1944), who described the foraging behavior by a bumble bee to flowers of *Melampyrum pratense:* ''After the bee has robbed a flower of nectar, she places herself on the edge of the upper lip, stretching her hindlegs across its mouth, and vibrates her wings rapidly. This results in pollen being showered on to her legs. When this same bee takes up her position on the next flower, her pollen-covered legs touch the projecting stigma, thus probably effecting pollination.''

Similar behavior, but in the opposite order, was noted by Macior (1966); bumble bee queens (*Bombus affinis)* would sometimes collect pollen from *Aquilegia canadensis* flowers before climbing up the outside of the nectar spur and robbing the nectar. He concluded that ''pollination is accomplished during pollen and nectar foraging even when nectar is secured by spur perforation.'' *Bombus terrestris* bumble bees behave in a similar manner on *Corydalis cava*, first foraging for pollen in a flower, then climbing outside the flower to rob nectar (Olesen 1996). Koeman-Kwak (1973) also noted this pattern of pollen collector–nectar robber. *Bombus terrestris* and *B. jonellus* first foraged for pollen while hovering beside the *Pedicularis palustris* flower, and then landed on the flower to rob the nectar. Flowers were pollinated during this process, and ''the seed production rate of flowers pollinated in this manner was comparable to that of flowers pollinated by legitimate collectors'' (Koeman-Kwak 1973).

Morris (1996) studied the behavior of two pollen collector–nectar robbers, *Bombus mixtus* and *B. frigidus*. These bumble bees would visit *Mertensia paniculata* flowers in their young (1st day), pink, pollen-producing stage to collect pollen, and visit the older (3rd–5th day), blue, nectar-producing flowers as nectar robbers. Individual bumble bees switched frequently between nectar robbing and pollen collection. Morris postulated that the nectar reward in the blue flowers may act as a key enticement to robbers, ''which then enhance plant reproduction by legitimately visiting early-stage flowers.''

Some nectar robbers do not bite holes in a flower's corolla. These ''secondary nectar robbers'' collect nectar through holes made by previous visitors. Honey bees (*Apis mellifera*) often behave as secondary nectar robbers. Rust (1979) observed that, ''During nectar foraging an individual *A. mellifera* might steal nectar from several cut spurs then switch and enter the saccate sepal for nectar, only to switch back to robbing after several pollinating visits.'' It is likely that these bees, too, are both robbers and pollinators.

These examples are of individuals that both rob and pollinate, sometimes simultaneously, and in other cases as separate activities, but in all cases, an individual bee may do both. In other cases, however, individual bees of the same species may only rob nectar, or only visit a flower legitimately and pollinate. Individual honey bees and bumble bees tend to specialize in both their choice of flowers and in their foraging tactic on those flowers (Heinrich 1976, Waser 1986, Villalobos and Shelly 1996). The most common explanation of this specialization is that an early learned behavior that is successful tends to be repeated to the exclusion of other behaviors. The species, then, could be considered as both a robber and a pollinator, even though the individuals of that species may behave as only one or the other. For instance, the bumble bee *Bombus terrestris* robs the flowers of red clover, but *Bombus terrestris* can also be the most effective pollinator of the crop (see Hawkins 1961, Free 1970). Bumble bee colony growth is dependent upon the rate of food intake (Oster 1976) so it is likely, although never tested, that robbers will contribute to the success of the colony by their collection of nectar. A successful colony will produce more bees, and if a certain percentage of these bees behave as legitimate pollinators, then a plant with a

long blooming period could, in theory, benefit from the robbers.

What Type of Organism Is the Robber?

It is interesting to note that almost all of these cases of robber-like pollinators involve bees. Most, but not all, of the pollination by robber bees is a result of the collection of pollen, an important food source for developing larvae. Carpenter bees or bumble bees were the robbers in 11 of the 12 studies that showed neutral or positive effects on seed set due to robbers (Table 3).

Trigona bee robbers, on the other hand, are always associated with negative effects on seed set (Table 3), perhaps because of their aggressive, territorial nature. *Trigona* bees have been known to chase away hummingbird pollinators, thus causing reduced seed set (Roubik 1982). Due to their small size, and the structure of the flowers they rob, it may take an individual *Trigona* bee up to 20 min to make a robbing hole; this investment of time may be the reason for their territoriality.

Because the ability of other types of robbers to pollinate has rarely been tested, it is unclear whether bee robbers should be considered as unique or typical, but most birds do not deliberately collect pollen, and so may be less likely to pollinate.

Does the Robber Change the Behavior of the Legitimate Pollinator?

In addition to, or perhaps instead of, directly pollinating flowers, robbers may influence plant fitness by changing the behavior of the legitimate pollinators (Heinrich and Raven 1972). Indirect effects (the effect of one species on another that occurs through mutual interactions with a third species) such as this have been shown to have substantial ecological consequences (Miller and Travis 1996).

Bumble bees fly longer distances after visiting a plant low in nectar (as could occur in the presence of robbers) and shorter distances after visiting a plant rich in nectar (Pyke 1978b, Waddington 1980, Heinrich 1983, Marden 1984, Zimmerman and Cook 1985, Kadmon and Shmida 1992). Also, when nectar volumes drop below a certain threshold, pollinators visit fewer flowers per inflorescence (Pyke 1982, Hodges 1985). A consequence of this change in pollinator behavior due to decreased nectar volume could be more outcrossed pollination and higher fitness. Table 4 summarizes the possible behavioral changes in pollinators caused by nectar robbers. The behavioral changes, and their consequences, will be discussed.

Table 4. Potential behavioral changes in pollinators caused by nectar reduction by nectar robbers. The probable result for the plant assumes that all other behaviors remain the same on robbed and unrobbed flowers.

Behavioral changes in pollinators	Probable result for plant
Flight distances increase	Pollen flow distance increases
Fewer flowers visited on each inflorescence	Reduces geitonogamy in self-fertile flowers
Visit more flowers per unit time	Pollen flow rate increases
Reduced time spent in each flower	Less pollen transfer
Change foraging tactic to pollen collection only	Depends upon the morphology of the plant
Avoidance of robbed flowers	Could increase pollen flow distance if pollinator does not switch to different species
Switching to a different plant species	No pollen transfer

Changing the flight distance of the pollinators

Longer pollinator flight distances generally translate into increased pollen flow and increased outcrossing rates (Gliddon and Saleem 1984, Fenster 1991). Many experiments show that outcrossing leads to increased seed set and improved survival rates of seedlings (e.g., Charlesworth and Charlesworth 1987, Fenster 1991, Husband and Schemske 1996). If nectar robbers are the cause of longer flight distances by the legitimate pollinators, they could be increasing the fitness of the robbed plants by promoting outcrossing. The robbers could then be considered mutualists. Zimmerman and Cook (1985) tested one component of this hypothesis. They artificially robbed some flowers of *Impatiens capensis* by making a hole in the nectar spur of the corolla and removing nectar with a syringe. The robbed patch generated a greater frequency of long-distance bee flights, and the authors concluded that pollen was transported greater distances, resulting in a greater neighborhood size (sensu Wright 1969) in the robbed patch. In a first test of this hypothesis on naturally robbed plants, bumble bees visiting robbed patches flew longer distances between inflorescences (Maloof 2000).

The tropical hummingbird *Lampornis clemenciae* feeds by traplining. When nectar-robbing birds (*Diglossa baritula)* remove nectar from flowers, the hummingbirds must increase their foraging area to gather the nectar they need (Hernandez and Toledo 1979). Hernandez and Toledo conclude, ''therefore, we must consider that robbers may have a positive effect on this plant species [*Erythrina leptorhiza*].''

Changing the number of flowers visited by the pollinators

Robbers may also increase outcrossing by creating conditions that cause legitimate pollinators to visit fewer flowers on the same inflorescence. Bumble bees almost always work upward on vertical inflorescences, visiting multiple flowers and departing when food rewards fall below a critical threshold (Heinrich 1983, Hodges 1985). Hummingbirds also leave an inflorescence when nectar rewards drop below a certain thresh-

old (Pyke 1978*a*). Visiting multiple flowers on the same plant may lead to geitonogamy (the pollination of flowers by pollen from other flowers on the same plant), which can have numerous deleterious effects on reproductive success (de Jong et al. 1993). If nectar rewards are reduced by robbers, the legitimate pollinators may depart the inflorescence sooner, thus reducing geitonogamy and increasing the pollen dispersal distance (Klinkhamer and de Jong 1993). This is especially important in plants that are self-fertile and have many flowers on an inflorescence. Hodges (1995) found that individual hawk moths visited more flowers on plants that contained more nectar, and that the increased visitation resulted in increased selfing rates.

Changing time spent per flower by pollinators

Besides changing flight distances and the number of flowers visited by pollinators, nectar robbers may change the amount of time spent by pollinators in each flower. Greater amounts of nectar result in longer visits, and longer visits may result in greater deposition of pollen (Thomson and Plowright 1980, Feinsinger 1983, Lanza et al. 1995, but see Mitchell and Waser 1992). How do nectar robbers figure into this equation? It is clear that they reduce nectar levels (e.g., McDade and Kinsman 1980, Zimmerman and Cook 1985, Maloof 1999), and therefore shorten the length of a visit (Zimmerman and Cook 1985, Thomson 1986), potentially resulting in less pollen deposition on the stigma. Pollen deposition is related to both male and female fitness, so it would seem that the robbers are having a detrimental effect on the plant. One benefit of the pollinator spending a shorter time in each flower, however, is that more flowers are visited per unit time (Cruden et al. 1983). This could be beneficial for the plant if it causes a greater percentage of flowers to be visited than would be visited otherwise.

Flying longer distances between inflorescences, visiting fewer flowers per inflorescence, and visiting more flowers per unit time all have the potential to increase pollen flow, if the total number of visits is not reduced. The critical question then becomes: do nectar robbers reduce the number of visits from legitimate pollinators? There has been very little experimental work on this question, and thus far, the results appear mixed. The response from the legitimate pollinator appears to depend upon the identity of the pollinator, the amount of nectar left in the flower by the robber, and the availability and quality of alternate food sources. Each of these will be examined.

What Is the Identity of the Legitimate Pollinator(s)?

If a pollinator can tell from a distance that a flower has been robbed, it is reasonable to assume that the pollinator might avoid the flower because of lower expected nectar reward. Thus, the behavior of a pollinator in the presence of nectar-robbed flowers would be dependent upon the sensory capabilities of the pollinator. Rust (1979) found that *Bombus vagans* and *B. impatiens* bumble bees (legitimate pollinators of *Impatiens capensis*) ''do not discriminate between robbed and unrobbed or even experimentally nectarless flowers.'' We found a similar lack of discrimination in *Bombus appositus* bumble bees visiting robbed and unrobbed patches of *Corydalis caseana* flowers (Maloof 2000). Likewise, Goulson et al. (1998) found that ''bumblebees could not detect the nectar levels in inflorescences that had not been visited, and so readily accepted inflorescences that had been depleted of nectar artificially. Thus they are unlikely to be using either direct vision of nectar, detection of humidity gradients, or nectar scent to discriminate between inflorescences.'' Despite the bumble bees' inability to determine nectar levels visually, there is some evidence that bumble bees can distinguish between rewarding and nonrewarding flowers of the same species (see Goulson et al. 1998). It appears that this discrimination ability is the result of scent marks left on the flowers by previous bee visitors. This area of research is in its infancy and, to date, no studies have been done concerning the type of scent marks, if any, left by nectar-robbing bumble bees. In a study by Richardson (1995), honey bees (*Apis mellifera*) avoided *Chilopsis linearis* flowers robbed by carpenter bees (*Xylocopa californica*), but bumble bees (*Bombus sonoris*) did not. It is unknown whether the divergence in behavior of the bees reflects a difference in response to scent marking or sensory capabilities.

There is no evidence that butterflies avoid flowers robbed by *Trigona* bees (Barrows 1976). On the other hand, there is some evidence that hummingbirds may be able to determine the nectar status of flowers visually prior to visiting (Gass and Montgomerie 1981). One study has shown that hummingbirds visit more flowers in lightly robbed patches than in heavily robbed patches (Irwin and Brody 1998). This could be due to hummingbirds leaving the robbed patches because of low nectar levels, or staying in a patch where the first visits were highly rewarding, but the possibility exists that hummingbirds are able to determine which flowers have been robbed *before* they visit. In five of the six studies in which nectar robbing was shown to have a negative effect on fruit set, the legitimate pollinators were hummingbirds (Roubik 1982, 1989, Roubik et al. 1985, Traveset et al. 1998, Irwin and Brody 1999). In most cases, the reduced fruit set was caused by reduced visitation rates, whereas in one case (Traveset et al. 1998), it was probably caused by damage to the flowers from robbers.

How Much Nectar is Left by the Robber?

The nectar-removing capabilities of the robber may strongly influence the subsequent behavior of the legitimate pollinators, and hence affect the ultimate outcome for the plant. In one study, in which almost 100% of the nectar was removed from *Justicia aurea* flowers

by robbers, the legitimate hummingbird pollinators almost entirely ceased visiting. This clearly had a negative effect on reproductive success. However, in another species, *Aphelandra golfodulcensis*, the robbers left behind ~4 μL of nectar and hummingbird pollinators continued to visit (McDade and Kinsman 1980). As the authors of that study note, ''These two different responses would result in decreased or increased reproductive success, respectively.'' Increased reproductive success might be expected in the case of *Aphelandra golfodulcensis* because the legitimate pollinators were able to extract the nectar remaining after a robber visit, but they had to visit more flowers to fulfill their energy requirements.

Bumble bee (*Bombus occidentalis)* robbers on *Corydalis caseana* flowers leave behind an average of 20% of the original nectar volume (Maloof 1999). That may explain why pollinator-dependent fruit set remains high (>80%) even though the flowers are commonly (40–80%) nectar robbed.

What Other Resources Are Available to the Pollinator?

If pollinators are able to determine whether or not flowers have been robbed, there are four possible responses: (1) visit more flowers of the same species, indiscriminately, to get the necessary nectar volume; (2) avoid those flowers that have been robbed, but visit unrobbed flowers of the same species; (3) switch to pollen collection; or (4) switch to species with higher rewards (see Table 4).

Switching would be possible only if there are other flowers nearby with adequate nectar that could be efficiently handled by the pollinator. Bumble bees may avoid switching because learning new flowers, especially complex ones, requires an investment of time (Laverty 1994) and there are costs involved in switching (Chittka and Thomson 1997). For butterflies, also, switching is avoided because of the learning costs (Lewis 1989). Another, infrequently discussed, reason for not switching is the variation in nectar chemistry, such as the amino acid content of various nectars (Baker et al. 1978). Nectar from a particular flower may contain an essential amino acid and, for that reason alone, a pollinator may remain constant despite the presence of nectar robbers and low nectar volumes. Additionally, nectar from robbed flowers may have higher concentrations of amino acids due to diffusion from damaged tissues (Camargo et al. 1984).

More research is needed to determine what conditions cause pollinators to switch species and how often, if ever, nectar robbers are responsible for that switching. More research on pollinating birds, in particular, would be useful.

Evolutionary Implications

Flower morphology

It is generally agreed that legitimate pollinators may direct flower evolution by selecting for certain shapes and colors (in addition to other traits), but the role of nectar robbers as agents of selection on flower morphology is a promising field of study that has virtually been ignored. If robbers have fitness effects on plants, whether positive or negative, then they, too, may be operating as selective agents, influencing which colors, shapes, etc., will be the most successful. In general, flowers with long corolla tubes and nectar spurs are the ones most likely to be robbed. The traditional view on this observation is that the long corollas and flower spurs are selected for because they result in increased pollen deposition on stigmas from the restricted suite of long-tongued legitimate pollinators (Nilsson 1988); robbers simply bypass these structures because they cannot reach the nectar any other way (Soberón and Martínez del Río 1985). However, if corolla tube length and spur length, beyond some minimum, do not affect the nectar robbers adversely, but may affect the legitimate pollinators adversely because of constraints on proboscis or bill length, then there may be selection on corolla morphology from the robbers. This selection could be mediated either through the direct effects that robbers have on plant fitness (such as pollination), or through the indirect effects that robbers have on plant fitness by causing changes in pollinator behavior.

For instance, if a local deme of legitimate pollinators could not reach the nectar in the bottom of a long nectar spur, it would be logical for them to forage on a different species, at least until nectar accumulated to a level that they could reach. But if, in this same location, there were robbers that could get to the nectar in the bottom of the spur, then the nectar would never accumulate to a level accessible to the pollinators. Now suppose that these nectar robbers also collected pollen from the flowers and pollinated in the process (as we have mentioned earlier, bumble bees are often robber-like pollinators). In such a case, the robber would be the agent of selection and, most likely, there would be positive, or at least neutral, selection for long corollas or nectar spurs, because long corollas do not prevent robbers from collecting nectar or pollinating. In fact, if the robbers were discriminating about which flowers they visited, they would most likely choose those with the longest corolla tubes, whose nectar was least available to the legitimate pollinators. Roubik et al. (1985) found that *Quassia amara* corolla lengths were longer in populations that were robbed than in an isolated population that had no robbers. This connection between corolla length and robbers is intriguing and should be studied further. Ocotillo (*Fouquiera splendens)* flowers, like many others, exhibit large geographic variations in morphology (Henrickson 1972). Waser (1979) believes that some of this variation may be due to evolutionary adaptations that allow robber-pollinators, such as carpenter bees, to pollinate in the process of nectar collection.

Flower location

Traveset et al. (1998) found that nectar-robbing birds (*Phrygilus patagonicus*) were more likely to rob *Fuchsia* flowers growing in a open area. These birds sometimes damaged a flower's ovary while robbing; consequently, flowers in open areas exhibited reduced seed set. Plants growing in the forest, on the other hand, had higher seed set because they were more likely to be visited by the legitimate pollinator, a hummingbird. This combination may be selecting for plants that are shade tolerant. In another case, involving hummingbird pollination of shrubby *Centropogon valerii*, the nectar-robbing bird (*Diglossa plumbea*) foraged mostly on the inner and lower flowers (Colwell et al. 1974). The researchers noted that fruit set was lower on these inner and lower flowers (although this was not documented) and suggested that selection might favor plants that produce flowers only in the upper and outer part of the shrub. In these two examples, the robbers are exerting selection against genotypes likely to be robbed, but there may be other instances in which robbers increase plant fitness and therefore exert positive selection.

Nectar volume

If a plant is robbed of nectar, yet a certain volume of nectar is needed to keep the most effective pollinators as constant visitors, then those plants, or populations, producing enough nectar for both robber and pollinator will be the most successful in fitness terms, and will leave the most progeny, leading to increased nectar production. In the terminology used by Pyke (1981), optimal rates of nectar production should be higher in the presence of nectar robbers. Barrows (1976) wrote that, ''coevolution of *Lantana camara*, its pollinators, and its nectar robber, *Trigona fulviventris*, has probably involved increased nectar production to feed both its pollinators and its robbers.'' Others have repeated the assumption that nectar production should be higher in heavily robbed populations (Soberón and Martínez del Río 1985, Morris 1996), but the only test of this idea was done by Roubik et al. (1985). They studied four different populations of *Quassia amara*, some that were robbed and others that were unrobbed. The flowers protected from visitors in an area of heavy robbing contained an average of 45.3 μL of nectar, whereas the flowers in an area without nectar robbers contained an average of 30.8 μL of nectar. One explanation of this observation is that plants in heavily robbed areas may have evolved increased nectar production, but further work should be done before this conclusion is accepted, as alternatives are possible (e.g., robbers preferentially use plants with higher nectar production).

Protective mechanisms

If nectar robbers had consistently negative effects on plant fitness, we would expect protective mechanisms to evolve. It is sometimes suggested that plants *have* evolved protection mechanisms (e.g., thickened calyces, dense inflorescences, latex sap, extrafloral nectaries; see Guerrant and Fiedler 1981, Inouye 1983, and references therein), but to our knowledge, none of these suggestions has been rigorously tested.

The plant genus that we study (*Corydalis*) occurs throughout North America, Europe, and Asia. It is apparently robbed throughout most of its range (Higashi et al. 1988, Olesen 1996; J. E. Maloof, *personal observation*), yet no protective mechanisms are evident. More research is needed to link variations in these putative protective mechanisms with variations in robbing rates and, ideally, plant fitness effects, before we can assume that traits have evolved to protect against nectar robbers.

Discussion

Are nectar robbers cheaters or mutualists? One thing we know for certain is that they cannot be assumed to be one or the other. Mutualists benefit each other. The benefit to nectar robbers from flowers seems obvious: they are an important, sometimes the sole, source of food (Scott et al. 1993). As we have shown, there may also be benefits to flowers from nectar robbers. These benefits may be direct (in the case of ''robber-like pollinators'') or indirect (mediated through a third species). Indirect benefits, especially, may be overlooked because of their subtlety or complexity. Some patterns are beginning to emerge and the conclusions listed here are just a beginning in our understanding of the complex ecology of nectar robbing.

1) It should not be automatically assumed that nectar robbers are not pollinating the flowers they visit. In many cases, nectar robbers are pollinators, too.

2) The effects of nectar robbers are complex and depend, in part, on four factors.

a) The identity of the legitimate pollinator. Hummingbirds may be able to sense and avoid robbed flowers, but insects may not. Hummingbirds do not collect pollen from plants as a food source; bees do, and pollen transfer (pollination) may occur as a result of this behavior.

b) The growth form of the plant. Geitonogamy may be detrimental to a plant, and could become a problem if there are many open flowers on an inflorescence. Nectar robbers may reduce geitonogamy by changing foraging patterns.

c) How much nectar robbers remove. If robbers remove all of the nectar, the legitimate pollinators may switch; if robbers leave some nectar behind, the legitimate pollinators may remain constant.

d) Resources available in the environment. If there is a scarcity of alternative nectar sources, the pollinators may be more likely to remain constant. Amino acid content of a nectar may also influence pollinator behavior.

3) Nectar robbing is a common phenomenon that may have evolutionary implications.

4) Evidence to date shows that robbers are often, but not always, mutualists.

We hope that this review will stimulate a new perspective on nectar robbing, an appreciation of its ecological and evolutionary complexities, and additional research into its consequences. We have emphasized bees as nectar robbers because of our own experience and the predominance of literature on bees as robbers, but the differences between bee- and bird-pollinated and robbed flowers suggest that additional work on robbers other than bees would be profitable.

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