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Rebecca E. Irwin · Alison K. Brody

Nectar robbing in *Ipomopsis aggregata*: effects on pollinator behavior and plant fitness

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Abstract Hummingbirds foraging in alpine meadows of central Colorado, United States, face a heterogeneous distribution of nectar rewards. This study investigated how variability in nectar resources caused by nectar-robbing bumblebees affected the foraging behavior of hummingbird pollinators and, subsequently, the reproductive success of a host plant (*Ipomopsis aggregata*). We presented hummingbirds with experimental arrays of *I. aggregata* and measured hummingbird foraging behavior as a function of known levels of nectar robbing. Hummingbirds visited significantly fewer plants with heavy nectar robbing (over 80% of available flowers robbed) and visited fewer flowers on those plants. These changes in hummingbird foraging behavior resulted in decreased percent fruit set as well as decreased total seed set in heavily robbed plants. These results indicate that hummingbird avoidance of nectar-robbed plants and flowers reduces plant fitness components. In addition, our results suggest that the mutualisms between pollinators and host plants may be affected by other species, such as nectar robbers.

Key words Bumblebees · Cheating behavior · Hummingbirds · *Ipomopsis aggregata* · Nectar robbery

Introduction

Animals foraging for nectar encounter a world of variable rewards (e.g., Baker et al. 1978; Pyke 1981a;

Pleasants 1983a; Wolf and Hainsworth 1986; Mitchell 1989). Plants may differ in nectar production, concentration, or standing crop due to inherent differences in genotype (Pederson 1953; Teuber and Barnes 1979), microhabitat (Shuel 1967; Zimmerman 1983), or recent depletion by legitimate visitors or nectar robbers (for reviews see Faegri and van der Pijl 1979; Jones and Little 1983; Real 1983; Proctor et al. 1996). Although the effect of legitimate pollinators in both producing and responding to variable nectar rewards has been studied extensively (e.g., Pyke et al. 1977; Pyke 1978a, b, c, 1981b, 1984; Heinrich 1979, 1983; Gass and Montgomerie 1981; Waddington and Heinrich 1981; Carpenter 1983; Wolf and Hainsworth 1986, 1990, 1991; Mitchell 1993), the effect of illegitimate visitors, such as nectar robbers, in creating variable nectar rewards has been relatively ignored (but see Heinrich and Raven 1972; McDade and Kinsman 1980; Pleasants 1983a; Arizmendi et al. 1996). Nectar robbers are animals that chew through floral parts to obtain nectar, thereby bypassing the floral openings used by legitimate pollinators (Inouye 1980). Nectar robbers decrease the standing crop of nectar (McDade and Kinsman 1980; Pleasants 1983a) and modify the sugar concentration of available nectar (Pleasants 1983a; Arizmendi et al. 1996). Thus, nectar robbers may significantly affect the distribution of rewards available to legitimate pollinators.

Surveys show that nectar robbing occurs most often on flowers adapted for hummingbird pollination (Barrows 1980; McDade and Kinsman 1980; Inouye 1983). However, detailed experimental and observational studies have most often focused on insect-pollinated plant species (Meidell 1944; Macior 1966; Free 1968; Koeman-Kwak 1973; Barrows 1976; Kendall and Smith 1976; Rust 1979; Wyatt 1980; Fritz and Morse 1981; Stephenson 1982; Galen 1983; Newton and Hill 1983; Zimmerman and Cook 1985; Higashi et al. 1988; Reddy et al. 1992; Morris 1996; Olesen 1996). These studies have shown that the effect of nectar robbing on insect-

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pollinated hosts may be positive, negative, or of no discernible consequence. Plants may benefit from nectar robbing if depletion of nectar rewards by robbers forces pollinators to move more often between plants (Heinrich and Raven 1972), and increased pollinator movement may enhance seed production by increasing outcrossing (Heinrich and Raven 1972; Zimmerman and Cook 1985). Nectar robbers may also benefit the plants they rob if they affect pollination by accidentally brushing against floral reproductive structures (Higashi et al. 1988) or by legitimately visiting flowers to collect pollen (Meidell 1944; Macior 1966; Koeman-Kwak 1973; Morris 1996). Alternatively, nectar robbing may be detrimental if robbers damage plant reproductive structures (McDade and Kinsman 1980), or if they deter legitimate pollinators from visiting plants (Fritz and Morse 1981; Reddy et al. 1992; but see Barrows 1976).

Only a handful of studies have examined the effects of nectar robbers on hummingbird-pollinated species (Colwell et al. 1974; Waser 1979; McDade and Kinsman 1980; Roubik 1982; Arizmendi et al. 1996; Irwin and Brody 1998). Nectar robbers may have either positive or negative effects on hummingbird-pollinated plants. Hummingbird-pollinated plants may benefit from nectar robbing if avian nectar robbers also act as low-efficiency pollinators (Arizmendi et al. 1996). Nectar robbing may be detrimental to plant fitness if nectar robbers deter hummingbird pollinators directly through interference competition or indirectly through exploitative competition for nectar resources. For example, territorial nectar-robbing bees physically chase hummingbird pollinators from floral patches of *Pavonia dasypetala* (Roubik 1982), and avian robbers and pollinators partition nectar resources in space to avoid interference competition for the nectar of *Centropogon valerii* (Colwell et al. 1974). Nectar robbers also reduce male and female fitness components of the hummingbird-pollinated plant *Ipomopsis aggregata* (Polemoniaceae) (Irwin and Brody 1998); however, the effect of the nectar-robbing bees on the foraging behavior of the hummingbird pollinators of *I. aggregata* is unknown. Furthermore, the indirect effects of nectar-robbing insects on hummingbird selectivity remain unexplored in cases where insect robbers and avian pollinators do not interact directly and where avian pollinators do not also act as robbers.

The aim of our study was to determine how nectar robbing by the bumblebee, *Bombus occidentalis*, indirectly affects the selectivity of hummingbird pollinators foraging on flowers of *I. aggregata*. We selected this system to study the indirect effects of nectar robbers on hummingbird selectivity and host plant fitness because *B. occidentalis* and hummingbird pollinators do not physically interact (i.e., *B. occidentalis* do not chase hummingbirds away from flower patches). Furthermore, there is a clear distinction between the activities of the two species. *B. occidentalis* robbers do not act as pollinators, and hummingbird pollinators do not rob *I. aggregata*. In 1995, we quantified nectar robber activity on naturally occurring *I. aggregata* to determine the rob-

bing rates that hummingbirds encounter, and we developed an artificial robbing technique that accurately mimics robbing by *B. occidentalis*. In 1996, we examined whether nectar robbing affects the selectivity of hummingbird pollinators by presenting birds with experimental *I. aggregata* that were heavily or lightly robbed. The experimental heavy and light robbing treatments corresponded to high and low robbing levels hummingbirds normally encountered in 1995. We asked whether nectar robbing affects (1) the frequency of pollinator visits to a plant and (2) the behavior of pollinators during each visit. We also measured the fruit and seed production of all experimental *I. aggregata*. Measuring the fruit and seed production of *I. aggregata* provided a direct link between hummingbird selectivity and host-plant fitness.

Methods

Study system

We conducted this study using *I. aggregata* plants in the vicinity of the Rocky Mountain Biological Laboratory (RMBL), elevation 2800 m, in the Elk Mountains of central Colorado, United States. Near the RMBL, *I. aggregata* is obligately outcrossed and is pollinated primarily by broad-tailed hummingbirds (*Selasphorus platycercus*) and rufous hummingbirds (*S. rufus*). Broad-tailed hummingbirds arrive at the RMBL in the spring as northward migrants and set up breeding and nesting territories soon after snowmelt (Waser 1976). Rufous hummingbirds arrive at the RMBL in mid-July as southward migrants and set up feeding territories (Calder 1987, 1993). Both hummingbirds spend approximately 10% of their daytime hours foraging for nectar (Waser 1976), and *I. aggregata* plants are their preferred hosts (Waser 1976, 1978). Broad-tailed and rufous hummingbirds preferentially visit nectar-rich patches of *I. aggregata* (Wolf and Hainsworth 1990), and they show preferences for taller plants with larger inflorescences (Wolf and Hainsworth 1990; Brody and Mitchell 1997). Both hummingbirds rely on abundant *I. aggregata* nectar to support their high metabolic rate, as hovering flight in hummingbirds costs an estimated 2.0–3.1 mg sucrose min⁻¹ (Calder and Calder 1992).

I. aggregata is a long-lived monocarpic perennial around the RMBL. It grows as a vegetative rosette for 2–7 years, flowers once, and then dies (Waser and Price 1989). In the year of flowering, most plants produce a single stalk of scarlet, trumpet-shaped flowers. Each plant flowers for 4–8 weeks and individual flowers last approximately 3–5 days. Nectaries are located at the base of the long (18–20 mm) floral tube, and nectar is produced at a nearly constant rate of 1–5 µl nectar flower⁻¹ day⁻¹, with a concentration of 20–25% sucrose equivalents (Pleasants 1983a). The standing crop of nectar in *I. aggregata* flowers is affected not only by visits from hummingbirds but also by visits from nectar robbers (Pleasants 1983a).

I. aggregata flowers are robbed by the bumblebee, *B. occidentalis*. The bees use their sharp, toothed mandibles to chew a hole through the side of the corolla near the basal nectaries. After chewing a hole, the robber will insert its proboscis into the hole and consume nectar without contacting the sexual parts of the flower (R.E. Irwin and A.K. Brody, personal observations). Nectar robbers often remove all available nectar from flowers in a single visit. Renewed standing crops of nectar in robbed flowers have a higher sugar concentration due to water evaporation out of the robber holes (Pleasants 1983a; R. E. Irwin and A. K. Brody, unpublished work). *I. aggregata* is the preferred host plant of *B. occidentalis* around the RMBL (Pyke 1982). There is no record of aggressive

behavior among *B. occidentalis* or among robbers and either hummingbird species for access to *I. aggregata* flowers (Heinrich 1979; Pleasants 1983b). Therefore, it is unlikely that robbers and pollinators interact directly.

Field procedures

Natural variation in nectar robbing

To determine natural levels of nectar robbing, we surveyed 15 randomly selected *I. aggregata* growing widely dispersed in the townsite of the RMBL over the 1995 flowering season. To randomly select plants, we mapped and numbered all *I. aggregata* that we had access to around the RMBL and then chose 15 numbered plants blindly using a computerized random number generator. Every 5 days, we recorded the number of robber visits to each plant by counting the number of robber holes in all open flowers. Because robbers make a new hole each time they rob a flower, even if a pre-existing hole is present, we could obtain an accurate measure of the amount of robbing plants and flowers received by counting the number of holes in corolla tubes. Furthermore, because *I. aggregata* flowers are only in bloom for 3–5 days, by censusing plants every 5 days, we were sure not to count the same robber holes twice. For each plant, we calculated the mean nectar robbing per plant as the total number of robber holes divided by the total number of flowers produced over the flowering season.

To determine the impact of natural variation in nectar robbing on female plant reproduction, we collected all of the fruits from each plant and counted the number of seeds in each successful fruit. We then performed regressions of mean percent fruit set per plant (arcsine square root-transformed) and mean seeds per fruit per plant (natural log-transformed) on mean nectar robbing per plant to access the relationship between plant reproduction and nectar robbing.

To determine if robbers damage floral reproductive structures, we randomly collected 17 pairs of flowers from 17 randomly selected *I. aggregata*. One member of each pair was naturally robbed by *B. occidentalis*, and the other flower was unrobbed. We chose flower pairs such that both were in the same reproductive stage and in similar positions on the plant. Under a dissecting microscope, we examined the robbed flowers visually for damage to stamens, styles, and ovaries. The unrobbed flower in each pair was examined to determine the natural morphology of flowers on the same plant and to control for any damage we may have caused during flower collection.

Artificial simulation of nectar robbing

In 1995, we examined how an artificial robbing technique (cutting a hole in the base of the corolla with a scalpel, inserting a 10- μ l micro-capillary tube into the hole, and drawing out all available nectar) mimicked natural robbing. At five sites near the RMBL, we randomly chose four plants with similarities in plant height, stem branching, and total number of buds. We randomly chose one plant and robbed 80% of its flowers (according to the methods above) every 5 days throughout the flowering season. For the other three plants, we recorded the percent of flowers naturally robbed every 5 days throughout the season. Plants were exposed to natural hummingbird pollination throughout their lifespans. We marked the calyces of all flowers with a small dot of varying color using a permanent, felt-tipped marker to distinguish the weeks that flowers were in bloom. Once plants ceased blooming, we collected all fruits and counted the seeds in each fruit.

To determine if our artificial robbing treatment simulated natural robbing in terms of plant response, we measured two response variables at the whole-plant level: percent fruit set per week (number of fruits that produced seeds/total number of flowers produced; arcsine square root-transformed) and average seeds per fruit per week (mean number of seeds produced per successful fruit; natural log-transformed). Response variables were calculated on a

weekly basis to separate variation in fruit and seed production caused by our treatments from variation caused by differential resource availability and/or seasonal stochastic effects (Campbell and Halama 1993). We compared weekly percent fruit set and seeds/fruit between artificially and naturally robbed plants using repeated-measures ANOVAs with treatment (artificial versus natural robbing) as a fixed effect, plant nested within treatment and site as random effects, bloom week as the repeated factor, and the percent of flowers robbed per week as a covariate.

Effects of experimental nectar robbing on hummingbird selectivity and plant fitness

In June 1996, we collected 20 pairs of flowering *I. aggregata* from a natural population growing 25 km south of the RMBL and transplanted them into individual flower pots. Pairs were chosen based on similarities in plant height, stem branching, and total number of buds and flowers. We placed plants in a greenhouse for 2 days and watered and fertilized them to reduce transplant shock.

We then randomly assigned members of each pair to one of two artificial robbing treatments – either “light” nectar robbing (10% of available flowers robbed) or “heavy” nectar robbing (80% of available flowers robbed). Levels of 10% nectar robbing and 80% nectar robbing represent common low and high levels of nectar robbing observed in nature (see Results). We artificially robbed flowers as described previously. This method adequately mimics natural robbing by *B. occidentalis* (see Results).

On each of 6 successive days, we robbed plants according to their assigned treatments. All newly robbed flowers were either in elongated bud or male phase. If a flower had been robbed previously, it was robbed again by extracting all available nectar through the existing hole. We marked the calyces of all 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 small red dot 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 was over. Each pair of plants was then randomly assigned to one of two experimental grids. Each grid consisted of 20 plants spaced 1 m apart in a square pattern in an open meadow at the RMBL; the grids were 5 m apart. We placed pairs in the same grid, but we did not keep the pairs together spatially. Because birds could easily forage on both grids in a single foraging bout, the grids were not statistically independent and were not considered in the statistical analyses. We rotated the plants from one grid to the other every second observation period to control for position effects; however, the relative positions of the plants within the grids remained the same throughout the experiment.

We placed plants in the field for 2 h each day and recorded all hummingbird visits to the plants. Using a hand-held tape recorder, we recorded the species and sex of each bird that entered the grid of experimental plants, the plant(s) visited, and the number of flowers visited per plant for each hummingbird foraging bout observed.

After each 2-h observation period, we returned plants to the greenhouse to allow them to replenish their nectar volumes over the next 24 h. The average standing crop of nectar in a flower was approximately 1 μ l before daily robbing treatments. This approximates the average standing crop of nectar in flowers in natural populations (Pleasants 1983a). Because this experiment was conducted in early June, *B. occidentalis* workers were not foraging; therefore, natural nectar robbing did not change our robbing treatment levels.

After 6 days of observations, the potted plants were left in the greenhouse and watered and fertilized daily. Once seeds were mature, we collected all fruit capsules from flowers that were open during the observation period. Partially developed capsules that did not produce seeds (aborted fruits) were recorded. We then counted all seeds produced in each successful fruit.

To determine if nectar robbing affected hummingbird foraging behavior on *I. aggregata*, we calculated the daily visitation rate to

flowers as: (total number of visits to each plant on a given day) \times (average percent of flowers probed per visit). From hereafter, we refer to this variable as "visitation rate". We then analyzed the effect of nectar robbing on visitation rate using a randomized-block, repeated-measures ANOVA with plant pairs as blocks (20 blocks), robbing treatment (10% and 80%) randomly assigned to plants within each block, and observation date as the repeated factor.

To determine if nectar robbing affected fruit and seed production, we analyzed percent fruit set (number of expanded fruits/total number of flowers; arcsine square root-transformed) and total seed set (number of seeds per plant) in the context of a randomized block design. Again, we considered plant pairs as blocks with the two robbing treatments randomly assigned to plants within each block. In the overall model, we used the mean visitation rate per plant over the course of the experiment as a covariate varying over plants within and across blocks. These analyses were run using BMDP, procedure 2V (BMDP Statistical Software 1985). By including the covariate in the model, we were able to tease apart variation in plant fitness caused by hummingbird visitation from potential variation caused by our robbing treatment. For example, if we found a significant effect of the covariate (hummingbird visitation rate) and an insignificant effect of the robbing treatment, we would have strong evidence that hummingbird selectivity, and not our robbing treatments per se, was causing the variation in percent fruit set and total seed set among plants with 10% and 80% robbing. Conversely, if we found a significant effect of robbing treatment and the effect of the covariate was insignificant, it would indicate that differences between the robbing levels in terms of fruit and seed production were caused by our robbing treatments rather than by hummingbird selectivity.

Results

Natural variation in nectar robbing

For plants surveyed in 1995, the mean percent nectar robbing per plant ranged from 0% to 96% of available flowers. Mean robbing per plant showed a bimodal distribution with peaks at low and high robbing levels (Fig. 1). Plants with higher nectar robbing produced fewer successful fruits ($r = 0.26$, $n = 15$ plants, $P = 0.04$) and fewer seeds per successful fruit ($r = 0.52$, $n = 15$ plants, $P < 0.01$). We found no evidence of visual physical damage to the stigmas, styles, or ovaries of the 17 robbed flowers we examined, suggesting that the decreased fertility of flowers robbed by *B. occidentalis* may be due to effects on pollinator visitation, rather than to destruction of plant reproductive parts.

Artificial simulation of nectar robbing

Artificially and naturally robbed plants did not differ in weekly percent fruit set or seed set per fruit (Table 1a, b). Because neither plant reproductive component varied significantly among sites in the overall model, we pooled the data across sites. As the season progressed, both artificially and naturally robbed plants produced fewer successful fruits and fewer seeds per fruit so that the effect of the repeated factor (bloom week) was significant in the overall model (Table 1a, b). Furthermore, percent

fruit set and seed set per fruit varied with percent of flowers robbed (Table 1a, b). Plants with higher percent robbing experienced lower percent fruit set and seed set per fruit.

Effect of experimental nectar robbing on hummingbird selectivity and plant fitness

Effect of experimental nectar robbing on hummingbird selectivity

Over the 12 h of observation at the two experimental arrays, we recorded 52 hummingbird foraging bouts, 273 visits to individual plants, and 1,699 visits to individual flowers. The 52 foraging bouts represented the foraging activity of at least three birds. All birds observed were male broad-tailed hummingbirds.

Nectar robbing had a significant effect on hummingbird visitation rate to *I. aggregata* (Table 2). Over the 6 days of observation, hummingbird visitation rate was significantly higher to plants and flowers in the light robbing treatment (mean \pm 1 SE = 59.4 ± 3.8) than to plants and flowers in the heavy robbing treatment (mean \pm 1 SE = 39.9 ± 3.4 ; Table 2). Visitation rate is the product of the number of times a plant was visited and the percentage of flowers probed per visit. Looking at each visitation rate component separately, plants in the light nectar robbing treatment were visited 1.28 ± 0.08 (mean \pm 1 SE) times per day, while plants in the heavy robbing treatment received only 1.02 ± 0.08 visits per day. On average, $43.4 \pm 2.9\%$ (mean \pm 1 SE) of flowers were probed per visit to lightly robbed plants, while only $32.3 \pm 2.8\%$ of flowers were probed per visit to heavily robbed plants. As the experiment progressed, visitation rate to all plants declined so that the effect of the repeated factor (day) was also significant in the overall model (Table 2).

Effect of experimental nectar robbing on plant fitness

Visitation rate explained a significant amount of the variation in percent fruit set and total seed set across all pairs of plants (Tables 3a, 4a). In fitting the model, BMDP first analyzed the effect of the covariate (visitation rate) across all pairs (blocks). In the next level of analyses, BMDP partitioned the variance attributable to the treatment effect and the effect of visitation rate within each pair. Once the effect of visitation rate was accounted for, we found no additional effect of robbing treatment on measures of fruit set or total seed set (Tables 3b, 4b). However, robbing treatment was highly significant when visitation rate was not included as a covariate in the model (percent fruit set: $F_{1,19} = 116.75$, $P < 0.0001$; total seeds: $F_{1,19} = 22.44$, $P = 0.0001$; Fig. 2), implying that robbing treatments changed fer-

Table 1 Repeated-measures ANOVAs examining the effect of natural and artificial nectar robbing on **a** percent fruit set and **b** seed set per fruit. In the model, robbing treatment (artificial vs. natural robbing) was treated as a fixed effect, plant nested within

Source	Sum of squares	df	Mean square	F	P
a %Fruit set					
Robbing treatment	0.253	1	0.253	0.249	0.6240
Plant (treatment)	18.220	18	1.012	1.037	0.4223
Bloom week	40.819	5	8.164	8.366	<0.0001
% Robbing	4.949	1	4.949	4.163	0.0431
b Seeds/fruit					
Robbing treatment	0.571	1	0.571	1.146	0.3000
Plant (treatment)	8.907	18	0.495	1.122	0.3416
Bloom week	9.116	5	1.823	4.136	0.0018
% Robbing	1.938	1	1.938	3.951	0.0494

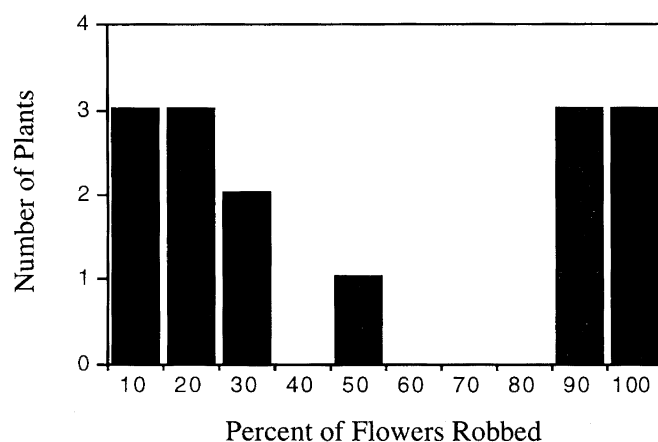


Fig. 1 Mean frequency of robbing by *Bombus occidentalis* on 15 randomly sampled *Ipomopsis aggregata* over the 1995 flowering season

Table 2 Randomized-block, repeated-measures ANOVA examining variation in visitation rate among plants with light and heavy robbing over the 6 days of the experiment. Plant pairs were treated as a random blocking factor, the robbing treatment (10% or 80%) as a fixed factor, and day as the repeated factor. Visitation rate was examined as a function of treatment and was calculated as: number of visits to each plant per day \times average percentage of flowers probed per visit. All main effects were tested over their appropriate interaction term

Source	Sum of squares	df	Mean square	F	P
Treatment	2.273	1	2.273	18.60	0.0001
Pair (block)	2.899	19	0.153	1.25	0.2372
Day	3.353	5	0.671	5.49	0.0002
Pair \times treatment	3.963	19	0.209	1.71	0.0482
Day \times pair	14.545	95	0.153	1.25	0.1369
Day \times treatment	0.649	5	0.129	1.06	0.3855

tility because they influenced hummingbird visitation rate. Not surprisingly, given the tight association between visitation rate and robbing treatment, the covariate was not significant between plants within each pair for either response variable because the magnitude

of plant-to-plant variability in fruit and seed set was relatively great when compared to the magnitude of differences in visitation rate.

Discussion

Nectar robbing of *I. aggregata* had a significant influence on the foraging selectivity of hummingbird pollinators. Our experimental manipulations of nectar robbing showed that hummingbirds avoided heavily robbed plants and flowers. Visitation rate to plants and flowers (the number of times a plant was visited multiplied by the average percent of flowers probed per visit) was significantly reduced in plants with heavy robbing. Our results suggest that the depletion of nectar caused by robbing, and not the robbers themselves, biased hummingbirds towards plants with low nectar robbing.

Similarly, the indirect effects of nectar robbing have been demonstrated in insect-pollinated systems (Fritz and Morse 1981; Reddy et al. 1992). For example, robbed flowers of *Vitex negundo* received less pollen and produced fewer seeds than unrobbed flowers, presumably due to pollinator avoidance of robbed flowers (Reddy et al. 1992). Also, robbed flowers of *Asclepias syriaca* initiated fewer seed pods than did unrobbed flowers (Fritz and Morse 1981). Reduced seed pod initiation may have been due to insect-pollinator avoidance of robbed flowers; however, this was not experimentally verified. Our data demonstrate that insect nectar robbers can indirectly affect hummingbird pollinators and that hummingbird selectivity of plants is a causal factor in the decline of fruit and seed production in plants with heavy robbing. These results provide a mechanistic explanation for reduced male and female fitness components of heavily robbed *I. aggregata* that we found in a previous field study (Irwin and Brody 1998).

Why do hummingbirds avoid nectar-robbed plants and flowers? In the temperate mountains of North America, broad-tailed hummingbirds face extreme energy demands (e.g., Lasiewski 1963; Wolf and Hainsworth 1971; Calder 1975), and yet, they must support

those energy demands on flowers that produce relatively small amounts of nectar (4 μ l/day in *I. aggregata*; Pleasants 1983a). Hummingbirds have adopted several strategies to overcome these energetic demands. For example, hummingbirds operate under a set of decision rules that maximize their net energy intake while minimizing their total energy spent foraging (e.g., Hainsworth and Wolf 1976; Pyke 1978a; Gass and Montgomerie 1981). One decision governing hummingbird foraging behavior is whether to visit a given plant (e.g., Pyke et al. 1977; Gass and Montgomerie 1981; Pyke 1981b). These decisions carry obvious energetic consequences. If birds visit poor nectar resources, they may not meet their daily energetic requirements (Gass and Montgomerie 1981). To aid in these foraging decisions, hummingbirds can learn to use floral cues to make decisions about which plants to visit. For example, hummingbirds foraging at *Malvaviscus arboreus* avoid old flowers that produce no nectar by cueing in on age-related floral color changes associated with no nectar reward (Gass and Montgomerie 1981).

Table 3 Randomized-block ANCOVA examining variation in percent fruit set among plants with light and heavy robbing. Plant pairs were considered as random blocks with the two robbing treatments (10% and 80%) randomly assigned to plants within blocks. In two separate models, we considered mean visitation rate as a covariate varying **a** across all pairs of plants, or **b** within each robbing treatment pair

Source	Sum of squares	df	Mean square	F	P
a.					
Mean visitation	0.3938	1	0.3938	5.47	0.0311
Error	1.2966	18	0.0720		
b.					
Treatment	0.1667	1	0.1667	2.05	0.1691
Mean visitation (covariate)	0.1009	1	0.1009	1.24	0.2797
Error	1.4617	18	0.0812		

Table 4 Randomized-block ANCOVA examining variation in total seed set among plants with light and heavy robbing. Plant pairs were considered as random blocks with the two robbing treatments (10% and 80%) randomly assigned to plants within blocks. In two separate models, we considered mean visitation rate as a covariate varying **a** across all pairs of plants, or **b** within each robbing treatment pair

Source	Sum of squares	df	Mean square	F	P
a.					
Mean visitation	7354.931	1	7354.931	7.93	0.0114
Error	16699.169	18	927.732		
b.					
Treatment	1103.063	1	1103.063	0.82	0.3784
Mean visitation (covariate)	4418.745	1	4418.745	3.27	0.0874
Error	24347.355	18	1352.631		

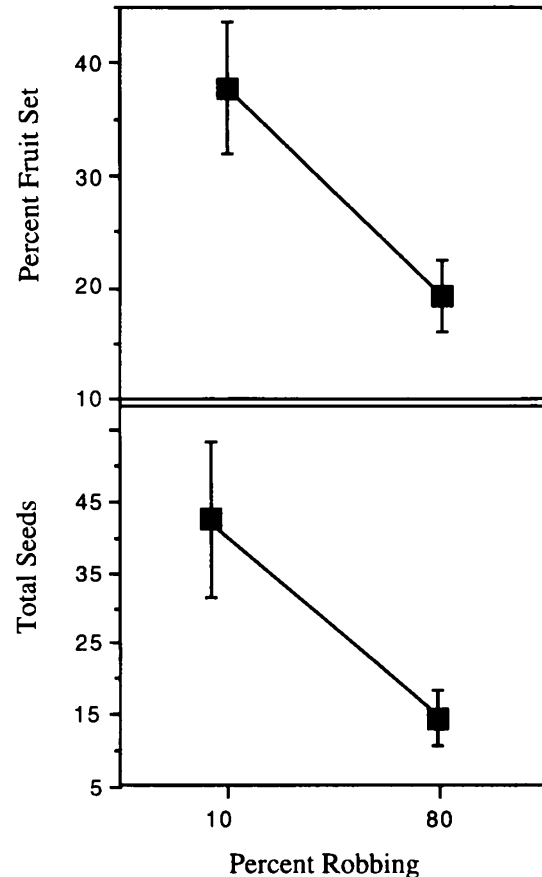


Fig. 2 The effect of light (10%) and heavy (80%) robbing on percent fruit set (mean \pm 1 SE) and total seeds (mean \pm 1 SE) per plant ($n = 20$ plants per treatment)

Likewise, hummingbirds foraging in patches of plants with variable amounts of nectar robbing may benefit from using cues that allow them to make decisions about which plants to visit. Our data suggest that birds do selectively avoid nectar-robbled plants. Such behavior may significantly increase their daily net rate of energy intake. We do not know what cues broad-tailed hummingbirds use to avoid robbed *I. aggregata*, but there are several possibilities. Nectar robbing changes *I. aggregata* flowers in three ways. It causes localized necrosis of petal tissue around the holes made by robbers, decreases the volume of nectar available, and increases the sugar concentration of nectar by as much as 10% because water in the nectar evaporates from the robbers' holes (Pleasants 1983a; R.E. Irwin and A.K. Brody, unpublished work). We are currently investigating which of these cues hummingbird pollinators use to avoid nectar-robbled *I. aggregata*.

Nectar robbers not only affect hummingbird selectivity among plants but also the number of flowers probed on plants. Wolf and Hainsworth (1986) found that if hummingbirds encounter flowers of low nectar reward, they are more likely to leave a plant early. In heavily robbed plants, there is a greater probability that

hummingbirds will forage on robbed flowers with low nectar rewards resulting in the early departure of pollinators. Thus, there should be a positive correlation between the average standing crop of nectar per flower on an inflorescence and the average number of flowers probed per hummingbird visit (Pyke 1981b). Our results support this hypothesis. Hummingbirds visited fewer heavily robbed plants and probed fewer available flowers on those plants.

The decline we found in hummingbird visitation rate to lightly and heavily robbed plants over the course of the experiment was not surprising. We began the experiment when few plants in the area were flowering, but as the experiment progressed, naturally-growing plants in the area came into bloom and competed with our experimental *I. aggregata* for hummingbird pollinators. Ultimately, the interactions among nectar robbers, hummingbird pollinators, and *I. aggregata* will be a function of all interacting members of the community.

Hummingbird avoidance of nectar-robbed plants resulted in reduced fruit and seed production in heavily robbed experimental *I. aggregata* and in plants heavily robbed by *B. occidentalis* in 1995. Mitchell and Waser (1992) found that increasing the number of visits to *I. aggregata* plants and flowers increased the amount of pollen deposited on stigmas. Because seed set in *I. aggregata* is typically limited by the pollen individual flowers receive, increased pollen deposition usually results in increased fruit set and total seed set (Hainsworth et al. 1985; Campbell 1991; Campbell and Halama 1993), and our study is consistent with this pattern. Even though we found that hummingbirds visited a higher percentage of open flowers on plants with light robbing, the benefits of multiple-flower visitation outweighed the potential disadvantages of within-plant pollen transfer. In addition, we detected no trade-off between percent fruit set at the whole-plant level and seed set per fruit, nor was one seen in previous experiments in this system (Brody and Mitchell 1997). We also found that nectar robbing did not damage the reproductive machinery of *I. aggregata* flowers. Therefore, differences in the reproductive success of plants with light and heavy robbing in this study appear to be due to differences in visitation rates by pollinators.

The interactions between pollinators and their host plants have most often been examined as two-species systems (for reviews see Faegri and van der Pijl 1979; Jones and Little 1983; Real 1983; Proctor et al. 1996). Here, we provide experimental evidence that a third species, the nectar robber *B. occidentalis*, has significant effects on the outcome of interactions between hummingbird pollinators and their hosts. These results emphasize the need to study pollinator selectivity and host plant reproduction in concert with other interacting organisms. We also found that *I. aggregata* experienced considerable variation in natural nectar robbing. Plants were either heavily robbed or virtually ignored by robbers (Fig. 1). This variability in nectar

robbing, combined with the negative effects of heavy nectar robbing on plant fitness, may make nectar robbers an important selective agent in *I. aggregata* populations. We are next examining the degree to which nectar robbing and hummingbird pollination act as dual selection pressures on the evolution of floral traits.

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References

- Arizmendi MC, Dominguez CA, Dirzo R (1996) The role of an avian nectar robber and of hummingbird pollinators in the reproduction of two plant species. *Funct Ecol* 10:119–127
- Baker HG, Opler PA, Baker I (1978) A comparison of the amino acid complements of floral and extrafloral nectars. *Bot Gaz* 139:322–332
- Barrows EM (1976) Nectar robbing and pollination of *Lantana camara* (Verbenaceae). *Biotropica* 8:132–135
- Barrows EM (1980) Robbing of exotic plants by introduced carpenter and honey bees in Hawaii, with comparative notes. *Biotropica* 12:23–29
- BMDP Statistical Software (1985) BMDP statistical software manual. University of California Press, Berkeley
- Brody AK, Mitchell RJ (1997) Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. *Oecologia* 110:86–93
- Calder WA (1975) Daylength and the hummingbird's use of time. *Auk* 92:81–97
- Calder WA (1987) Southbound through Colorado: migration of rufous hummingbirds. *Nat Geogr Res* 3:40–51
- Calder WA (1993) Rufous hummingbird (*Selasphorus rufus*). In: Poole A, Gill F (eds) *The birds of North America*, no 53. Academy of Natural Sciences, Philadelphia, pp 1–20
- Calder WA, Calder LL (1992) Broad-tailed hummingbird (*Selasphorus platycercus*). In: Poole A, Stettenheim P, Gill F (eds) *The birds of North America*. Academy of Natural Sciences, Philadelphia, pp 1–16
- Campbell DR (1991) Effects of floral traits on sequential components of fitness in *Ipomopsis aggregata*. *Am Nat* 137:713–737
- Campbell DR, Halama KJ (1993) Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology* 74:1043–1051
- Carpenter FL (1983) Pollination energetics in avian communities: simple concepts and complex realities. In: Jones CE, Little RJ (eds) *Handbook of experimental pollination biology*. Van Nostrand Reinhold, New York, pp 215–234
- Colwell RK, Betts BJ, Bunnell P, Carpenter FL, Feinsinger P (1974) Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flower-piercer *Diglossa plumbea*, and its evolutionary implications. *Condor* 76:447–452
- Faegri K, Pijl L van der (1979) *The principles of pollination ecology*, 3rd edn. Pergamon, Oxford
- Free JB (1968) Behavior of bees visiting runner beans (*Phaseolus multiflorus*). *J Appl Ecol* 5:631–638

- Fritz RS, Morse DH (1981) Nectar parasitism of *Asclepias syriaca* by ants: effect of nectar levels, pollinia insertion, pollinaria removal and pod production. *Oecologia* 50:316–319
- Galen C (1983) The effect of nectar-thieving ants on seedset in floral scent morphs of *Polemonium viscosum*. *Oikos* 41:245–249
- Gass CL, Montgomerie RD (1981) Hummingbird foraging behavior: decision-making and energy regulation. In: Kamil AC, Sargent TD (eds) Foraging behavior: ecological, ethological, and psychological approaches. Garland, New York, pp 159–194
- Hainsworth FR, Wolf LL (1976) Nectar characteristics and food selection by hummingbirds. *Oecologia* 25:101–114
- Hainsworth FR, Wolf LL, Mercier T (1985) Pollen limitation in a monocarpic species, *Ipomopsis aggregata*. *J Ecol* 73:263–270
- Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge
- Heinrich B (1983) Insect foraging energetics. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology, Van Nostrand Reinhold, New York, pp 187–214
- Heinrich B, Raven PH (1972) Energetics and pollination ecology. *Science* 176:597–602
- Higashi S, Ohara M, Arai H, Matsuo K (1988) Robber-like pollinators: overwintered queen bumblebees foraging on *Corydalis ambigua*. *Ecol Entomol* 13:411–418
- Inouye DW (1980) The terminology of floral larceny. *Ecology* 61:1251–1253
- Inouye DW (1983) The ecology of nectar robbing. In: Bentley B, Elias T (eds) The biology of nectaries, Columbia University Press, New York, pp 153–173
- Irwin RE, Brody AK (1998) [CE1] Nectar-robbing bumblebees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology*, in review
- Jones CE, Little RJ (1983) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York
- Kendall DA, Smith BD (1976) The pollinating efficiency of honeybee and bumblebee visits to flowers of runner bean *Phaseolus coccineus* L. *J Appl Ecol* 13:749–752
- Koeman-Kwak M (1973) Pollination of *Pedicularis palustris* by nectar thieves (short-tongued bumblebees). *Acta Bot Neerl* 22:608–615
- Lasiewski RC (1963) Oxygen consumption of torpid, resting, active, and flying hummingbirds. *Physiol Zool* 36:122–140
- Macior LW (1966) Foraging behavior of *Bombus* (Hymenoptera: Apidae) in relation to *Aquilegia* pollination. *Am J Bot* 53:302–309
- McDade LA, Kinsman S (1980) The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. *Evolution* 34:944–958
- Meidell O (1944) Notes on the pollination of *Melampyrum pratense* and the “honeystealing” of humble-bees and bees. *Bergens Mus Arbok* 11:5–11
- Mitchell RJ (1993) Adaptive significance of *Ipomopsis aggregata* nectar production: observation and experiment in the field. *Evolution* 47:25–35
- Mitchell RJ, Waser NM (1992) Adaptive significance of *Ipomopsis aggregata* nectar production: pollination success of single flowers. *Ecology* 73:633–638
- Mitchell WA (1989) Informational constraints on optimally foraging hummingbirds. *Oikos* 55:145–154
- Morris WF (1996) Mutualism denied? Nectar-robbing bumble bees do not reduce female or male fitness of bluebells. *Ecology* 77:1451–1462
- Newton SD, Hill GD (1983) Robbing of field bean flowers by the short-tongued bumble bee *Bombus terrestris* L. *J Apic Res* 22:124–129
- Olesen JM (1996) From naiveté to experience: bumblebee queens (*Bombus terrestris*) foraging on *Corydalis cava* (Fumariaceae). *J Kans Entomol Soc* 69(4, suppl): 274–286
- Pederson MW (1953) Seed production in alfalfa as related to nectar production and honeybee visitation. *Bot Gaz* 115:129–138
- Pleasants JM (1983a) Nectar production in *Ipomopsis aggregata* (Polemoniaceae). *Am J Bot* 70:1468–1475
- Pleasants JM (1983b) Structure of plant and pollinator communities. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp 375–393
- Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Timber, Portland, Oregon
- Pyke GH (1978a) Optimal foraging in hummingbirds: testing the marginal value theorem. *Am Zool* 18:739–552
- Pyke GH (1978b) Optimal foraging in bumblebees and coevolution with their plants. *Oecologia* 36:281–293
- Pyke GH (1978c) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor Popul Biol* 13:72–98
- Pyke GH (1981a) Optimal nectar production in a hummingbird-pollinated plant. *Theor Popul Biol* 20:326–343
- Pyke GH (1981b) Optimal foraging in nectar-feeding animals and coevolution with their plants. In: Kamil AC, Sargent TD (eds) Foraging behavior: ecological, ethological, and psychological approaches. Garland, New York, pp 19–38
- Pyke GH (1982) Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* 63:555–573
- Pyke GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–575
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- Real L (1983) Pollination biology. Academic Press, London
- Reddy TB, Rangaiah K, Reddi EUB, Reddi CS (1992) Consequences of nectar robbing in the pollination ecology of *Vitex negundo* (Verbenaceae). *Curr Sci* 62:690–691
- Roubik DW (1982) The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63:354–360.
- Rust RW (1979) Pollination of *Impatiens capensis*: pollinators and nectar robbers. *J Kans Entomol Soc* 52:297–308
- Shuel RW (1967) The influence of external factors on nectar production. *Am Bee J* 107:54–56
- Stephenson AG (1982) Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *J Chem Ecol* 8:1025–1034
- Teuber LR, Barnes DK (1979) Environmental and genetic influences on quantity and quality of alfalfa nectar. *Crop Sci* 19:874–878
- Waddington KD, Heinrich B (1981) Patterns of movement and floral choice by foraging bees. In: Kamil AC, Sargent TD (eds) Foraging behavior: ecological, ethological, and psychological approaches. Garland, New York, pp 215–230
- Waser NM (1976) Food supply and nest timing of broad-tailed hummingbirds in the Rocky Mountains. *Condor* 78:133–135
- Waser NM (1978) Competition for hummingbird pollination and sequential flowering in two co-occurring wildflowers. *Ecology* 59:934–944
- Waser NM (1979) Pollinator availability as a determinant of flowering time in Ocotillo (*Fouquieria splendens*). *Oecologia* 39:107–121
- Waser NM, Price MV (1989) Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* 43:1097–1109
- Wolf LL, Hainsworth FR (1971) Time and energy budgets of territorial hummingbirds. *Ecology* 52:980–988
- Wolf LL, Hainsworth FR (1986) Information and hummingbird foraging at individual inflorescences of *Ipomopsis aggregata*. *Oikos* 46:15–22
- Wolf LL, Hainsworth FR (1990) Non-random foraging by hummingbirds: patterns of movement between *Ipomopsis aggregata* (Pursch) V. Grant inflorescences. *Funct Ecol* 4:149–157

- Wolf LL, Hainsworth FR (1991) Hummingbird foraging patterns: visits to clumps of *Ipomopsis aggregata* inflorescences. *Anim Behav* 41:803–812
- Wyatt R (1980) The impact of nectar-robbing ants on the pollination system of *Asclepias curassavica*. *Bull Torrey Bot Club* 107:24–28
- Zimmerman M (1983) Plant reproduction and optimal foraging: environmental nectar manipulations in *Delphinium nelsonii*. *Oikos* 41:57–63
- Zimmerman M, Cook S (1985) Pollinator foraging, experimental nectar-robbing and plant fitness in *Impatiens capensis*. *Am Midl Nat* 113:81–84