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IMPACT OF NECTAR ROBBING ON ESTIMATES OF POLLEN FLOW: CONCEPTUAL PREDICTIONS AND EMPIRICAL OUTCOMES

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Abstract. Pollen movement within and among plants affects levels of inbreeding and plant fitness as well as the spatial scale of genetic differentiation. Pollen movement has primarily been studied as a function of the direct relationships between plants and pollinators; however, nonpollinating floral visitors, such as some nectar robbers, may have indirect effects on pollen dispersal by altering plant–pollinator interactions. Theory predicts that nectar robbing should have indirect positive effects on plants by increasing pollen dispersal distance and reducing self-pollen transfer (geitonogamy) and inbreeding through changes in pollinator behavior associated with reduced nectar rewards. Here I experimentally tested the indirect effects of the nectar-robbing bumble bee, *Bombus occidentalis*, on the distance of pollen movement among plants and levels of pollen movement within plants (estimated using powdered fluorescent dyes as pollen analogues) using the self-incompatible, hummingbird-pollinated host, *Ipomopsis aggregata*. Empirical results did not fully support the theoretical predictions. Heavy levels of nectar (>80% of available flowers robbed) had no effect on the mean and mean-squared distance of dye dispersal within populations. However, hummingbird pollinators were 50% more likely to depart from a population after visiting a plant with low robbing relative to a plant with high robbing, suggesting that pollen dispersal among populations might be reduced in plants with high robbing relative to plants with low robbing. Heavy nectar robbing reduced levels of self-dye transfer by one-half. However, when I manipulated robbing levels and access to self-pollen, the costs associated with increased robbing and reduced pollinator visitation (e.g., reduced seed production) outweighed any advantages associated with reduced geitonogamy. Taken together, these results suggest that the negative indirect effects of robbing on plant reproduction through decreased pollinator visitation and changes in pollinator departure from plants far exceed any positive effects associated with decreased geitonogamy. Given the widespread nature of plant attack by nectar robbers, these indirect effects are likely common phenomena structuring natural plant populations.

Key words: Bombus occidentalis; *geitonogamy; indirect effects;* Ipomopsis aggregata; *nectar robbing; plant reproductive success; pollen dispersal.*

INTRODUCTION

Pollen dispersal has many important consequences in natural plant populations. For example, pollen movement within and among plants can influence levels of inbreeding, plant fitness, and the magnitude and scale of spatial genetic differentiation (e.g., Wright 1943, Endler 1977, 1979, Snow et al. 1996). A wealth of studies have provided a detailed understanding of how plant and floral characters mediate the movement of pollinators within and among plants and the patterns of pollen and gene flow that result (e.g., Galen and Plowright 1985, Campbell and Waser 1989, Campbell and Dooley 1992, Galen 1992, Harder and Barrett 1996, Williams et al. 2001). However, pollinators are not the only visitors attracted to plants. Nonpollinating visitors, such as herbivores, florivores, and seed predators, often change the relationships between plants and pollinators (interaction modifications, sensu Wootton 1993), and recent studies highlight the importance of these antagonists to male and female reproductive success of plants through changes in pollinator behavior (Karban and Strauss 1993, Strauss et al. 1996, Brody 1997, Gronemeyer et al. 1997, Juenger and Bergelson 1997, 2000, Krupnick et al. 1999, Mothershead and Marquis 2000). Unfortunately, we know relatively little about the direct and indirect links among floral antagonists, pollinator movement, and spatial patterns of pollen and gene flow in natural populations. Here I focus on the indirect impacts of nectar robbers on estimates of pollen movement and potential gene flow. The predictions and results presented are likely applicable to other floral antagonists that modify plant–pollinator relationships through changes in nectar rewards.

Nectar robbers are animals that remove floral nectar by biting or piercing holes in flowers, circumventing the floral opening used by legitimate floral visitors (Inouye 1980). Nectar robbing is very common among flowering plants; most plant species with tubular flow-

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TABLE 1. Conceptual predictions and empirical outcomes of the indirect effects of nectar robbing on pollen movement among and within *Ipomopsis aggregata* plants through changes in plant–pollinator relationships.

Measure	Prediction		Empirical outcome in this system	
	Effect of robbing	Outcome on plant	Effect of robbing	Outcome on plant
(A) Pollinator flight distance among plants	Increases pollinator flight distance	Beneficial: increased outcrossing distance	Within populations: no effect	Within populations: no effect
			Between populations: Decreases pollinator departures	Between populations: Detrimental: potential decreased dispersal between populations
(B) Pollinator visitation rate to plants	Decreases pollinator visitation rate	Detrimental: decreased pollen donation and receipt	Decreases pollinator visitation rate (Irwin and Brody 1998)	Detrimental: decreased pollen donation and receipt (Irwin and Brody 1999)
(C) Pollinator per-flower visitation within plants	Decreases pollinator per-flower visitation	Beneficial: decreased geitonogamy, inbreeding	Decreases pollinator per-flower visitation	No effect: negative effects of robbing outweigh advantage of decreased geitonogamy

Notes: The column entitled ''effect of robbing'' refers to the impact of nectar robbing on (A) pollinator flight distance among plants, (B) pollinator visitation to plants, and (C) pollinator per-flower visitation within plants. The column entitled ''outcome on plant'' refers to the beneficial or detrimental impact robbing has indirectly on plant reproduction through changes in pollinator or pollen movement. Prediction (B) was tested in a previous study in this system, as noted.

ers or flowers with nectar spurs experience some form of floral larceny (R. E. Irwin and J. E. Maloof, *unpublished data*). Nectar robbers can directly affect plants, for example, by acting as pollinators as well as robbers in the same or different floral visits (e.g., Morris 1996), or by damaging floral reproductive structures (e.g., Galen 1983, 1999, Traveset et al. 1998). In addition, nectar robbers can indirectly affect plants by changing direct plant–pollinator relationships via at least three different mechanisms: (1) the flight behavior of pollinators between plant visits, (2) the overall pollinator visitation rate to plants, and (3) the percentage of flowers probed per plant (e.g., Zimmerman and Cook 1985, Irwin and Brody 1998, 1999, Maloof 2001). Each of these mechanisms could have positive and/or negative effects on pollen and gene movement through changes in the quantity or quality of pollen delivered to and deposited on stigmas (Table 1).

Assuming that pollinators use area-restricted foraging tactics to move out of unrewarding ''patches'' of robbed plants (Gill and Wolf 1977, Pyke 1978, Zimmerman 1982, Heinrich 1983, Kadmon and Shmida 1992), an increase in interplant flight distances by pollinators in response to low nectar rewards in robbed plants could increase pollen flow distances (Zimmerman and Cook 1985, Maloof 2001), contributing to beneficial effects on outcrossing distance while decreasing the spatial genetic structure of plant populations (Table 1A). However, the beneficial effects of robbing associated with increased pollinator flight may be offset by overall lower visitation rates to robbed plants (Table 1B). Pollinator avoidance of unrewarding, nectar-robbed plants and flowers can decrease pollen donation and pollen receipt (Irwin and Brody 1999), lower male and/or female fitness components (e.g., Irwin and Brody 2000, Navarro 2001), and, in turn, reduce the number of plants in a genetic neighborhood. In facultatively selfing species, pollinator avoidance of robbed plants could also affect the genetic neighborhood due to a reduction in the proportion of outcross to self-pollen movement. The detrimental effects of pollinator avoidance of robbed plants could, however, be moderated by reduced within-plant pollen movement (geitonogamy). Pollinators often visit fewer available flowers on unrewarding, robbed plants (Irwin and Brody 1998, Maloof and Inouye 2000). Thus, robbing may indirectly reduce geitonogamy, resulting in a beneficial plant effect by reducing inbreeding in facultatively selfing species and reducing stigma clogging while increasing the delivery of outcross pollen and seed set for obligately outcrossing species (de Jong et al. 1992, Klinkhamer and de Jong 1993) (Table 1C). Moreover, nectar robbing may indirectly reduce the male cost of geitonogamy via a reduction in pollen discounting (Harder and Barrett 1995). The detrimental vs. beneficial effects of nectar robbing will ultimately depend on the relative strength of each of these interactive mechanisms on pollen movement and subsequent gene flow in natural populations. Their combined effect remains unexplored.

That nectar robbers will have indirect effects on pollen and gene flow rests on one critical assumption, namely that there are direct links between pollinator movement, estimates of pollen flow, and realized gene flow. The linkage between each of these measures is often tenuous, at best. For example, pollinator move-

ment may misrepresent pollen and gene flow due to, among other factors, pollen carryover or pollinator grooming (Waser and Price 1982, Thomson 1986, Thomson and Thomson 1989, Harder 1990, Broyles and Wyatt 1991, Karron et al. 1995, Rademaker et al. 1997, Johnson et al. 2001). And pollen flow may underestimate realized gene flow if there is preferential fertilization by outcrossed pollen over near-neighbor pollen (e.g., Schemske and Paulter 1984, Sobrevila 1988, Waser and Price 1989, Fischer and Matthies 1997), or if there are rare long-distance gene flow events, which are hard to track by following pollen movement (e.g., Thomson and Thomson 1989, Campbell 1991, Campbell and Dooley 1992, Broyles et al. 1994, Nason et al. 1996, Schulke and Waser 2001). Interpretation of the indirect effects of robbing must incorporate the strength of the links among pollinator, pollen, and gene movement.

Here I examine the indirect impacts of the nectar-robbing bumble bee *Bombus occidentalis* on the distance of pollen movement among plants and levels of pollen movement within plants using the self-incompatible herb *Ipomopsis aggregata*. The work goes one step beyond previous studies (Zimmerman and Cook 1985, Maloof 2001) by measuring the indirect effects of robbing on pollinator movement and estimates of pollen movement rather than on pollinator movement alone. *Ipomopsis aggregata* provides an ideal model plant with which to address the indirect importance of robbing on estimates of pollinator movement and pollen flow for two reasons. First, a wealth of studies have quantified the links among pollinator movement, pollen dispersal distances, and realized gene flow (Campbell and Waser 1989, Campbell 1991, Campbell and Dooley 1992). In addition, previous studies have found that high levels of nectar robbing of *I. aggregata* reduce pollen donation, pollen receipt, and seeds sired and produced due to pollinator avoidance of robbed plants (Irwin and Brody 1998, 1999, 2000). Therefore, *B. occidentalis* has an indirect negative effect on *I. aggregata* mediated though hummingbird pollinators, and this interaction modification may have additional implications, both positive and negative, for pollen dispersal distances and geitonogamy. In the present study, I further investigate this indirect interaction by asking: (1) Does nectar robbing influence estimates of the distance of pollen dispersal within populations? (2) Does nectar robbing impact levels of within-plant pollen movement (geitonogamy)? and (3) Does robbing mediate the potential for long-distance pollen-flow events, estimated using pollinator departure from plants with low vs. high robbing? Finding that plants with low nectar robbing experienced higher levels of geitonogamy, I then manipulated robbing levels and access to self-pollen to ask, (4) Does the fitness cost of self-pollination differ between plants with low and high robbing levels?

Methods

Study system

I studied the indirect effects of nectar robbing on the montane perennial herb *Ipomopsis aggregata* (Polemoniaceae), near the Rocky Mountain Biological Laboratory (RMBL), elevation 2800 m, in the Elk Mountains of central Colorado. At this field site, *I. aggregata* grows in open alpine meadows in relatively dense populations (mean $\pm$ 1 SE = 2.7 $\pm$ 0.7 *I. aggregata*/m^2 in the populations examined in this study). *I. aggregata* experiences late-acting self-incompatibility (Waser and Price 1991) and does not reproduce vegetatively; therefore, seed production relies on interplant pollen movement (Waser and Price 1983). In addition, *I. aggregata* is monocarpic, allowing measurement of lifetime reproductive success in one flowering season (Waser and Price 1989). The numerous, red, trumpet-shaped flowers of *I. aggregata* are hermaphroditic, protandrous, and pollinated primarily by Broad-tailed Hummingbirds (*Selasphorus platycercus*) and Rufous Hummingbirds (*S. rufus*) around the RMBL (Waser 1978). Individual flowers bloom for ~3–5 d. *I. aggregata* experiences nectar robbing by the bumble bee *Bombus occidentalis*. The bees use their toothed mandibles to chew holes through the sides of corollas, through which they insert their proboscis and remove all available nectar. They do so without pollinating the plants and without damaging the plants' reproductive or nectar-producing structures (Irwin and Brody 1998). Renewed standing crops of nectar in robbed *I. aggregata* flowers have 6–10% higher sugar concentration because water in the nectar evaporates out of the nectar-robber holes (Pleasants 1983); however, this change in nectar concentration does not influence pollinator visitation rate to plants (Irwin 2000). Levels of robbing per *I. aggregata* within populations range from 0% to 100% of flowers robbed throughout a flowering season with a peak robbing activity across seven years and 30 *I. aggregata* populations of 66.14 $\pm$ 12.14% (R. E. Irwin and J. E. Maloof, *unpublished data*).

Pollen dispersal is a major component of gene flow in *I. aggregata* populations, with relatively little dispersal by seeds. On average, hummingbird pollinators fly ~0.8 m between successive plant visits (Waser 1982), and this restricted pollen flow promotes local kinship structure within populations that is further augmented by restricted seed dispersal (Campbell and Dooley 1992). The mean-squared distance of pollen dispersal (estimated using powdered fluorescent dyes) ranges from 3.2 to 10.1 m^2 and the genetic neighborhood area ranges from 10.0 to 31.8 m^2 (Campbell and Waser 1989, Campbell 1991). (Mean-squared distance is interrelated with the genetic neighborhood size as approximate $\pi \times$ mean-squared distance [Wright 1943, Crawford 1984].) Pollen dispersal underestimates realized gene flow in *I. aggregata* populations likely due to postpollination events (such as biparental inbreeding

depression) and rare long-distance gene flow (Campbell 1991, Campbell and Dooley 1992). To ameliorate underestimates of gene flow by pollen dispersal due to rare long-distance pollen flow, I estimated both pollen movement within populations (using powdered fluorescent dyes as pollen analogues) *and* long-distance pollen movement among populations (using estimates of pollinator movement) between plants with low and high levels of robbing. Further, in all studies, I investigated differences in these estimates of pollen dispersal between robbing treatments and did not use the estimates as surrogates for *realized* gene flow.

Pollen movement within *I. aggregata* plants also has important fitness consequences. Geitonogamy in *I. aggregata* can reduce seeds per fruit by 25–42% and pollen export to other plants by 14% (Waser and Price 1991, de Jong et al. 1992). Histological studies with *I. aggregata* indicate that self-pollen can germinate on self-stigmas and develop pollen tubes that penetrate ovules. However, these selfed ovules are unsuccessful, likely via late-acting self-incompatibility rather than via inbreeding depression (Waser and Price 1991).

Field Experiments

Effects of nectar robbing on estimated pollen movement within populations

I studied the effects of robbing on estimated pollen movement in three *I. aggregata* populations in the summer of 1996. Each population was $\sim 10 \times 10$ m in area, and the three populations were separated from each other by >1 km. Previous studies have shown that 95% of *I. aggregata* pollen and dye are expected to stay within populations of this size (e.g., Waser and Price 1983).

I mapped the *x*, *y* coordinates of all bolting *I. aggregata* in each population to the nearest 10 cm and then chose six *I. aggregata* at the center of each population (focal plants) that were similar in size (plant height and inflorescence diameter) and floral morphology (corolla length and width). In each population, three focal plants each were randomly assigned to one of two artificially imposed robbing treatments, either light robbing (10% of available flowers robbed) or heavy robbing (80% of available flowers robbed). The light and heavy robbing levels in this experiment simulate low and high robbing levels commonly found in natural populations of *I. aggregata* (Irwin and Brody 1998). Plants were assigned at random to these robbing treatments based on the size characters measured above (MANOVA: $F_{4,13} = 0.62$, $P = 0.66$).

To artificially impose robbing on plants, I robbed newly opened flowers by cutting a small hole ($\sim$1 mm in diameter) in the side of corollas near the base using dissecting scissors. I then removed all available nectar from each ''robbed'' flower using a 10-μL microcapillary tube inserted into the hole. If a flower was robbed a previous day, I robbed it again by inserting the microcapillary tube into the existing hole and removing all available nectar. This method of robbing adequately mimics natural robbing by *B. occidentalis* measured in the currency of plant reproduction (Irwin and Brody 1998). To ensure that unrobbed flowers did not get robbed naturally by *B. occidentalis*, I covered the corollas with pieces of clear, plastic drinking straws to deter robbers. This collaring manipulation has no adverse impact on the pollination or reproduction of *I. aggregata* (Irwin and Brody 1999).

I estimated pollen movement from plants with simulated low and high robbing using powdered fluorescent dyes as pollen analogues (Waser and Price 1982). Averaged over multiple *I. aggregata* flowers, dye movement provides an accurate estimate of pollen movement (Waser and Price 1982). At the beginning of the season, each plant was randomly assigned a different color of dye for the duration of its lifetime (either blue, green, red, orange, pink, or chartreuse) (Series JST-300, Radiant Color, Richmond, California). Each week during the blooming season, I robbed plants according to their assigned robbing status in the morning between 0800 and 1100 hours and applied dye particles every day for four consecutive days. I applied dye particles with a toothpick to all of the anthers of newly opened flowers on the focal plants in male phase. Because dye was only applied to newly opened flowers in male phase prior to stigma opening (*I. aggregata* flowers are protrandrous), it is unlikely that I inadvertently applied ''self-dye'' to stigmas. Moreover, I robbed and collared flowers prior to applying dye; therefore, it is unlikely that the treatment manipulations resulted in dye movement. I recorded the number of open flowers on each of the study plants and the number of male-phase flowers dyed. Each afternoon after dye application, I randomly selected 15 mapped outer plants in the population and collected stigmas from one-half of the flowers in female phase to estimate the distance of dye donation to outer plants. In addition, I collected one-half of the stigmas from each of the focal plants to estimate levels of within-plant dye transfer per flower dyed as well as dye transfer among the focal plants. Stigmas were brought back to the laboratory and the number of dye particles of each color donated to the stigmas was counted under a dissecting microscope. In a previous study in these populations, plants with high robbing donated 80% fewer dye particles and received 30% fewer dye particles than plants with low robbing (Irwin and Brody 1999).

In the data analyses, I first examined the distance of dye movement from plants with low vs. high robbing. For each mapped plant that received dye from the focal plants, I calculated the distance between the outer plant and the treatment plant from which it received dye. I then calculated the mean and mean-squared dye donation distance per focal plant per day. As noted above, mean-squared distance is related to genetic neighborhood size as $\pi \times$ mean-squared distance (Wright 1943,

Crawford 1984). Because both the mean and mean-squared dispersal distance estimates represent means over large numbers of plants from which stigmas were collected, their frequency distributions are expected to be normal irrespective of the underlying distribution form (Campbell and Waser 1989). To test for differences between robbing treatments for both the mean and mean-squared dispersal distance, I used a mixed-model repeated-measures ANOVA using nectar-robbing treatment as a fixed effect, plant nested within treatment and site as random effects, day as the repeated factor, and interaction terms between them. The treatment effect was tested over the plant nested within treatment term; all other effects were tested over the residual. Site was removed as a factor from the final model because it was not statistically significant (mean distance: $F_{2, 341} = 0.91$, $P = 0.40$; mean-squared distance: $F_{2, 341} = 0.40$, $P = 0.67$), and there were no significant interaction terms including site ($P > 0.13$ in all cases). In addition, the day $\times$ treatment interaction term was not statistically significant and was removed from the model as well (mean distance: $F_{15, 341} = 0.80$, $P = 0.68$; mean-squared distance: $F_{15, 341} = 0.55$, $P = 0.91$) Separate analyses performed on means and medians produced similar results. All statistical analyses described here and below were performed using JMP statistical software (SAS Institute, version 4.0.4, Cary, North Carolina).

To determine the importance of robbing to within-plant dye movement, for each plant I calculated the mean number of self-dye particles received per flower dyed per day. Self-dye receipt was normalized using the natural-log transformation and analyzed using a mixed-model repeated-measures ANOVA, as above. The following factors were removed from the final analysis because they were not statistically significant: site ($F_{2, 130} = 1.95$, $P = 0.15$), site $\times$ robbing treatment ($F_{2, 130} = 1.44$, $P = 0.24$), and day $\times$ robbing treatment ($F_{15, 130} = 0.78$, $P = 0.70$).

Effects of nectar robbing on the likelihood of pollinators to leave a population

Dye-particle movement provides an accurate measure of pollen movement from plants with low vs. high robbing *within* populations. However, ~16% of all seeds produced within a population are sired by a father that grows outside that population (Campbell and Dooley 1992), and nectar robbing may also influence the magnitude of this long-distance pollen movement, especially if pollinators are more likely to leave a population after visiting an unrewarding plant with high robbing. If such is the case, high levels of nectar robbing would result in pollen being moved over relatively large distances. To estimate the effects of robbing on long-distance pollen transport, I quantified the likelihood of pollinators to leave an experimental *I. aggregata* population after visiting plants with low vs. high robbing. The movement patterns of hummingbird foragers and the transfer of pollen from large populations to small, isolated populations in another alpine-flowering species (*Delphinium nuttallianum*) suggests that pollen picked up on a pollinator's body in a foraging bout has the potential to be transferred to another population (Schulke and Waser 2001). Here I am suggesting that pollen from the last plant visited in a foraging bout would potentially have the greatest probability of being transferred to another population (i.e., a long-distance pollen-flow event).

I quantified pollinator visitation to 20 pairs of potted, flowering *I. aggregata* in June 1996. One member of each pair was randomly assigned to receive either a low or a high simulated nectar-robbing treatment (as described in *Effects of nectar robbing on estimated pollen movement within populations*). On each of six successive days, I robbed plants in the morning according to their assigned robbing treatments and then placed plants out in the field in two experimental arrays for 2 h of observation (from ~0800 to 1000 hours). Each array consisted of 10 plant pairs in a rectangular grid in an open meadow. Plants were assigned at random to positions in the array on each day of observation. Hummingbirds can remember the spatial location of food sources after a limited number of visits (e.g., Miller et al. 1985, Hurly 1996, Hurly and Healy 1996); therefore, it is likely that within days, hummingbirds could learn the spatial location of rewarding plants with light robbing. However, by rerandomizing the positions of plants on each day of the experiment, I prevented hummingbirds from learning the positions of rewarding plants with light robbing among days. I rerandomized the positions of plants each day to disassociate position effects (due to external factors such as the location of trees and trails near the arrays) from robbing-treatment effects on hummingbird behavior. Plants were spaced 1 m apart in the arrays, and the two arrays were 5 m apart. Because hummingbird pollinators could easily forage on both arrays in a single foraging bout, the arrays were not statistically independent and thus not considered as such in the statistical analysis. In each 2-h observation period, I recorded the number of times hummingbird pollinators left the arrays after foraging on a plant with low vs. high robbing. I repeated the study in 1997 using the same experimental design but over 11 successive days of observation. In a previous study using this experimental design at this study site, hummingbirds visited more plants and flowers with low robbing than with high robbing (Irwin and Brody 1998). Here, I was interested only in the likelihood that a hummingbird would leave the arrays after visiting plants with low vs. high robbing, as pollen from this last plant visit could have a greater chance of being donated outside of the experimental population.

Over the 12 h of observations in 1996, the arrays received 45 hummingbird-foraging bouts, and over the 22 h of observations in 1997, 170 hummingbird-for-

TABLE 2. Mean and mean-squared dye dispersal distance in marked *Ipomopsis aggregata* did not vary among plants with experimental low and high nectar robbing, revealed by mixed-model repeated-measures ANOVAs.

Source	df	Mean distance			Mean-squared distance		
		SS	*F*	*P*	SS	*F*	*P*
Robbing treatment	1	4.16	1.01	0.3192	169.59	1.02	0.3159
Plant(Robbing treatment)	16	97.73	1.97	0.0161	3188.22	1.42	0.1350
Day	15	111.65	2.28	0.0043	3927.14	1.75	0.0405
Error	360	1174.42			53899.78		

aging bouts. For each year of the study, I used log-likelihood ratio goodness-of-fit tests to compare the number of times birds left the arrays after foraging on plants with low vs. high robbing to the null hypothesis, namely equal probability of leaving the arrays after visiting plants from either treatment (Sokal and Rohlf 1995).

Effects of nectar robbing on geitonogamy and female plant reproduction

In the previous section, I tested whether nectar robbing indirectly influenced within-plant pollen transfer estimated with dye-particle analogues; in this experiment I tested the indirect effects of nectar robbing on geitonogamy measured in the currency of female plant reproduction. I selected 80 *I. aggregata* as they initiated flowering in a natural population in the summer of 2000. Twenty plants each were randomly assigned to one of four treatments corresponding to a factorial cross of two levels of nectar robbing (simulated low vs. high robbing, as described in *Field Experiments: Effects of nectar robbing on estimated pollen movement within populations*, above) by two levels of access to self-pollen (control vs. emasculation). By emasculating flowers, I removed the potential for self-pollen movement within plants to measure the relative importance of nectar robbing vs. self-pollination to female plant reproduction and whether the costs of self-pollination (i.e., reduced seed set) differ between plants with low and high robbing. The use of an emasculation treatment to remove within-plant pollen movement has been employed in previous studies using *I. aggregata* (e.g., de Jong et al. 1992, Juenger and Bergelson 2000) and assumes that emasculation does not alter the attractiveness or ''fit'' of flowers to pollinators. Treatments were applied at the whole-plant level throughout the blooming season. Plants were assigned at random to the treatments based on five plant and floral characters (plant height, corolla length, corolla width, bloom date, and flower production) (MANOVA: $F_{15, 199} = 1.47$, $P = 0.12$).

To impose robbing treatments on plants, I artificially robbed and collared flowers every other day that plants were in bloom. I also performed the emasculation treatment every other day by carefully removing all anthers from all floral buds prior to anther dehiscence using fine-point forceps. In the control treatment, floral buds were probed with the forceps (to control for mechanical handling), and one anther was removed from each bud (to control for filament damage associated with removing anthers that could induce some unknown physiological response). Forceps were cleaned with ethanol between plants to avoid any unsuspected pollen movement.

Once plants ceased blooming, I collected and counted all of the fruits and seeds produced by each of the study plants. For each plant, I calculated three measures of plant reproduction: (1) percentage fruit set (number of seed-bearing fruits divided by total flower production, arcsine square-root transformed), (2) mean number of seeds per fruit (mean number of seeds produced per seed-bearing fruit), and (3) seed production (total seeds produced per plant). All flowers on each plant were scored for fruit production, and I counted all of the seeds produced in each successful fruit. To test for differences among the robbing and emasculation treatments for these three variables simultaneously, I used a MANOVA with robbing treatment (low vs. high), access to self-pollen treatment (control vs. emasculation), and their interaction as fixed effects. A significant MANOVA was followed by univariate ANOVAs and Tukey's hsd tests.

RESULTS

Effects of nectar robbing on estimated pollen movement within populations

Within populations, I found no significant differences in the mean and mean-squared distance of dye dispersal from plants with experimental low vs. high robbing (mean ± 1 SE; dispersal distance, low vs. high robbing: 2.24 ± 0.20 m vs. 1.84 ± 0.22 m; mean-squared distance, low vs. high robbing: 8.68 ± 0.71 m^2 vs. 6.27 ± 1.35 m^2; Table 2). A power analysis indicated that to achieve a significant difference between robbing treatments in dispersal distance at $\alpha = 0.05$, I would have needed >500 plants per treatment. These results contradict predictions that high nectar robbing should increase pollen dispersal distance (Table 1A); in the *Ipomopsis aggregata* populations studied here, nectar robbing had no effect on the distance of dye dispersal within populations. Dye dispersal distance varied among plants as well as among days of the experiment, with a slight increase in dispersal distance as the season progressed (Table 2).

TABLE 3. *Ipomopsis aggregata* with simulated low robbing received significantly more self-dye per flower dyed than did plants with simulated high robbing, as shown by a mixed-model repeated-measures ANOVA.

Source	df	SS	*F*	*P*
Robbing treatment	1	21.40	8.28	0.01
Plant(Robbing treatment)	16	42.54	3.20	<0.0001
Day	15	22.02	1.77	0.04
Error	169	140.55		

However, plants with low and high robbing differed in levels of self-dye receipt (geitonogamy) (Table 3). Plants with low robbing received over two times more self-dye per male-phase flower dyed than plants with high nectar robbing (Fig. 1), matching predictions that robbing should reduce geitonogamy (Table 1C). Self-dye receipt per flower dyed differed among plants as well as among days of the experiment, but with no seasonal trend per se (Table 3).

Effects of nectar robbing on the likelihood of pollinators to leave a population

In 1996, pollinators were almost 50% more likely to leave the experimental arrays after visiting plants with low nectar robbing relative to plants with high robbing ($\chi^2 = 3.80$, df = 1, $P = 0.05$; Fig. 2). And in 1997, pollinators were >80% more likely to leave the arrays after visiting plants with low robbing relative to plants with high robbing ($\chi^2 = 96.58$, df = 1, $P < 0.001$; Fig. 2). These results further contradict predictions that high nectar robbing should increase pollen movement through increased pollinator flight (Table 1A). In the arrays studied here, pollinators were more likely to leave the experimental populations, and potentially more likely to influence long-distance pollen movement, after visiting rewarding plants with low nectar robbing.

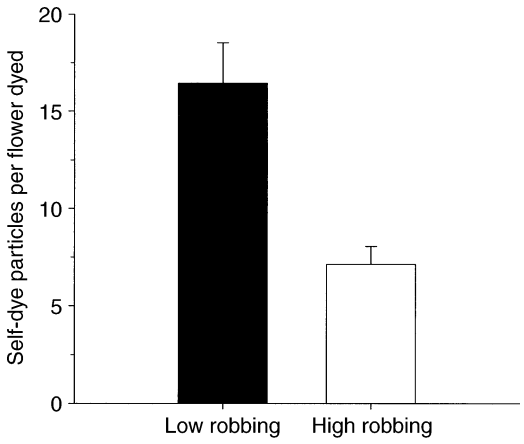

FIG. 1. *Ipomopsis aggregata* with simulated low robbing (10% of available flowers robbed) received significantly more self-dye per flower dyed than did plants with simulated high robbing (80% of available flowers robbed). Bars are means + 1 SE.

Effects of nectar robbing on geitonogamy and female plant reproduction

Irrespective of emasculation treatment, plants with low robbing had higher female reproductive success than plants with high robbing (MANOVA, robbing treatment: $F_{3,74} = 14.60$, $P < 0.0001$; Fig. 3). I found no significant effect of emasculation treatment nor a significant robbing × emasculation interaction for any measures of female-fitness components (MANOVA, emasculation treatment: $F_{3,74} = 0.71$, $P = 0.55$; robbing × emasculation: $F_{3,74} = 0.45$, $P = 0.72$). Plants with low nectar robbing produced significantly more fruits (ANOVA, $F_{1,76} = 26.29$, $P < 0.0001$), more seeds per fruit (ANOVA, $F_{1,76} = 17.88$, $P < 0.0001$), and more total seeds (ANOVA, $F_{1,76} = 26.85$, $P < 0.0001$) than plants with high nectar robbing across emasculation treatments (Fig. 3). These results suggest that the negative effects typically associated with self-pollen transfer (i.e., reduced seed production) are outweighed by the benefits associated with increased outcrossing in plants with low nectar robbing.

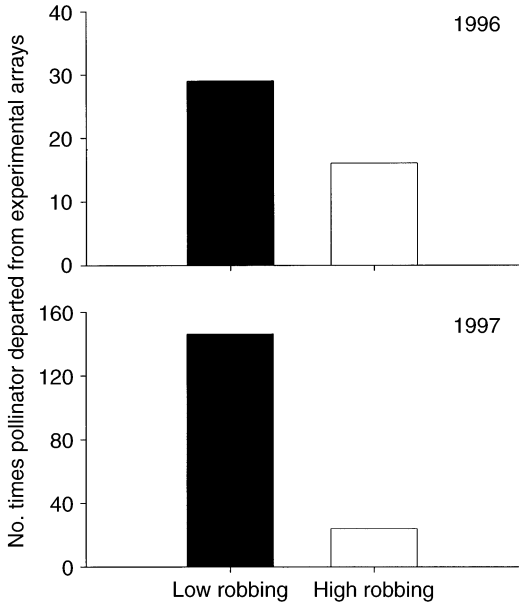

FIG. 2. Number of times pollinators left the experimental arrays after visiting *Ipomopsis aggregata* with simulated low vs. high nectar robbing (10% vs. 80% of available flowers robbed) in 1996 and 1997.

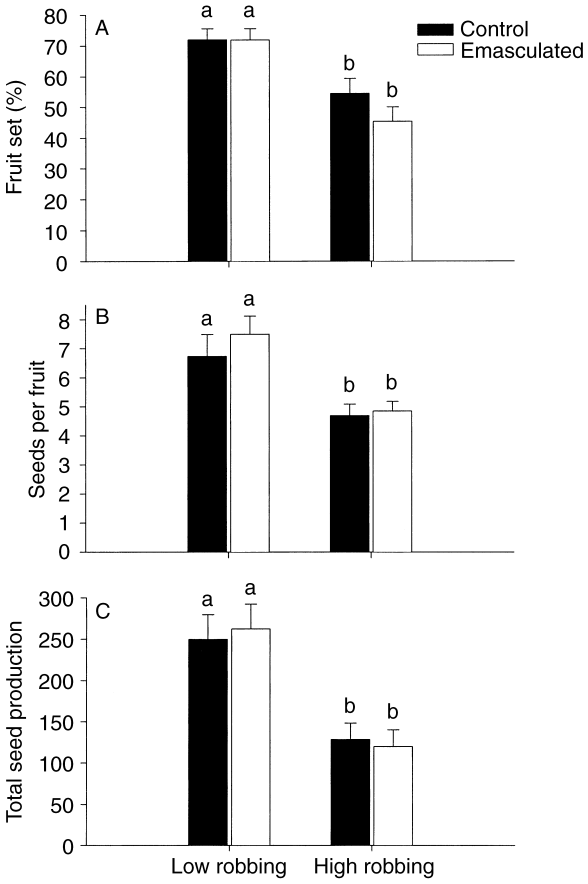

FIG. 3. The effects of simulated nectar robbing and emasculation treatments on (a) fruit set, (b) seeds per fruit, and (c) total seed production. Irrespective of emasculation treatment, *Ipomopsis aggregata* with low robbing (10% of available flowers robbed) produced more fruits, seeds per fruit, and total seeds than plants with high robbing (80% of flowers robbed) (MANOVA, $F_{3,74} = 14.60$, $P < 0.0001$). Different lowercase letters above the bars represent means that are significantly different based on Tukey's hsd tests. Bars are means + 1 SE.

DISCUSSION

Effects of nectar robbing on estimated pollen movement and pollinator flight

Pollen dispersal, an important component of gene flow in natural plant populations, has primarily been studied in light of the direct relationships between plants and pollinators; however, nectar robbers may have important indirect effects, both positive and negative, on pollen dispersal by altering plant–pollinator interactions. Results presented here suggest that nectar robbing does not influence the distance of dye (pollen-analogue) dispersal within plant populations. Mean and mean-squared distance of dye dispersal from plants in the present study were slightly lower than estimates reported in a previous study on *Ipomopsis aggregata* using similar techniques (Campbell and Waser 1989), likely because the density of flowering *I. aggregata* was higher in the present study populations over those of Campbell and Waser (1989; D. R. Campbell, *personal communication*). However, pollinators were more likely to leave a patch of plants after visiting plants with low vs. high robbing. Until more direct measures of pollen and gene movement among populations are in hand, I can only speculate that plants with high robbing experienced lower interpopulation pollen and gene movement relative to plants with low robbing. These results suggest that high levels of nectar robbing could adversely affect outcrossing among plant populations.

Foraging theory predicts (1) an inverse relation between nectar reward level and interplant pollinator flight distance (e.g., Pyke 1978) and (2) that a forager should leave a patch when its rate of energy intake falls below the overall potential net rate of energy intake in the habitat (marginal value theorem; Charnov 1976). Thus, if hummingbirds in this study forage in accordance with optimal foraging theory, they should fly further within a population and be more likely to leave a population after visiting unrewarding plants with high robbing. Such behavior would result in increased pollen dispersal within and among populations, assuming direct links between pollinator visitation and pollen flow. However, the results I found in the present study contradict these foraging predictions (Table 1) as well as those found in two previous studies examining the effects of nectar robbing on pollinator movement among plants (Zimmerman and Cook 1985, Maloof 2001).

One possible explanation for these surprising and unpredicted results is that previous studies in this system suggest that hummingbirds have a priori knowledge of the reward and robbing status of plants prior to floral visitation, although the exact cues that hummingbirds use to select rewarding plants are unknown (Irwin and Brody 1998, Irwin 2000). The above theories, however, were based on pollinators that had no knowledge of the reward status of flowering units prior to visitation. A priori knowledge of reward status could significantly change predictions about pollinator foraging behavior. For example, with a priori knowledge, hummingbirds should avoid plants with high robbing, which has been shown previously in this system (Irwin and Brody 1998, Irwin 2000), and only leave a patch of plants when their energy requirements are satisfied or after visiting most or all of the rewarding plants, in this case plants with low robbing. I unfortunately do not know whether or not birds left the experimental arrays when they were energetically satisfied; however, birds did visit significantly more plants with low robbing vs. high robbing before departing (Irwin and Brody 1998).

It should be noted that it may not be the last plant that a hummingbird visits that determines its leaving probability, but rather the series of visits within a patch. Although the experiments in this study were not designed to expressly test this mechanistic hypothesis

concerning hummingbird foraging, I did collect data on the series of plants visited with low and high robbing within the experimental arrays that can shed light on this supposition. I used a Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1995) to compare the temporal sequence of visits to plants with low vs. high robbing. I found that the two distributions did not differ significantly ($K = 0.53$, $N = 16$ distributions, $P = 0.94$), indicating that, in this system, the temporal sequence of plants visited with low vs. high robbing does not predict when a pollinator will depart from a patch of plants. However, as described above, hummingbird foragers visit significantly more plants and probe significantly more flowers with low vs. high robbing (Irwin and Brody 1998), suggesting that energetics may play an important role in the timing of bird departures, although the sequence of plants visited and competitive interactions with other hummingbirds (e.g., Paton and Carpenter 1984) cannot yet be ruled out as alternatives. Moreover, although this question was not examined in this study, birds may make decisions about departure from plant populations at the population level, not at the plant or flower level (as assumed in this study), and very different results may be obtained comparing bird departure from *populations* with low vs. high robbing, which could influence estimates of pollen and gene movement. More work is needed to understand the importance of nectar robbing and nectar-reward levels to the timing of pollinator departure from plant populations and their subsequent impacts on pollen and gene movement.

One caveat about the interpretation of this study is that pollen dispersal distance is just one of many components that influence gene flow and genetic structure in plant populations (e.g., Wright 1943, Crawford 1984). The *total* gene contribution through pollen, not just the distance that pollen is donated, also influences spatial genetic structure (Campbell and Waser 1987). For example, pollinator avoidance of robbed *I. aggregata* reduces pollen donation by 80% (Irwin and Brody 1999). A reduction in pollen donation can reduce the number of individuals in a genetic neighborhood. Moreover, gene flow occurs through both pollen and seed contributions (e.g., Crawford 1984). *I. aggregata* seeds have restricted dispersal distances, and robbing could influence genetic structure by changing the number of seeds input into populations by different plants. How robbing indirectly affects gene movement via pollen and seeds deserves further attention.

Effects of nectar robbing on geitonogamy and female plant reproduction

Robbing not only indirectly influenced the likelihood that a pollinator would leave a patch but also levels of pollen movement within individual plants. Plants with low levels of nectar robbing received 50% more self-pollen than plants with high robbing, supporting predictions concerning the effects of robbing on geitonogamy (Table 1). Previous work in this system has shown positive correlations between the nectar provided by plants, the average number of flowers probed per pollinator visit (Mitchell 1993, Irwin and Brody 1998), and levels of self-pollen transfer (de Jong et al. 1992). These patterns may be common in other plant–pollinator–robber systems as well (Maloof and Inouye 2000).

For *I. aggregata*, geitonogamy can be extremely costly to plant reproductive success, reducing seeds per fruit by 25–42% and pollen export to other plants by 14% (Waser and Price 1991, de Jong et al. 1992). However, when I manipulated robbing levels and access to self-pollen (using an emasculation treatment), I found no benefit of emasculation to components of female reproductive success. Plants with low robbing levels outperformed plants with high robbing levels, irrespective of emasculation treatment. In plants with low nectar robbing, I did find a slight benefit of emasculation over nonemasculation (a 5% difference in seed production; Fig. 3); however, this difference was not statistically significant. Levels of geitonogamous pollen movement should depend on floral display size (e.g., de Jong et al. 1992, Harder and Barrett 1995); however, in this study there was no difference in flower production among treatments that might have confounded interpretation of the effects of the robbing and emasculation treatments (see *Methods*: *Effects of nectar robbing on geitonogamy*). Nectar robbers are not the only plant antagonists that indirectly influence geitonogamy through changes in plant–pollinator relationships. Juenger and Bergelson (2000) found that emasculation of *I. aggregata* had a slight fitness benefit to plants when they were protected from mammalian herbivores; however, emasculation had no beneficial effects when plants were subjected to mammalian antagonists, a result similar to that found here. Pollen and/or resource limitation in the year of study may explain these results.

The negative effects of geitonogamy should only be evident when plants receive high amounts of pollen, both selfed and outcrossed, allowing for pollen competition on the stigma surface (de Jong et al. 1992). Plants with heavy robbing may not experience positive effects associated with reduced geitonogamy because they often are extremely pollen limited (Irwin and Brody 1998, 1999). For plants with low robbing, I expected to find larger differences in female reproduction between emasculated and nonemasculated plants because these plants receive more pollen than robbed counterparts (Irwin and Brody 1999). That I didn't find differences may be related to pollen and/or resource limitation in plants with light robbing in the year of study. The former would reduce pollen competition between selfed and outcrossed pollen grains on the stigma, easing the disadvantages associated with geitonogamy. The latter would diminish the ability of plants to respond to the advantages of low geitonogamy, reducing

the difference between emasculation and nonemasculation treatments. Resource and hand-pollination manipulations would need to accompany the robbing and emasculation treatments to tease apart these factors.

Conclusions

Although previously considered unimportant and novel floral visitors, nectar robbers are widespread (Irwin et al. 2001) and can have important indirect consequences on estimates of pollen flow in natural plant populations. I found that nectar robbing had no effect on the mean and mean-squared distance of dye dispersal within populations; however, pollinators were >50% more likely to leave experimental arrays after visiting plants with low robbing vs. high robbing, suggesting that pollen dispersal among populations might be reduced in plants with high robbing relative to plants with low robbing. Furthermore, high levels of robbing reduced within-plant dye transfer by one-half, but the reproductive benefits of reduced self-pollination in plants with high robbing were outweighed, likely by the disadvantages associated with decreased pollinator visitation and subsequent reduced seed production in unrewarding, robbed plants. Together, these experiments, combined with previous experiments in this system, suggest that the negative indirect effects of high robbing through decreased pollinator visitation (Irwin and Brody 1998), reduced male and female plant fitness estimates (Irwin and Brody 1999, 2000), and potential decreased outcrossing among populations (estimated via pollinator departures from patches) likely exceed the positive effects associated with decreased geitonogamy. Additional work is needed before we understand the general ecological and evolutionary significance of plant–pollinator–robber interactions to pollen flow and gene flow in natural populations. Given the ubiquity of nectar robbers, their indirect effects on plant–pollinator mutualisms are likely to have widespread importance in structuring plant populations in nature.

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