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PREDICTING THE EFFECTS OF NECTAR ROBBING ON PLANT REPRODUCTION: IMPLICATIONS OF POLLEN LIMITATION AND PLANT MATING SYSTEM[1]

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The outcome of species interactions is often difficult to predict, depending on the organisms involved and the ecological context. Nectar robbers remove nectar from flowers, often without providing pollination service, and their effects on plant reproduction vary in strength and direction. In two case studies and a meta-analysis, we tested the importance of pollen limitation and plant mating system in predicting the impacts of nectar robbing on female plant reproduction. We predicted that nectar robbing would have the strongest effects on species requiring pollinators to set seed and pollen limited for seed production. Our predictions were partially supported. In the first study, natural nectar robbing was associated with lower seed production in *Delphinium nuttallianum*, a self-compatible but non-autogamously selfing, pollen-limited perennial, and experimental nectar robbing reduced seed set relative to unrobbed plants. The second study involved *Linaria vulgaris*, a self-incompatible perennial that is generally not pollen limited. Natural levels of nectar robbing generally had little effect on estimates of female reproduction in *L. vulgaris*, while experimental nectar robbing reduced seed set per fruit but not percentage of fruit set. A meta-analysis revealed that nectar robbing had strong negative effects on pollen-limited and self-incompatible plants, as predicted. Our results suggest that pollination biology and plant mating system must be considered to understand and predict the ecological outcome of both mutualistic and antagonistic plant–animal interactions.

Key words: *Bombus occidentalis*; Colorado; *Delphinium nuttallianum*; *Linaria vulgaris*; meta-analysis; nectar robbing; pollen limitation; self-compatibility.

Mutualisms, interspecific interactions in which both members undergo a net fitness benefit, are ubiquitous in natural systems (Bronstein, 2001a) and bestow critical ecosystem services (e.g., Kearns et al., 1998). However, exploitation of mutualisms, including those between flowering plants and their pollinators, is also widespread (reviewed in Bronstein, 2001b). Exploiters gain access to rewards without providing services or rewards in return. Cheaters of plant–pollinator mutualisms are common among both plants and floral visitors. For example, mate-mimicking or nectarless orchids cheat their pollinators of nectar rewards, thus ensuring pollination service without incurring the potential costs of producing nectar (e.g., Gigord et al., 2002; Thakar et al., 2003). Conversely, nectar robbers are animals that access floral nectar by biting holes in the sides of flowers, often without providing pollination service (Inouye, 1980; Maloof and Inouye, 2000; Irwin et al., 2001). This paper focuses on nectar robbing and its impacts, in conjunction with pollen limitation and plant mating system, on female plant reproductive success. Cheaters in mutualistic systems are universal (Bronstein, 2001b), and investigating the mechanisms by which the impacts of cheaters are reduced or strengthened will provide a better understanding of their role in community interactions.

Nectar robbers are widespread both geographically and taxonomically (Irwin and Maloof, 2002), and robbing may affect up to 100% of flowers in some plant populations (e.g., Stout et al., 2000; Irwin and Maloof, 2002; Newman and Thomson, 2005). In one review, Maloof and Inouye (2000) list reports of negative, neutral, and positive fitness effects of robbing on female plant function. Alternatively, Irwin et al. (2001) used a meta-analysis approach and found, on average, a marginal negative effect of nectar robbing. Despite the abundance of robbing in nature and the wealth of attention this form of exploitation has received (e.g., Arizmendi et al., 1996; Morris, 1996; Irwin and Brody, 1999; Maloof and Inouye, 2000; Navarro, 2000; Lara and Ornelas, 2001; Irwin, 2003; Kjonaas and Rengifo, 2006), it remains difficult to predict the degree to which robbers will affect plant fitness. Irwin et al. (2001) found that both the identity of the robber and the pollinator (i.e., insects vs. birds) influenced the effects of robbers on plant reproduction. A number of other potential variables, such as the diversity of other floral resources available in the community, the effect of robbers on nectar-standing crop, and the scarcity of nectar in the environment, have also been suggested as factors determining the plant fitness impacts of robbers (Maloof and Inouye, 2000). While these variables are clearly important, some of them (in particular, nectar availability in the environment) are difficult to measure (Pleasants and Zimmerman, 1983) and may be too variable across populations and across systems (Schmida and Kadmon, 1991) to draw general conclusions. Nectar robbing may be context dependent to some degree, but some characters may be robust as predictor variables of the effects of robbing on plant reproduction. Here, we propose that two alternative

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variables may strongly predict the degree to which robbing affects female plant reproduction: (1) the extent to which plants are pollen limited and (2) the plant mating system. Although the notion that pollen limitation and the plant mating system may be used to predict the effects of robbing on female reproductive success is not new (e.g., Arizmendi et al., 1996; Stout et al., 2000; Arizmendi, 2001), the importance of these two variables has not been stringently tested. We are focusing here on cases in which robbers do not damage female reproductive organs (e.g., stigmas, styles, ovaries) while robbing. Moreover, we are focusing on the effects of robbing on female plant reproduction because too few studies have tested the effects of robbing on male plant reproduction to draw any general conclusions (e.g., Morris, 1996; Irwin and Brody, 2000).

Pollen limitation—If robbed plants receive fewer pollinator visits than unrobbed plants (e.g., Roubik, 1982; Irwin and Brody, 1998) and if plant reproduction is limited by pollinator visits and pollen receipt (e.g., Young and Young, 1992; Burd, 1994; Ashman et al., 2004), then the fitness costs associated with robbing may be high. Thus, the degree to which plants are pollen limited should strongly impact the effects of robbers on plant reproduction. Conversely, the costs of robbing to female plant fitness may be negligible if pollinator visitation is sufficient to fertilize all available ovules. Such might be the case if pollinators cannot identify robbed flowers (Goulson et al., 1998), if alternative nectar sources are scarce (Irwin et al., 2001), if legitimate visitation increases as a consequence of reduced nectar volume in robbed flowers (Maloof and Inouye, 2000), or if robbing animals also occasionally visit legitimately (Morris, 1996) or pollinate while robbing (e.g., Higashi et al., 1988). Robbing may also have no effect on female plant reproduction if seed production is limited by resources rather than pollinators (Campbell and Halama, 1993). Additionally, robbing may not affect female plant reproduction if pollinators discriminate between robbed and unrobbed flowers but deposit fewer pollen grains of higher quality on stigmas of robbed flowers because of longer pollinator flights between consecutive visits (Maloof, 2001); this argument assumes that increased pollen quality balances reduced pollen deposition for female plant reproduction and that plant populations have strong spatial genetic structuring. Although pollen quality may be important to the effects of robbing on plant reproductive success (Aizen and Harder, 2007), we focused here on a quantitative perspective of pollen limitation in relation to nectar robbing. Finally, positive indirect effects of nectar robbers, such as increasing the number of flowers and plants visited by legitimate pollinators, presumably due to changes in nectar rewards, has also been observed (e.g., Lara and Ornelas, 2002).

Plant mating system—Life history traits of plants, such as mating system, may also strongly affect the plant fitness consequences associated with robbing. For example, for plants that are predominantly selfing, changes in pollinator behavior following robbing may have little consequence on plant reproductive success. The same might be expected for plant species with mixed mating systems that suffer little or no fitness consequences as a result of selfing (Travers and Mazer, 2000). Alternatively, plants with mixed mating systems can incur strong selfing consequences due to early-acting inbreeding depression (Husband and Schemske, 1996). For self-incompatible plants, pollinator behavior following robbing may strongly impact plant reproductive success through, for example, changes in outcrossing distance (Maloof, 2001) or geitonogamy (Irwin, 2003). Self-incompatibility is typically defined as a genetic mechanism that reduces or inhibits self-fertilization (de Nettancourt, 2001). Here, we distinguish between self-incompatible species that can autogamously self-pollinate from those that require pollinators to move self-pollen from anthers to stigmas within flowers or plants. This distinction highlights all cases in which pollinator visitation is important for female plant reproduction.

To understand the effects of pollen limitation on the outcome of plant–nectar robber interactions, we compared the effects of nectar robbing on the female reproductive success of two subalpine plants, *Delphinium nuttallianum* (Ranunculaceae) and *Linaria vulgaris* (Scrophulariaceae). The two species share a common nectar-robbing bumble bee, *Bombus occidentalis* (Apidae), but differ in the degree of pollen limitation. Seed set of *D. nuttallianum* is generally limited by pollinator visitation (Waser and Price, 1990), whereas that of *L. vulgaris* is generally not limited by pollinator visits (R. E. Irwin, unpublished data). Using a combination of observational and experimental studies, we measured the effects of robbing on female plant reproductive success in both species. We predicted that robbing would have a stronger negative effect on *D. nuttallianum* than on *L. vulgaris* because female reproduction in *D. nuttallianum* is more strongly pollen limited. We then combined existing published studies with the results presented in this paper and conducted a meta-analysis to more broadly understand the degree to which pollen limitation and plant mating system (self-compatibility) affect the outcome of robbing on female plant reproduction. A meta-analytical approach is advantageous in that it allows us to generalize across a wide variety of systems involving nectar robbers. Although this work focused on nectar robbers and their impacts on female plant reproduction, the concepts presented are applicable to other species interactions that involve exploitation and the traits that mitigate or compound the costs of exploiters (for a review, see Bronstein, 2001b). Investigating the fitness consequences of cheating is a first step toward understanding the ecological and evolutionary implications of cheating on populations and communities.

MATERIALS AND METHODS

Study system—Fieldwork was conducted from June through September from 1997 to 1999 in and around the Rocky Mountain Biological Laboratory, Colorado, USA (RMBL; 38°57′29″ N, 106°59′06″ W; altitude, 2900 m a.s.l.). *Delphinium nuttallianum* Pritzel (= *D. nelsonii* Greene) blooms in the early summer around the RMBL (late May to early July; Saavedra et al., 2003). *Delphinium nuttallianum* is a perennial (mean life span until first flower = 3–7 years; Waser and Price, 1991), producing 1–10 purple, zygomorphic flowers on 1–2 racemose inflorescences (Waser, 1978). The flowers of *D. nuttallianum* have a nectar spur in which nectar collects (nectar production rate, 0.02 μL/h; percentage of sugar concentration, 51.2 ± 0.7% [mean ± SE]; Waser, 1978). The major pollinators of *D. nuttallianum* around the RMBL are broad-tailed hummingbirds (*Selasphorus platycercus* Swainson, Trochilidae), queen bumble bees (*Bombus appositus* Cresson, *B. flavifrons* Cresson, *B. californicus* F. Smith, and *B. nevadensis* Cresson; Apidae), and to a lesser extent, small solitary bees and other insect visitors (Waser, 1978, 1982; Waser and Price, 1990). Although the flowers of *D. nuttallianum* are self-compatible to some degree (Price and Waser, 1979), protandry prevents autogamous self-pollination, and plants require pollinators to transfer even self-pollen within flowers and plants (Waser and Price, 1990); *D. nuttallianum* sets very few seeds in the absence of pollinator visitation (Waser, 1978). Only 7% of seeds on average are produced from selfing, with some variation among populations (Williams et al., 2001). Seed set is often limited by pollinator visitation (Waser and Price, 1990), with greater pollinator visitation increasing stigma pollen loads and seed set as a saturating function (Bosch and Waser, 1999).

Linaria vulgaris Mill. blooms in the late summer around the RMBL (late July to early October). Native to Europe, *L. vulgaris* was introduced into areas around the RMBL in the late 1800s. *Linaria vulgaris* is a perennial (mean root lifespan, 3.8 yr; Robocker, 1974), with a single stalk producing 26.8 ± 2.6 yellow, zygomorphic flowers (R. E. Irwin, unpublished data). Nectar production rate of *L. vulgaris* flowers averages 0.09 μL/h, with a sugar concentration of 37% in eastern North America (Arnold, 1982). Around the RMBL, the sugar concentration of *L. vulgaris* can reach as high as 61.0 ± 1.6% (R. E. Irwin, unpublished data). *Linaria vulgaris* reproduces extensively by clonal growth (Saner et al., 1995) as well as through seeds. An individual stalk can produce >5000 seeds (Zilke and Coupland, 1954), and a genet can produce up to 30 000 seeds (Saner et al., 1995). At the RMBL, the self-incompatible flowers of *L. vulgaris* are pollinated primarily by bumble bees (*B. appositus*, *B. californicus*, *B. fervidus*, *B. flavifrons*, *B. frigidus*) and to a lesser extent, small solitary bees and rufous hummingbirds (*S. rufus*). Pollen limitation of female reproductive success varies among regions in which *L. vulgaris* occurs. In eastern North America, pollinator visitation likely limits seed production (Arnold, 1982); however, stalks are generally not pollen limited for seed production around the RMBL (R. E. Irwin, unpublished manuscript). For example, in 2002, 35 stalks each across two sites were provided with supplemental pollen or left open to natural levels of pollination. There was no significant effect of hand pollination on seed production per stalk relative to stalks without hand pollination ($F_{1,67} = 1.14$, $P = 0.29$; Appendix S1, see Supplemental Data with online version of this article). We would have needed at least 238 stalks per treatment to find a significant effect of hand pollination at $\alpha = 0.05$ (R. E. Irwin, unpublished data).

The nectar spurs of both *D. nuttallianum* and *L. vulgaris* are robbed by the bumble bee *Bombus occidentalis* Greene, Apidae. The bee uses its toothed mandibles to chew a hole through the sides of the nectar spurs; it then inserts its proboscis into the hole and removes nectar, bypassing the floral opening used by legitimate visitors. Data on natural nectar-robbing rates on *D. nuttallianum* and *L. vulgaris* have been published previously (Irwin and Maloof, 2002); here we expand our understanding of plant–nectar robber interactions in these plant species with the inclusion of new data to assess the relationship between natural levels of nectar robbing and plant reproduction and with the inclusion of experimental data from manipulating nectar robbing and measuring plant response. Robbing rates on *D. nuttallianum* range from 0 to 100% of available flowers with peak robbing of 56.5 ± 8.5% (mean ± 1 SE) of available flowers robbed (Irwin and Maloof, 2002). The effects of robbing on *D. nuttallianum* reproductive success are unknown. Robbing rates on *L. vulgaris* range from 0 to 100% of available flowers robbed with peak robbing of 79.3 ± 15.4% (mean ± 1 SE) of available flowers robbed (Irwin and Maloof, 2002). For *L. vulgaris* growing in southern England, high levels of robbing (96% of open flowers robbed) by *B. lapidarius*, *B. lucorum*, and *B. terrestris* had no effect on female reproductive success (Stout et al., 2000); however, the effects of nectar robbing by *B. occidentalis* on *L. vulgaris* in western North America are unknown.

Field methods—*The effects of nectar robbing on Delphinium nuttallianum*—We measured the effects of natural and experimental nectar robbing on female reproductive success of *D. nuttallianum* in 1999.

Observational study—To understand the relationship between natural levels of nectar robbing and female plant function, we randomly chose 50 budding *D. nuttallianum* at two sites (30 plants at site 1, 38°57′41.27″ N, 106°59′05.05″ W; 20 plants at site 2, 38°57′39.60″ N, 106°59′01.43″ W) in early June 1999. We measured robbing levels by counting the number of open flowers and the number of nectar robber holes in each flower once per week throughout the flowering season (Irwin and Maloof, 2002).

When plants senesced, we collected and counted all of the fruits and seeds produced by each plant. In addition, we counted the number of aborted ovules in each fruit under a dissecting microscope. For each plant, we calculated percentage of seed set (number of seeds produced divided by the total number of ovules per plant) and total seed set as measures of female plant reproduction. Percentage of seed set and total seed set were the most biologically relevant measures of female reproductive success for *D. nuttallianum* (as opposed to percentage of fruit set) because an individual plant does not produce many flowers in a given year, and the vast majority of flowers set fruit (almost 90% of flowers set fruit in this study). Moreover, percentage of seed set takes into account the finite number of ovules and underlying resource status of the plant, and total seeds is indicative of whole-plant reproductive success.

To assess the relationship between female plant reproduction and natural levels of nectar robbing, we performed regressions of percentage of seed set per fruit and total seeds per plant (log-transformed) on mean nectar robbing per plant (proportion of robbed flowers per plant, arcsine-square root transformed). Percentage of seed set and total seed production per plant were not significantly correlated ($r = 0.27$, $N = 28$, $P = 0.17$) and thus were analyzed separately. To avoid the confounding influence of a correlation between nectar robbing and female plant reproduction among sites, rather than among individuals within sites (the relevant hypothesis), we tested for homogeneity of the covariance structure between nectar robbing and mean percentage of seed set and total seed set across sites (PROC DISCRIM, option POOL = TEST, SAS version 8; SAS Institute, 2001). We combined the data across sites because we found no evidence to reject the null hypothesis of homogeneity of the covariance structure for percentage of seed set or total seed set (in both cases, $\chi^2 < 5.55$, $p = 0.14$). Nectar robbing may affect not only plant success but also per flower success, especially if pollinators discriminate on a per flower, rather than on a per plant, basis or if unrobbed flowers within plants can compensate for those that are robbed (Irwin and Brody, 1999). Thus, we also examined percentage of seed set per fruit and number of seeds per fruit of robbed and unrobbed flowers using a MANOVA. By using a multivariate approach here and for analysis of experimental data, we could test the effects of nectar robbing on several interrelated measures of female plant reproduction (Scheiner, 1993; Rencher, 1995). We removed 12 plants from all statistical analyses because they were consumed by unknown herbivores before we could collect the fruits.

Experimental manipulation—From the observational study, we cannot tease apart the correlative effects of robbing on plant reproduction from the causal effects; thus, we also measured the effects of experimental nectar robbing on female plant reproduction in *D. nuttallianum*. In 1999, we randomly chose 60 budding *D. nuttallianum* at a third site (38°57′36.57″ N, 106°58′58.78″ W) with naturally low robbing rates. We randomly assigned 30 plants each to an artificially superimposed "unrobbed" treatment (0% of available flowers robbed) or "complete nectar-robbing" treatment (100% of available flowers robbed). These levels of robbing are common in the field for *D. nuttallianum* (Irwin and Maloof, 2002). Because natural nectar robbing was uncommon at this site, we did not need to collar flowers to deter robbers. Nectar robbing by *B. occidentalis* was recorded and made up less than 11% of the available flowers open on control plants. To our knowledge, *D. nuttallianum* flowers do not respond positively to repeated nectar removal. Originally, we had an equal number of plants per robbing treatment (30 plants per treatment); however, six plants in the unrobbed treatment (final $N = 24$ plants) and three plants in the complete robbing treatment (final $N = 27$ plants) were consumed by unknown herbivores and thus were excluded from the study.

To rob flowers artificially, we made a small hole in the side of the nectar spur with dissecting scissors and removed all available nectar through the hole with a 10-μL microcapillary tube. Robbing treatments were performed every other day throughout the blooming season of each plant. If flowers had been robbed previously, the flowers were robbed again through the existing holes. This method of artificial robbing has been used successfully to mimic the effects of robbing by *B. occidentalis* on a co-occurring plant species, *Ipomopsis aggregata* (Polemoniaceae) (Irwin and Brody, 1998). To ensure that our experimental robbing treatment mimicked natural robbing in terms of plant response by *D. nuttallianum*, we used an ANOVA to compare mean percentage of seed set from plants with naturally vs. artificially robbed flowers. We found no difference in percentage of seed set between natural and artificial robbing ($F_{1,44} = 0.22$, $P = 0.64$), suggesting that our nectar-robbing method mimics natural robbing by *B. occidentalis*. Plants in the unrobbed treatment were left unmanipulated, but the flowers on these plants were physically handled each day to control for the effects of flower handling associated with the robbing treatments.

Once plants ceased blooming, we collected all of the fruits and measured percentage of seed set per fruit and total seeds for each plant, as described earlier. To understand the effects of experimental nectar robbing on female plant reproduction, we used a MANOVA with robbing treatment as a fixed effect and percentage of seed set and total seeds (square-root transformed) as response variables. A significant MANOVA was followed by univariate ANOVAs for each response variable.

The effects of nectar robbing on Linaria vulgaris—We also measured the effects of natural and experimental nectar robbing on female reproductive success in *L. vulgaris*. The methods for *L. vulgaris* differed slightly from those

TABLE 1. Yearly differences in percentage of robbing, percentage of fruit set, numbers of seeds per fruit, and number of seeds per stalk in natural populations of *Linaria vulgaris*. Values are mean ± 1 SE.

Year	Percentage of robbing	Percentage of fruit set	No. seeds per fruit	No. seeds per stalk
1997	39.5 ± 5.8	75.1 ± 3.8	90.7 ± 7.1	2306.0 ± 291.1
1998	23.1 ± 3.0	65.7 ± 2.9	88.4 ± 4.6	2991.7 ± 285.3
1999	95.4 ± 0.6	25.2 ± 2.4	100.9 ± 8.1	770.8 ± 94.1

of *D. nuttallianum* because of differences in life history characteristics and robbing levels between the two species.

Observational study—We quantified the relationship between natural levels of nectar robbing and female plant reproduction from 1997 to 1999 in one large site in the RMBL town site (38°57′32.39″ N, 106°59′24.36″ W). We measured natural robbing by *B. occidentalis* on focal stalks once per week throughout the flowering season, as described for *D. nuttallianum*. We measured robbing on 24 stalks in 1997, 35 stalks in 1998, and 50 stalks in 1999 (Irwin and Maloof, 2002). We realize that the best unit of replication would have been to measure the effects of nectar robbing on a whole-plant basis. However, *L. vulgaris* is clonal, and it is difficult to determine which stalks (ramets) are connected without digging up an entire population. Although working with ramets has disadvantages (i.e., we are not measuring whole-plant reproduction), ramet dynamics have been successfully compared to genet dynamics in other systems (e.g., Caswell, 1985; Eriksson and Jerling, 1990; Silvertown et al., 1993). In addition, there is competition for resources within *L. vulgaris* genets, and undamaged ramets may not direct resources toward damaged ramets (Hellstrom et al., 2006). If, however, resource translocation occurs from damaged to undamaged ramets, our results could be biased toward finding effects of nectar robbing.

Once plants ceased blooming, we collected all expanded fruit capsules and recorded aborted fruits. Because an individual *L. vulgaris* stalk can produce >5000 seeds (Zilke and Coupland, 1954), counting the number of seeds produced per stalk was not practical. Instead, for each stalk we measured the mass of 10 seeds on a microbalance (UMX2 Mettler Toledo Ultramicro Balance, Columbus, Ohio, USA) to the nearest 0.0001 g. Then we measured the mass of all seeds the stalk produced. We estimated the number of seeds produced per stalk by calculating seed number as: number of seeds = (mass of total seeds × 10 seeds)/mass of 10 seeds. Seed masses were only calculated for black seeds (likely viable seeds; Saner et al., 1995). White seeds are inviable (L. A. Burkle, personal observation) and were not included in the total seed number. For each stalk, we calculated three measures of female plant reproduction: (1) percentage of fruit set (number of expanded fruits divided by the total number of flowers produced; arcsine square-root transformed), (2) number of seeds per fruit (number of seeds divided by the number of successful fruits), and (3) seed production (total seeds produced per stalk; log transformed). We used this suite of variables to estimate female plant reproduction to identify the mechanisms by which robbers might affect plant reproduction. For example, if robbers affect percentage of fruit set and total seeds but not seeds per fruit, this would suggest that robbers affect total seeds by changing the probability that a plant will produce a successful fruit.

To assess the relationship between female plant reproduction and natural levels of nectar robbing, we performed multivariate regressions of percentage of fruit set, number of seeds per fruit, and seed production on mean nectar robbing per stalk in each year. Separate analyses were performed in each year of the study because (1) robbing levels, percentage of fruit set, number of seeds per fruit, and seed production varied significantly among years (MANOVA: $F_{6,184} = 52.6$, $P = 0.0001$; Table 1) and (2) the relationship between robbing level and female reproduction was confounded with year (PROC DISCRIM, option POOL = TEST, SAS version 8; in all cases $\chi^2 > 24.03$, $p < 0.001$). We also compared percentage of fruit set and number of seeds per fruit between robbed and unrobbed flowers within stalks in each year using Hotelling's T^2; we only included stalks that had robbed and unrobbed flowers in this analysis.

Experimental manipulation—We experimentally manipulated nectar robbing and measured subsequent effects on female plant reproduction in 1997. We haphazardly chose 21 stalks in the one large population of *L. vulgaris* in which we recorded natural robbing. We randomly assigned 10 stalks to an experimental "unrobbed" treatment (0% of available flowers robbed) and 11 stalks to an experimental "complete nectar-robbing" treatment (100% of available flowers robbed) for which flowers on each stalk were either artificially robbed as described for *D. nuttallianum* or naturally robbed by *B. occidentalis*. We removed all of the available nectar per flower in this robbing treatment because the bumble bees typically remove all available nectar when robbing flowers of *L. vulgaris*. These levels of robbing are common in the field for *L. vulgaris* by *B. occidentalis* (Irwin and Maloof, 2002).

Artificially and naturally robbed flowers were marked with small dots of different colors of indelible ink on their calyces. For the low robbing treatment, nectar spurs were either "collared" to deter robbers, or flowers were left unmanipulated. The collars were made of small pieces of translucent drinking straws; one end was folded over and stapled shut with a small stapler. The other end was placed over the spur, and the collar was tied to the pedicel and stalk of the plant using thread. The unmanipulated flowers were visited each day to determine whether they had been naturally robbed. Once the flowers fell off, all flowers that were not robbed by *B. occidentalis* were marked with small dots of ink on their calyces. Collared flowers were marked with a different color of ink. To ensure that our artificial robbing treatments and collaring treatments mimicked naturally robbed and unrobbed flowers, we compared percentage of fruit set (arcsine-square root transformed) and number of seeds per fruit for (1) artificially vs. naturally robbed flowers and (2) collared vs. unrobbed flowers using paired *t* tests within stalks. We found no difference between artificial and natural nectar robbing for percentage of fruit set ($t_{10} = 0.43$, $P = 0.68$) or for number of seeds per fruit ($t_{10} = 1.31$, $P = 0.22$). Moreover, we found no difference between collared and naturally unrobbed flowers for percentage of fruit set ($t_8 = 0.20$, $P = 0.85$) or number of seeds per fruit ($t_8 = 1.32$, $P = 0.22$). These results suggest that our artificial treatments mimicked natural conditions in terms of female plant response.

To determine the effects of the experimental robbing treatments on female reproductive success, we used a MANOVA with robbing treatment (artificially robbed vs. collared) as a fixed effect and percentage of fruit set (arcsine-square root transformed) and number of seeds per fruit as response variables. We calculated percentage of fruit set and number of seeds per fruit as mean values on treated flowers on a per stalk basis.

Meta-analysis: the influence of pollen limitation and plant mating system on the effects of nectar robbing on female plant reproduction—We performed a meta-analysis (Gurevitch and Hedges, 2001) to examine quantitatively the degree to which pollen limitation and plant mating system influence the effects of nectar robbing on female plant reproduction. Using the keyword nectar rob* (with an asterisk as a wild card), we searched the published literature on Web of Science from 1945 to 2007 as well as literature-cited sections from papers on nectar robbing. We included all studies that we found (27 total) that reported a measure of female reproductive success of robbed and unrobbed flowers or plants for which we could also locate information on self-compatibility and pollen limitation (see Table 2 for the list of studies included in the meta-analysis). Studies were excluded if robbers directly damaged female reproductive organs while robbing (i.e., Galen, 1983) in order to focus the meta-analysis on the indirect effects of robbing on female reproduction via changes in pollination. An effect size (*d*) was calculated for each study, expressing the difference in mean female reproduction in plants or flowers that were robbed or unrobbed, divided by their pooled SD and corrected for bias due to small sample size. Negative effects of robbing are specified by a negative effect of size and vice versa. An effect size of 0.2 (absolute value) is considered small, 0.5 medium, 0.8 large, and ≥1 very large (Cohen, 1969). The overall impact of nectar robbing on female plant reproduction was weak but negative ($d = -0.25$), with effect sizes ranging from −3.02 to +2.74. Our results are comparable to those found in a similar meta-analysis by Irwin et al. (2001; $d = -0.27$), with the current analysis containing 10 additional studies. We then calculated effect sizes for groups of studies that had plants with evidence of the presence vs. absence of pollen limitation of female reproductive success in at least one year of study (recognizing that pollen limitation can vary annually; Ashman et al., 2004) and plants with different mating systems (self-compatible vs. self-incompatible). The between-class homogeneity statistic (Q_b) was used to statistically analyze these comparisons. *Delphinium nuttallianum* was the only species that we could find in which the literature distinguished between the genetic mechanism of self-compatibility vs. the requirement that pollinators move both selfed and outcrossed pollen in a genetically self-compatible species. Thus, we performed the meta-analysis twice, with *D. nuttallianum* classified as self-compatible or functionally self-incompatible (requiring pollinators to move self and outcross pollen). Because the outcome of the statistical comparison was the same whether *D. nuttallianum* was classified as self-compatible or self-incompatible, we report the results for only the latter test.

Table 2. Studies included in the meta-analysis and plant characters (pollen limitation and self-compatibility). Dashed lines indicate species whose pollen limitation is unknown or whose pollen limitation for seed set varied to such a degree that the plant could not be classified. We included studies that examined the effects of nectar robbers (organisms that steal nectar by biting holes through flowers) and nectar thieves (organisms that steal nectar without pollinating because of a mismatch between floral and visitor morphology; Inouye, 1980).

Plant species	Reference	Pollen limited	Self-compatible
Aconitum lycoctonum	Utelli and Roy (2001)	—	yes
Anthyllis vulneraria	Navarro (2000)	no	yes
Aphelandra sinclairiana	McDade and Weeks (2004)	no	no
Asclepias curassavica	Wyatt (1980)	—	no
Asclepias syriaca	Fritz and Morse (1981)	yes	no
Centaurea solstitialis	Agrawal et al. (2000)	yes	yes
Chilopsis linearis	Richardson (2004)	yes	no
Corydalis ambigua	Higashi et al. (1988)	—	no
Corydalis caseana	Maloof (2001)	no	yes
Delphinium nuttallianum	This study	yes	no
Fouquiera splendens	Waser (1979)	yes	yes
Frasera speciosa	Norment (1988)	—	no
Fuchsia magellanica	Traveset et al. (1998)	—	yes
Fuchsia microphylla	Arizmendi et al. (1996)	no	yes
Hamelia patens	Lasso and Naranjo (2003)	yes	no
Impatiens capensis	Rust (1979)	yes	yes
Impatiens capensis	Temeles and Pan (2002)	yes	yes
Ipomoea heredifolia	Lara and Ornelas (2001)	—	no
Ipomopsis aggregata	Irwin and Brody (1999)	yes	no
Linaria vulgaris	This study	no	no
Linaria vulgaris	Stout et al. (2000)	—	no
Mertensia paniculata	Morris (1996)	—	no
Pavonia dasypetala	Roubik (1982)	—	yes
Petrocoptis grandiflora	Guitian et al. (1994)	no	no
Quassia amara	Roubik et al. (1985)	—	no
Salvia iodantha	Arizmendi (2001)	—	yes
Salvia mexicana	Arizmendi (2001)	no	yes
Salvia mexicana	Arizmendi et al. (1996)	no	yes
Symphytum officinale	Goulson et al. (1998)	no	no
Vaccinium ashei	Dedej and Delaplane (2004)	yes	no

We also performed these same meta-analyses on a subset of the studies, including only one entry per plant genus and only one entry per study, to minimize the possibility of biases due to author or species (Appendix S2, see Supplemental Data with online version of this article). In addition, we explored other traits as predictors of the ecological outcomes of nectar robbing for the meta-analysis, including flower color, flower shape, and plant species distribution (temperate vs. tropical/subtropical; Appendix S2).

RESULTS

The effects of nectar robbing on Delphinium nuttallianum—*Observational study*—At the plant level, there was no relationship between percentage of seed set and natural nectar robbing ($r^2 = 0.02$, $N = 28$, $P = 0.46$), but we found a significant negative relationship between total number of seeds per plant and robbing ($r^2 = 0.15$, $N = 28$, $P = 0.04$, Fig. 1). At the flower level, there was no statistically significant effect of robbing on female plant reproduction (MANOVA, Wilks' $\lambda = 0.17$, $F_{2,29} = 2.52$, $P = 0.10$; percentage of seed set, unrobbed, 67.8 ± 4.5%; robbed, 52.7 ± 4.6%; number of seeds per fruit, unrobbed, 25.8 ± 2.8 seeds per fruit; robbed, 21.0 ± 2.4 seeds per fruit [mean ± SE]). However, we had low power to detect a significant difference (power = 0.25 at $\alpha = 0.05$, using MACRO MPOWER in SAS version 8; SAS, 2001).

Experimental manipulation—In the experimental population of *D. nuttallianum*, nectar robbing had a significant effect on female plant reproduction (MANOVA, Wilks' $\lambda = 0.25$, $F_{2,48} = 6.08$, $P = 0.004$). Complete nectar robbing reduced the percentage of seed set by 22% and total seed set by 49% compared to unrobbed plants (percentage of seed set, $F_{1,49} = 5.42$, $P = 0.02$, Fig. 2A; total number of seeds per plant, $F_{1,49} = 12.29$, $P = 0.001$, Fig. 2B).

The effects of nectar robbing on Linaria vulgaris—*Observational study*—At the plant level in all three years of the study, we found no significant relationship between measures of *L. vulgaris* female plant reproduction per stalk and natural levels of nectar robbing (Table 3).

At the flower level, however, when we compared robbed vs. unrobbed flowers, the results were variable among years. We found no difference in measures of female reproduction (percentage of fruit set and number of seeds per fruit) between robbed and unrobbed flowers in 1997 (Hotelling's $T^2_{2,32} = 3.51$, $P > 0.05$) and 1998 (Hotelling's $T^2_{2,64} = 1.47$, $P > 0.05$). However, in 1999, there was a significant difference between robbed and unrobbed flowers in measures of female reproduction (Hotelling's $T^2_{2,36} = 19.86$, $P < 0.01$). This result was driven by a difference in number of seeds per fruit between robbed and unrobbed flowers ($t_{19} = 3.77$, $P = 0.0013$). Surprisingly, robbed flowers produced almost three times more seeds per fruit than unrobbed flowers (robbed flowers, 111.44 ± 13.47 seeds per fruit; unrobbed flowers, 41.79 ± 13.96 seeds per fruit). There was no difference in percentage of fruit set between robbed and unrobbed flowers in 1999 ($t_{19} = 0.11$, $P = 0.91$).

Experimental manipulation—We found a significant difference in female plant reproduction between artificially robbed and unrobbed (collared) flowers (MANOVA, $F_{2,17} = 3.98$, $P = 0.038$), with unrobbed flowers having, on average, more than twice as many seeds per fruit as artificially robbed flowers (ANOVA, $F_{1,18} = 8.3$, $P = 0.01$; unrobbed, 150.25 ± 22.31 seeds; robbed, 63.62 ± 20.18 seeds). There was no significant difference in percentage of fruit set between artificially robbed and unrobbed flowers (ANOVA, $F_{1,18} = 0.11$, $P = 0.74$; artificially robbed, 68.2 ± 10.2%; unrobbed, 74.1 ± 11.8%).

Meta-analysis: the influence of pollen limitation and plant mating system on the effects of nectar robbing on female plant reproduction—Both the presence vs. absence of pollen limitation ($Q_b = 51.23$, df = 1, $P < 0.0001$, $N = 19$) and self-compatibility ($Q_b = 21.5$, df = 1, $P < 0.0001$, $N = 25$) significantly affected the outcome of nectar robbing on plant reproduction. A very large negative effect of robbing was observed for pollen-limited plants ($d = -1.13$, $N = 10$ studies) compared to plants with no evidence of pollen limitation ($d = -0.22$, $N = 9$ studies). The effect of robbing on female reproduction was medium and negative in self-incompatible species ($d = -0.53$, $N = 17$ studies) and weak and negative in self-compatible species ($d = -0.25$, $N = 13$ studies).

DISCUSSION

The effects of nectar robbing on plant reproductive success have received extensive attention (reviewed in Maloof and Inouye, 2000; Irwin et al., 2001). Yet the range of effects has

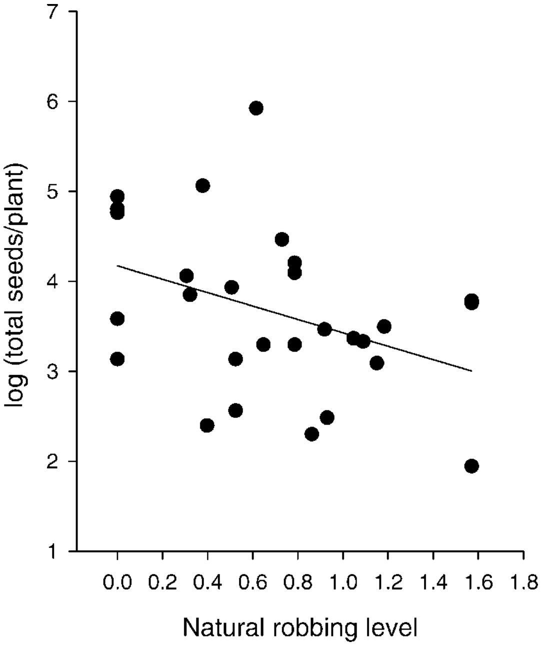

Fig. 1. Relationship between total seeds per plant and natural nectar robbing in *Delphinium nuttallianum*. The relationship [Log(total seeds) = 4.2 − 0.74 × robbing; arcsine square-root transformed] was negative and significant.

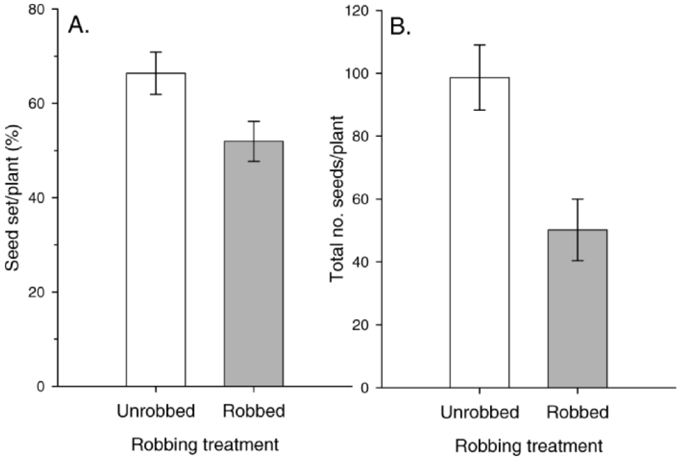

Fig. 2. Effects of experimental nectar robbing on *Delphinium nuttallianum*. (A) Percentage of seed set per plant and (B) total seeds per plant. Both variables were significantly higher in unrobbed plants (0% of available flowers robbed; $N = 24$ plants) than in experimentally robbed plants (100% of available flowers robbed; $N = 27$ plants). Bars indicate mean ± 1 SE.

precluded broad generalizations about the impacts of robbing on female plant reproduction. Here we hypothesized that the degree of pollen limitation and plant mating system (self-compatibility) would predict the effects of nectar robbing on female plant reproduction. Our predictions were partially upheld in the case studies involving montane plants (*D. nuttallianum* and *L. vulgaris*) and fully upheld in the meta-analysis. Natural nectar robbing of *D. nuttallianum*, a pollen-limited perennial, reduced total seed set at the plant level, and experimental nectar robbing reduced percentage of seed set and total seed set at the plant level. Conversely, in *L. vulgaris*, a species that is generally not pollen limited at our study site, natural nectar robbing did not affect most estimates of ramet (1997–1999) or per-flower (1997–1998) reproduction, but experimental nectar robbing reduced seed set per fruit and not percentage of fruit set. When we broadened our results to include other studies in a meta-analysis, we found a stronger negative effect of robbing on plants that were pollen limited for seed set and on plants that were self-incompatible.

Because *D. nuttallianum* is pollen limited, we predicted that high levels of nectar robbing would reduce estimates of female reproductive success. This prediction assumes that pollinators of *D. nuttallianum* detect and avoid nectar-robbed plants and flowers. The behavior of *D. nuttallianum* pollinators in response to nectar robbing in other plant systems partially supports this assumption. *Delphinium nuttallianum* is pollinated both by broad-tailed hummingbirds and by queen bumble bees (Waser and Price, 1990). Previous studies with broad-tailed hummingbirds have shown that these birds can avoid nectar-robbed plants and flowers in the sympatric *Ipomopsis aggregata* (Irwin and Brody, 1998), likely by detecting and avoiding flowers with reduced nectar volume (Irwin, 2000). Conversely, bumble bees around the RMBL do not avoid nectar-robbed plants and flowers of *Corydalis caseana* (Maloof, 2000), and bumble bees do not discriminate between robbed and unrobbed flowers in other plant species (Rust, 1979; Richardson, 2004). If hummingbirds can discriminate between robbed and unrobbed flowers and bumble bees cannot, then the negative effects of robbing observed here may be driven primarily by hummingbird pollinators. Thus, the effects of robbing on plant reproduction may be strongly affected by the relative abundance of hummingbird vs. bumble bee pollinators, which can vary both spatially and temporally (e.g., Pyke, 1982; Inouye et al., 1991). Given the strong effects of nectar robbing on *D. nuttallianum* reproduction observed here, further studies quantifying hummingbird and bumble bee pollinator foraging behavior in response to robbing are warranted.

One caveat about the effects of robbing on *D. nuttallianum* is that we found negative effects of natural nectar robbing on total seed set at the plant level, but we found no relationship between natural robbing and percentage of seed set at the plant level or on measures of female plant reproduction at the flower level. We know that this result is not due to increased rates of fruit abortion because *D. nuttallianum* rarely aborted fruits in our study. Instead, this result may be driven in part by the behavior of robbers. If percentage of seed set remains consistent across robbing levels while total seed set per plant decreases with robbing, then nectar robbers may be selecting plants with fewer total ovaries. Although we did not measure floral traits of *D. nuttallianum*, there may be trade-offs in resource allocation between the production of ovaries vs. floral rewards. For example, plants with low ovary production may have relatively more resources to allocate to characters associated with pollinator attraction, such as higher nectar production, which could attract more nectar robbing. In contrast, we assigned robbing treatments randomly to plants when we experimentally manipulated robbing to *D. nuttallianum*. Thus, robbing was superimposed on random levels of ovule production and floral attractive characters. Studies assessing the manner in which nectar-robbing bees select *D.*

TABLE 3. Relationship between measures of *Linaria vulgaris* female plant reproduction and natural levels of nectar robbing. The relationship was insignificant for all three years.

Year	Wilks' λ	df	*F*	*P*
1997	0.077	3, 15	0.38	0.77
1998	0.017	3, 31	0.17	0.92
1999	0.019	3, 46	1.75	0.83

nuttallianum to forage on would provide additional insight into the mechanisms driving the patterns we observed.

In the primarily bumble bee-pollinated *Linaria vulgaris*, we found that natural nectar robbing had no effect on ramet measures of reproduction in any year of study and had no effect on per-flower reproductive success in 1997 and 1998. These results are consistent with those reported for the effects of nectar robbing on *L. vulgaris* reproduction in southern England (Stout et al., 2000). Stout et al. (2000) reported that bumble bee pollinators of *L. vulgaris* continued to visit plants even with 96% of available flowers robbed. These results also match studies described previously in this paper suggesting that bumble bee pollinators do not discriminate between robbed and unrobbed plants and flowers (also reviewed in Maloof and Inouye, 2000). Pollinators may not discriminate between robbed and unrobbed flowers if robbing has little effect on nectar standing crop or if pollinators cannot identify potentially unrewarding robbed plants and flowers. Distinguishing between these two hypotheses would require manipulating robber holes and nectar availability and measuring the foraging behavior of bumble bee pollinators (as in Irwin, 2000 with hummingbirds). We did, however, find an effect of experimental robbing on *L. vulgaris* reproduction. Experimental nectar robbing reduced the number of seeds produced in each successful fruit but not the probability that a flower would produce a successful fruit. Mechanistically, this result suggests that robbed and unrobbed flowers both received enough pollen to produce similar numbers of seeds; however, the mechanism driving reduced seeds per fruit is not clear, especially because *L. vulgaris* generally are not pollen limited for seed production around the RMBL (R. E. Irwin, unpublished data). Moreover, that we found no consistent effect of natural nectar robbing on plant performance but a reduction in seeds per fruit when we manipulated nectar robbing suggests again that robbers may not be choosing plants at random (see earlier in Discussion for *D. nuttallianum* and Irwin, 2006). In this case, one relevant hypothesis is that nectar robber selection of plants may positively covary with plant resource status. Mechanistic work to assess how robbing affects pollinator visitation, the quantity and quality of pollen received, and seeds produced under different resource environments as well as the factors that impact robber selection of plants may provide some insight.

We found one anomalous result with respect to nectar robbing in *L. vulgaris*. In 1999, naturally robbed flowers produced significantly more seeds per fruit than unrobbed flowers on the same stalk. The mechanisms explaining this result are not completely clear. At the very least, we can rule out one factor. Anatomically, nectar robbers cannot pollinate while they rob flowers of *L. vulgaris*; thus, pollinating while robbing does not explain this result. One factor that may be involved in this unexpected result is that the percentage of flowers robbed per stalk in 1999 was significantly higher than in 1997 and 1998 (Table 3), suggesting that primary (and likely secondary) nectar robbers were dominant floral visitors in 1999. Bumble bees require both nectar and pollen to provision their larvae. If *B. occidentalis* were robbing flowers for nectar and then visiting those same flowers legitimately to collect pollen, then robbed flowers might have received higher quantity and/or quality of pollen loads, although we did not estimate pollen limitation of seed production for *L. vulgaris* in 1999. The same logic may also apply to bumble bees that act as secondary nectar robbers and pollinators in different floral visits (i.e., *B. flavifrons* is a dominant pollinator and secondary robber of *L. vulgaris*). Because we did not observe rates of robber or pollinator visits, we do not know how often *B. occidentalis* and secondary nectar-robbing bees switch between robbing and pollinating behaviors nor the relative abundances of pollinators vs. robbers in the year of study. Nectar robbers, however, are known to switch between secondary robbing and legitimate pollination in this system (Newman and Thomson, 2005), and behavioral switches are common for other bee species (e.g., Rust, 1979; Morris, 1996).

When we incorporated our results from *D. nuttallianum* and *L. vulgaris* into a meta-analysis with other published studies, we found that nectar robbing had the strongest negative effects on species that were pollen limited for female reproduction and that were self-incompatible. The degree of pollen limitation of a plant is driven, at least in part, by the rate of pollinator visitation, as well as pollen availability within the community (Ashman et al., 2004). Moreover, self-incompatible plants require pollinators for successful reproduction. These results suggest that understanding the effects of nectar robbing on female plant reproduction requires not only an understanding of plant mating system but also a multispecies perspective, including pollinators as well as nectar robbers and plants. There is growing appreciation that the ecological and evolutionary outcomes of multispecies interactions are difficult to predict from the outcome of pairwise relationships (e.g., Strauss and Irwin, 2004; Morris et al., 2007). Future studies that incorporate the activity of pollinators and plant life history traits into plant–robber interactions will likely provide strong ecological and evolutionary insights (see Results and online Appendix S2). Finally, pollen limitation and plant mating system are certainly not the only traits that may be strong predictors of the effects of nectar robbing on female plant reproduction. For example, little attention has been paid to the importance of flower longevity; nonetheless, long-lived flowers may be at higher risk to robbing relative to short-lived flowers and may suffer the strongest negative effects, assuming robbing has not selected for resistance or tolerance to robbing. In addition, the sequence of nectar robbing and pollination is likely important for long-lived flowers; if pollination occurs before nectar robbing, robbing may have little effect on plant reproduction. The importance of alternative traits in predicting the effects of robbing on female (and male) plant reproduction warrants further attention.

The work presented here is focused solely on the effects of nectar robbing on female plant reproduction. Only one study, to our knowledge, has examined the effects of robbing on realized male reproduction (seeds sired; Irwin and Brody, 2000), although a number of studies have examined the effects of robbing on estimates of male reproduction (pollen removal, donation, and/or dispersal distance; Wyatt, 1980; Morris, 1996; Irwin and Brody, 1999; Maloof, 2001; Temeles and Pan, 2002; Richardson, 2004). Given that a large number of angiosperms are hermaphroditic (Weiblen et al., 2000), studies are desperately needed that test the effects of nectar robbing, in combination with pollen limitation and plant life history traits, on male plant function. Male reproduction is often more strongly limited by pollinator visits than female reproduction (i.e., Young and Stanton, 1990); thus, we may expect to find stronger effects of pollinator activity on plant–robber interactions through male than female plant reproduction (but see Irwin and Brody, 2000).

In conclusion, we found that nectar robbing can have variable effects on female plant reproduction. This variation can be explained, at least in part, by the mating system and level of pollen limitation of the plant, with self-incompatible and pollen limited plants suffering from strong negative effects of robbing. In combination with a wealth of previous research, this study has highlighted the effects of nectar robbing on plants (Maloof and Inouye, 2000; Irwin et al., 2001). The time is ripe to move from the plant perspective to the perspective of the pollinators in order to understand more fully how robbing affects pollinator-foraging behavior and fitness. Only studies that combine such a dual perspective will provide insight into how nectar robbers affect coevolutionary relationships between plants and pollinators.

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