Ecology, 89(11), 2008, pp. 3093–3104
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MECHANISMS OF TOLERANCE TO FLORAL LARCENY IN TWO WILDFLOWER SPECIES

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Abstract. Tolerance of foliar damage is widely recognized as an effective defense against herbivores and pathogens. However, tolerance of the impacts of antagonists on pollination success is less well understood. Here, we extend the framework of tolerance to foliar damage to understand how plants mitigate the pollination and fitness costs of floral larceny (i.e., the consumption of floral nectar often without pollination). We focused on two mechanisms: high nectar rewards per flower to feed all floral visitors and high flower production to compensate for reproductive losses under reduced pollination and seed set. We compared the efficacy of these mechanisms in two plant species: *Polemonium viscosum* and *Ipomopsis aggregata*. In *Polemonium*, ants acting as larcenists reduce nectar accumulation but do not completely empty flowers. When nectar reserves were augmented, ant consumption increased, negating the efficacy of this putative tolerance mechanism. Similarly, in *Ipomopsis*, nectar addition had little effect on tolerance to larceny by bumble bees, perhaps because residual intact flowers do not have enough nectar to compensate for lost rewards. Flower production in both species mitigated some of the negative impacts of larceny on seed set. In *Polemonium*, flower number was not plastic in response to larceny, but large inflorescences enhanced female fitness only when larcenists were present, suggesting that "surplus" flowers in large inflorescences can function to replace reproductive losses due to larceny. In *Ipomopsis*, high rates of larceny induced flower production, but the fecundity benefits of making more flowers declined inversely to larcenist intensity. Overall, our results suggest (1) that tolerance to floral larceny involves "banking" extra flowers to replace lost reproduction rather than maintaining pollination of ones with larceny, and (2) that the efficacy of flower production as a tolerance mechanism varies inversely to larceny rate.

Key words: compensation; floral larceny; Ipomopsis aggregata; *nectar robbing; plant–animal interactions;* Polemonium viscosum; *pollination; tolerance.*

Introduction

Plant damage by herbivores and pathogens is ubiquitous (Crawley 1983, Morris et al. 2007) and can limit individual plant fitness as well as drive natural selection on plant defensive traits (Fritz and Simms 1992). Plants employ at least two defensive strategies against herbivores and pathogens: resistance (the capacity of plants to reduce the frequency of damage or the fitness of the consumer) and tolerance (the capacity of plants to compensate for damage through regrowth and reproduction; Painter 1951, 1958). Herbivores and pathogens, however, represent only two classes in a diversity of consumers who feed on plants. Many plant species are susceptible to floral larcenists: Nectar robbers and thieves that steal nectar from flowers often without providing pollination service (Inouye 1980). There is growing recognition that the concept of resistance can be applied to other antagonistic interactions, such as floral larceny (Irwin et al. 2004*b*), providing a unifying framework across species interactions. However, little is known about the ecology and evolution of tolerance as an additional mechanism ameliorating the impact of floral larcenists. This lack of information is surprising given that tolerance is a common mechanism for how plant and animal hosts cope with competition and cheating in other mutualisms (Pellmyr and Huth 1994, Wise and Abrahamson 2007). The goal of this study was to extend the existing thematic framework of tolerance to include plant–floral larcenist interactions and to explore how putative mechanisms of tolerance for the loss of pollinator service and for reproductive losses inflicted by larcenists can affect plant–larcenist–pollinator interactions.

Floral larcenists are common visitors to flowering plants, especially those with tubular flowers or nectar spurs (Irwin and Maloof 2002). On average, larcenists

Manuscript received 14 January 2008; revised 4 March 2008; accepted 13 March 2008. Corresponding Editor: D. R. Strong.
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have a detrimental effect on female and male plant reproduction (Irwin et al. 2001), and in some cases, their effects on plant performance are comparable in magnitude and similar in mechanism to those inflicted by other plant consumers (Juenger and Bergelson 1997, Irwin and Brody 2000, Ashman and Penet 2007). Floral larcenists can affect plant reproduction directly, by damaging reproductive organs (Traveset et al. 1998, Galen 1999), and indirectly, by modifying plant interactions with pollinators (Roubik 1982, Irwin and Brody 1998). As with plant–herbivore and plant–pathogen interactions, the effects of floral larceny on plant fitness vary greatly among plant species and populations and even among individual plants within populations (Maloof and Inouye 2000). Such variation raises the question: Are tolerance mechanisms acting at variable degrees to mitigate the effects of larcenists on plants?

We examined tolerance to floral larceny via two nonmutually exclusive traits or mechanisms: nectar and flower production. We took a trait-based approach to understand tolerance, reasoning that a focus on traits and their associated mechanisms may provide generality across the myriad species-specific floral-larceny systems (for the use of trait-based approaches more broadly, see Strauss et al. 2005, McGill et al. 2006, Ackerly and Cornwell 2007). Each trait we examined provides a potential mode of tolerance analogous to a mechanism of plant tolerance to herbivory: (1) high nectar production aligns with high growth (or production) to replace resources lost to foliar consumers, and (2) high flower production aligns with resource reallocation via the deployment of stored reserves to replace lost fitness due to consumption (Strauss and Agrawal 1999, Stowe et al. 2000, Tiffin 2000). Reward or flower production that is either induced in response to larceny impact (compensation) or constitutively high in advance of losses (a bet-hedging strategy) could maintain sufficient residual nectar or flowers for pollinator attraction and plant reproduction despite losses and damage by larcenists.

For plants to tolerate floral larceny by making enough nectar to feed both pollinators and larcenists requires that individual larcenists satiate at relatively low reward levels, that consumption by larcenists fails to keep pace with any enhancement of floral rewards, that pollinators respond to increased rewards and plants are pollinator-limited for reproduction, and that the plant-fitness benefits of increased pollinator visitation outweigh any potential resource costs (e.g., photosynthate, water) arising from the production of surplus nectar. Unfortunately, resource costs of nectar production are largely unknown for most species, and are likely to vary widely within species and among habitats from year to year (e.g., Campbell 1996, Boose 1997, Carroll et al. 2001). If rewards for pollinators are costly to produce (Pyke 1991, but see Ornelas and Ordano 2007), compensation via nectar production should increase the cost of investment in the pollination mutualism; however, if as theory predicts, nectar represents a relatively cheap investment of resources to acquire more expensive ones (Schwartz and Hoeksema 1998), then even elevated investment in floral rewards may be trivial compared to the benefits.

In addition, plants may tolerate floral larceny by making more flowers after damage, or by having constitutively high flower to fruit ratios, allowing losses in damaged or un-pollinated flowers to be mitigated by gains in "surplus" intact flowers. In a similar vein, plants can tolerate pollinating seed predators that lay too many eggs in flowers by abscising those flowers and reallocating resources to other flowers on the plant (Pellmyr and Huth 1994, Bronstein 2001). And plants can tolerate florivore damage by increasing fruit and seed production in later, undamaged flowers (Holtsford 1985). Here, surplus flowers reduce the costs of cheating by providing new opportunities for pollinators to confer fitness benefits. As in plant–herbivore interactions, the degree of compensation via flower production may vary among species depending on plant architecture, growth plasticity, life-history schedules, and the timing of flower-number determination (Strauss and Agrawal 1999, Tiffin 2000).

We compared tolerance via nectar and flower production between two host plants that vary in the causal pathways of larcenist impact on plant fitness: *Polemonium viscosum* (Polemoniaceae, larcenists primarily directly damage reproductive organs) and *Ipomopsis aggregata* (Polemoniaceae, larcenists primarily indirectly affect plants via changes in pollinator behavior). Our comparison allowed us to address the extent to which common traits and mechanisms of tolerance predominated in species impacted through direct vs. indirect causal pathways. It is important to note that potential mechanisms of tolerance for floral larceny in these two systems (and others) likely have evolved in response to other species interactions, such as plant–pollinator interactions, or are under selection related to physiological or life-history traits (Armbruster 1997). Moreover, we realize that tolerance is typically estimated using clones or closely related plants in damaged and undamaged states (Simms and Triplett 1994). However, in this study, we used long-lived, wild-growing plants of unknown genetic relatedness to test whether specific mechanisms mitigated the pollination or fitness costs of floral larceny. In all cases, we assigned plants at random to damage treatments, and in some cases, we also manipulated the putative tolerance traits. Even so, we sacrificed some inference for realism.

In investigating the two putative tolerance mechanisms of reward and flower production, we asked the following questions: (1) Does enhanced nectar production ameliorate the loss of rewards (*Polemonium*) and plant-fitness costs (*Ipomopsis*) under floral larceny? (2) Does flower production mitigate the plant-fitness costs of floral larceny (both species)? These experiments shed light on whether diverse mechanisms of tolerance have

the potential to ameliorate both the direct and indirect effects of floral larceny on plant reproduction.

Methods

Study systems

Polemonium viscosum and *Ipomopsis aggregata* (hereafter referred to as *Polemonium* and *Ipomopsis*) are herbaceous perennials with showy, animal-pollinated flowers. Individuals of both species are obligate outcrossers (Waser 1978, Galen and Kevan 1980). In both species, seed set is often pollen limited, although the strength of pollen limitation varies among populations and years (Irwin 2006, Galen and Geib 2007). *Polemonium* are iteroparous, and individuals flower for 1–2 weeks each summer. They produce ~5–25 flowers (mean = 14; Galen and Butchart 2003) in a ball-like raceme, about half of which are open simultaneously. *Ipomopsis* grows as a vegetative rosette for 2–7 years, flowers once, and then dies. Plants flower for 4–8 weeks, producing few to several hundred flowers, each open for 3–5 days; mean (±SE) floral-display size is 5.0 ± 0.2 flowers (range = 1–31 flowers; R. E. Irwin, *unpublished data*). Flower number is not heritable in either species, but varies with plant size (*Polemonium*; Galen 1996) and maternal environment (*Ipomopsis*; Campbell 1997). In *Ipomopsis*, but not *Polemonium*, inflorescence size has a positive impact on pollination success (Galen 1996, Brody and Mitchell 1997). Nectar production in both species continues throughout a flower's lifetime and correlates with corolla size (Cresswell and Galen 1991, Campbell 1996). The genetic basis of nectar production is unknown in *Polemonium* and negligible in *Ipomopsis* (Campbell 1996). Primary pollinators for both species preferentially visit plants with higher nectar rewards per flower (Cresswell and Galen 1991, Mitchell 1993*a*). In *Polemonium*, nectar is produced at a rate of 0.54 μL (38% sucrose equivalents by mass) per flower per day (Galen and Kevan 1980). In *Ipomopsis*, nectar production is relatively constant during the day with a reduced rate at night, irrespective of whether nectar is removed; average nectar production is ~4 μL per flower per day in 1–2 day old flowers (Pleasants 1983). All *Ipomopsis* used were single stalked; in the few cases of *Polemonium* producing multiple inflorescences, inflorescence number was matched between treatments. All experiments were conducted within seasons (required for *Ipomopsis* because it is monocarpic, although some experiments were repeated over multiple years on new plants each year).

We studied a population of *Polemonium* on an alpine tundra slope at 3650–3700 m on Pennsylvania Mountain, Colorado (Park County, Colorado, USA). Although *Polemonium* exhibit a floral scent polymorphism (Galen and Kevan 1980), sweet-flowered plants predominate at this site; thus, all experiments were confined to the sweet morph. At this location, *Polemonium* are mainly pollinated by nectar-collecting *Bombus kirbyellus* queens (Galen 1996). *Formica neorufibarbis gelida* ants consume nectar from *Polemonium* flowers without pollinating, causing flower damage, including pistil and occasionally anther loss. The total number of flowers damaged per plant per day increases with the number of ants observed ($r^2 = 0.42$, $F_{1,20} = 14.56$, $P < 0.001$), but the shallow slope for this relationship (0.3 ± 0.1 damaged flowers per visit) suggests that several ant visits are necessary to dislodge the style (C. Galen, J. J. Ranenold, and A. McKinley, *unpublished data*). Thus, damage to pistils does not occur in all ant visits to flowers, but increases in likelihood with successive ant visitation per flower (Galen and Butchart 2003). Plants protected from ants have higher seed set than unprotected neighbors (Galen 1999). Ant visitation may also reduce male fitness because exposure of anthers to ants decreases pollen germination (Galen and Butchart 2003). Indirect effects of ants on bumble bee pollination of *Polemonium* are negligible (Galen and Geib 2007).

We studied *Ipomopsis* around the Rocky Mountain Biological Laboratory (RMBL; Gunnison County, Colorado, USA) where Broad-tailed (*Selasphorous platycercus*) and Rufous Hummingbirds (*S. rufus*) are the primary pollinators, and *Bombus occidentalis* is a floral larcenist. During foraging, the bee chews a hole through the corolla and inserts her proboscis into it, removing available nectar in a single visit. Bees steal nectar from 0% to 100% of available flowers per plant, varying over the flowering season. At peak flowering, larcenists empty about two-thirds of a plant's flowers on average (Irwin and Maloof 2002). *Bombus occidentalis* do not pollinate flowers while stealing nectar, and unlike *F. n. gelida*, they do not damage reproductive or nectar-producing organs (Irwin and Brody 1998). Thus, direct effects of these larcenists on plants via damage to floral tissues are likely negligible. High levels of larceny, however, make plants less attractive to hummingbird pollinators, indirectly reducing seeds sired and produced by 50% (Irwin and Brody 2000). Hummingbird pollinators use nectar as a proximate cue to avoid non-rewarding flowers with floral larceny, irrespective of spatial cues or other simple visual cues, such as the hole in the flower (Irwin 2000).

In drawing together this "tale of two species," we struggled with an admittedly incomplete data set where some experiments and nearly all field methods (described in the next section) were species specific. Partly, this reflects differences in past research on the two systems. For example, the impact of larcenists on nectar rewards is already known for *Ipomopsis* (Irwin and Brody 1998), but not *Polemonium*. Additionally, designing experiments that simultaneously test whether nectar production (1) is outweighed by larcenist consumption and (2) mitigates the impact of larcenists on pollinator behavior is not possible since the first objective requires pollinator exclusion and the second pollinator visitation. Other differences in technique and methodology simply reflect variation in best practices between species. For example, for *Polemonium*, nectar is too viscous for

accurate measurement via microcapillary extraction and refractometry; yet these techniques work for *Ipomopsis* (Pleasants 1983). Despite these caveats, this synthesis offers a more general understanding of tolerance to floral larceny than might be gleaned from examining either species alone. We used the approach that identifying and understanding common traits or mechanisms can facilitate the generalization of results (Liebold and Tessier 1998, Werner 1998).

Does enhanced nectar production ameliorate the loss of rewards and plant fitness due to floral larceny?

Can enhanced nectar in Polemonium *flowers maintain rewards for pollinators in the face of floral larceny?*—In July 2006, we enriched nectar rewards in *Polemonium* flowers (to simulate high nectar production) and monitored the amount of nectar remaining after plants were visited or bypassed by naturally foraging ants in the field. Control inflorescences with unmanipulated rewards were sampled simultaneously, to determine whether ants completely eliminate nectar rewards for pollinators under natural conditions. Flying insects were excluded from all inflorescences using transparent plastic cones so that we could examine the impact of ants on reward levels independent of other flower visitors. Cones were at least 2.5 cm above the ground, and we ensured that the sides of the cones were away from flowers to reduce possible temperature effects. Inflorescences were collected into water picks one day before the experiment, trimmed to six flowers each to standardize floral display, and assigned to control and nectar-enrichment at random ($n = 15$ inflorescences per treatment). One control inflorescence wilted, reducing the total sample size to 29. We supplemented nectar by adding 1 μL of 30% sucrose solution to three marked (with acrylic paint on the calyx) flowers per inflorescence using a Pipetman precision microliter pipette (Rainin Instrument Company, Oakland, California, USA). The resulting sugar content doubled average sugar rewards per flower (Cresswell and Galen 1991). We probed three marked flowers on each control inflorescence with an empty pipette to control for handling. We randomly assigned one control and one nectar-enriched inflorescence to different sides of 15 *F. n. gelida* nests where ants had visited bouquets of *Polemonium* two days earlier. We placed inflorescences next to nests between 08:00–10:00 hours (Mountain Daylight Time, MDT) and counted the number of ants foraging on the inflorescences at 25-min intervals over a 6-h period (until 14:00–16:00 hours).

Before and after exposure to ants, we extracted all of the available nectar from marked flowers on each inflorescence. Nectar sampling required flower removal, so for pre-treatment measures, we removed nectar from only one marked flower per inflorescence. For post-treatment measures, we removed nectar from the two remaining marked flowers, and total sugar content was divided by two to determine rewards on a per flower basis. We rinsed nectar out of the corolla with water (Cresswell and Galen 1991), froze samples, and measured total sugar in sucrose equivalents by photocolorimetry (McKenna and Thomson 1988).

Respectively, for plants with enriched and control rewards, ants visited eight of 15 and five of 14 total inflorescences. We used a repeated-measures analysis of variance (rm-ANOVA, Proc GLM, SAS, version 6.12; SAS Institute 1995) to test whether sugar enrichment could maintain rewards for pollinators despite ant consumption. The rm-ANOVA included treatment (enriched or control rewards), ant visitation (inflorescence visited or bypassed by ants), and timing (pre- or post-foraging trials) as fixed effects. A significant interaction between treatment and ant visitation would suggest that ants alter the degree to which nectar enrichment maintains rewards for pollination service.

Do enhanced rewards mitigate the impact of larcenists on pollination and female fitness in Ipomopsis*?*—In 2003 and 2005, we tested whether nectar addition could alleviate the negative effects of floral larceny on female reproduction of *Ipomopsis*. We randomly assigned single-stalked, flowering *Ipomopsis* to one of four factorial treatments applied at the whole-plant level: nectar addition (nectar addition vs. control) crossed by floral larceny (high vs. none) (n per treatment = 15 plants in 2003 and 25 plants in 2005). We performed treatments four days per week (approximately every other day) throughout blooming.

For plants in the nectar-addition treatment, we added 2 μL of 25% sucrose solution to all open flowers in the early morning to simulate constitutively higher levels of nectar availability. The addition of 2 μL of 25% sucrose solution is in the range of natural nectar production (Pleasants 1983). We added nectar to flowers in 2003 using an Eppendorf Repeater Plus pipettor (Brinkmann Instruments, Westbury, New York, USA) with a narrow tip (0.1-mL Combitip Plus), and in 2005 using a glass syringe with a blunt tip and repeater dispenser (PB600-1, Hamilton, Reno, Nevada, USA). The pipette tip or syringe needle was cleaned with alcohol between flowers to avoid transferring pollen. In the control treatment, we handled flowers and probed them with the empty pipettor or syringe.

For plants in the high floral-larceny treatment, we artificially damaged and stole nectar from ≥80% of open flowers per plant midday, which represents a high, but commonly observed level of floral larceny in some years (Irwin and Maloof 2002). On these flowers, we cut a hole, ~1 mm in diameter, in the side of the corolla using fine-tipped dissecting scissors and removed all available nectar using a microcapillary tube inserted through the hole. This method causes similar floral damage and nectar loss as natural visitation by *B. occidentalis* (Irwin and Brody 1998). On plants that did not receive floral larceny, we handled, but did not puncture, flowers or remove nectar. We did not protect flowers to deter *B. occidentalis* on these plants because natural visitation by *B. occidentalis* was low in the years of study. At the end

of the flowering season, we collected all fruits and counted total seed set per plant. We calculated relative fitness in each year based on seed set per plant.

To test whether nectar addition mitigated the negative effects of floral larceny on relative female fitness, we used a three-way ANOVA with year, nectar-addition treatment, floral-larceny treatment, and their interactions as factors. If nectar addition mitigates the negative effects of larceny on female reproduction, we would find a significant interaction between nectar-addition and floral-larceny treatments. A significant three-way interaction would suggest that the ability of nectar addition to mitigate floral larceny was not consistent between years. Sample sizes in both years were reduced due to loss of plants (two in 2003 and one in 2005; high floral larceny, no nectar added) to deer or meloid beetles.

In addition, in 2003, we tested two assumptions for mitigation of larcenist costs by nectar rewards. First, we tested the assumption that nectar addition increases pollinator visitation by measuring stigma pollen loads on plants in the experiment as a proxy for pollinator visitation (Engel and Irwin 2003). Twice during peak flowering (9 and 25 July), we collected 20% (up to six) of available stigmas from plants with no floral larceny in nectar-addition and control treatments once the corollas had fallen off. Conspecific pollen loads ($\geq$97% of pollen per stigma) were stained in basic fuchsin (Kearns and Inouye 1993) and counted under a compound microscope. We calculated mean pollen receipt per stigma per plant, averaged over the two dates, to test the hypothesis that nectar addition increases pollen receipt (square-root transformed to improve normality) relative to controls using a one-tailed t test.

Second, we used a hand-pollination treatment to test the assumption that pollen receipt limited seed set. Because *B. occidentalis* primarily have indirect effects on *Ipomopsis* mediated through changes in pollinator behavior, if plants are not pollen-limited for seed set, changes in pollinator visitation and pollen deposition are unlikely to have effects on plant reproduction. We randomly chose 15 plants near individuals in the experiment and hand-pollinated all flowers with receptive stigmas two times per week throughout flowering. Pollen from haphazardly chosen (nonexperimental) donors was added by rubbing dehiscing anthers on receptive stigmas. We collected fruits and counted all of the seeds per plant. We compared total seed set per plant between pollen-supplemented and control plants (from the experiment above) using a one-tailed t test to test the prediction that pollen supplementation increases female reproduction.

Does flower production mitigate the plant-fitness costs of floral larceny?

Polemonium.—We assessed the impact of flower number on seed set in ant-damaged and undamaged (control) plants in June–July 2005. To avoid confounding possible resistance mechanisms with tolerance, we matched flower phenotypes that restrict access to foraging ants (corolla tube length and corolla flare; Galen and Cuba 2001) between damaged and control plants. We searched at 42 randomly selected points for the closest sweet-flowered plant with one or more ant-damaged flowers. Corolla tube length and flare were measured with digital calipers for two mature female-phase flowers per plant. We then randomly chose a neighboring *Polemonium* with no ants or ant damage as a paired control, provided that the dimensions of its mature flowers were within ± 1 SD unit of the ant-damaged individual and that plants had equal numbers of inflorescences. Floral traits were highly correlated between paired damaged and control plants (for corolla tube length and flare, $r = 0.83$, $r = 0.76$, $n = 42$ plants, $P < 0.0001$).

Ants were excluded from flowers of controls by fitting tangle-foot coated plastic tubing cut from drinking straws around each stem (Galen 1983). We counted open flowers and buds on damaged and control plants to score total flower production. We surveyed damaged plants every 2–3 days until wilting for cumulative number of flowers damaged. For all plants, pollen receipt per flower was scored by removing the style of a wilted flower, storing it in 3:1 (ethanol : acetic acid) fixative, and staining it with aniline blue dye. Self-incompatible pollen fails to germinate and is washed from the stigma during staining, leaving germinated outcross grains for visualization under fluorescence microscopy (Galen and Cuba 2001). After all flowers wilted, we enclosed inflorescences in cages made of plastic mesh to exclude deer and elk. In late August, we collected fruits and counted seeds. Despite fencing, we lost some plants to grazers, reducing sample sizes to 33 damaged plants and 25 controls.

We used path analysis (Proc Calis in SAS, ML option; SAS Institute 1995) to assess the role of flower production in compensating for ant damage. We first developed separate a priori path models for ant-damaged plants and matched controls that included direct effects of total flower number, pollen receipt per flower (a proxy for pollinator visitation; Galen and Stanton 1989), and date of peak flowering on relative fitness (based on seed set per plant), and specified a covariance between flowering date and total flowers (C. Galen, *unpublished data*). To account for phenological variation in pollinator activity, both models included the direct effect of peak flowering date on pollen receipt. For ant-damaged plants, we also included two additional direct effects: the impact of total flowers on the number of flowers damaged and the impact of the number of flowers damaged on seed set. To assess whether the relationship of flower number to seed set differed between damaged plants and controls, we used a nested-models procedure (Mitchell 1993*b*). This procedure tested the significance of the reduction in goodness-of-fit of the control path model when the path coefficient for the direct effect of flower number on seed

set was constrained to its value in the analysis of ant-damaged plants.

Ipomopsis.—We tested whether *Ipomopsis* compensated for floral larceny by producing more flowers using 66 single-stalked plants randomly assigned to high ($\geq$80% of available flowers damaged) and low floral larceny ($\leq$10% of available flowers damaged). We conducted floral larceny treatments four days per week throughout the blooming season, as described in the previous section. We handled similar numbers of flowers on plants in the high and low treatments to control for any effects of flower handling. We counted the number of open flowers (four days per week) and determined total flower number at the end of the season to assess whether floral larceny affected floral-display size or the total number of flowers produced per plant, respectively. We collected and counted all seeds from each plant.

To test how floral larceny affected weekly average floral-display size, we used rm-ANOVA with floral-larceny treatment as a fixed effect, week as the repeated factor, and floral-display size (square-root transformed) as the response variable. We tested how larceny affected the number of days that plants remained in bloom and the total number of flowers produced (square-root transformed) using a MANOVA with floral-larceny treatment as a fixed effect. A significant MANOVA was followed by univariate ANOVAs for each response variable (Scheiner 1993). To assess whether floral larceny enhanced the fitness benefit of flower production, we used an ANCOVA with floral-larceny treatment, total flower production, and their interaction as factors and total seed set (square-root transformed) as the response variable. A significant interaction between larceny treatment and flower production would suggest that floral larceny altered the fitness returns of flower production.

Results

Does enhanced nectar production ameliorate the loss of rewards and plant fitness due to floral larceny?

Can enhanced nectar in Polemonium *flowers maintain rewards for pollinators in the face of floral larceny?*—Enrichment with artificial nectar yielded a fourfold increase in sucrose per flower compared to unmanipulated controls at the onset of the experiment (treatment effect, $F_{1,25} = 32.84$, $P < 0.0001$; Fig. 1; Appendix A). In the absence of ants, nectar accumulated over the course of the day in flowers of both treatment groups, with enriched flowers maintaining the initial fourfold sucrose advantage (Fig. 1). However, after ant visitation, the difference in sucrose content between control and enriched flowers was much smaller and not significant ($P > 0.18$; time by ant interaction, $F_{1,25} = 5.29$, $P < 0.03$; Fig. 1; Appendix A). This pattern suggests that enhanced nectar production would largely feed ants, leaving little additional nectar accumulated for legitimate pollinators. The impact of ants on nectar accumulation tended to increase with reward level: In control flowers ants had a relatively small impact on

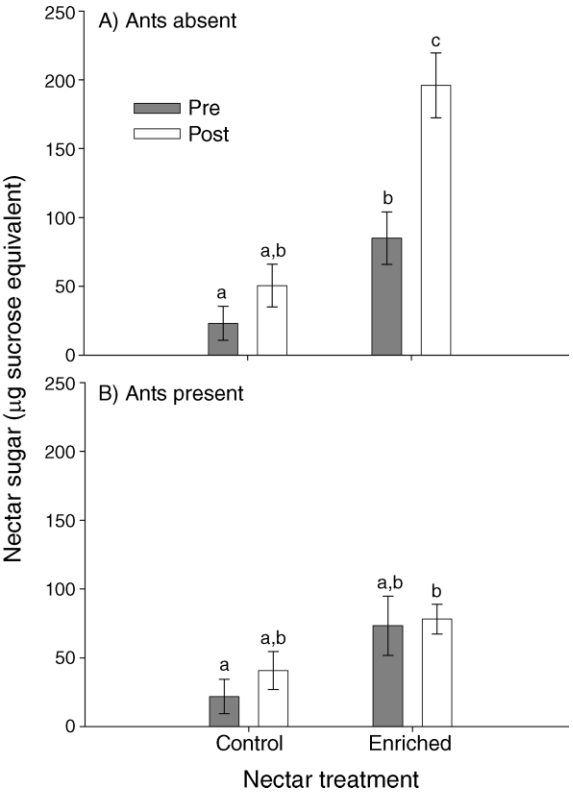

FIG. 1. Impact of floral larceny by ants on *Polemonium* nectar rewards in inflorescences with control or enriched nectar. Bars (±SE) show mean nectar standing crops in flowers with ants (A) absent and (B) present before (pre) and after (post) potential ant visitation. Letters above bars indicate groups that are significantly different at $P < 0.05$.

standing crop (ant by time by treatment interaction, $F_{1,25} = 3.84$, $P < 0.06$). Results suggest that nectar consumption by ants increases and largely keeps pace with energetic rewards, negating potential benefits of enhanced production.

Do enhanced rewards mitigate the impact of larcenists on pollination and female fitness in Ipomopsis*?*—Although we predicted that nectar addition would mitigate the negative effects of experimental floral larceny on female reproduction in *Ipomopsis*, we found no support for this hypothesis. Across both years, nectar addition had no effect on relative seed set ($F_{1,149} = 1.32$, $P = 0.25$), nor did it mitigate the negative effects of floral larceny on relative seed set ($F_{1,149} = 0.01$, $P = 0.92$; Fig. 2). High floral larceny significantly reduced relative seed set ($F_{1,149} = 5.02$, $P = 0.03$), but the magnitude of the larceny effect varied between years ($F_{1,149} = 5.42$, $P = 0.02$). Floral larceny had no effect on relative seed set in 2003 ($F_{1,54} = 0.003$, $P = 0.95$), but reduced relative seed set by 37% in 2005 ($F_{1,95} = 13.77$, $P = 0.0003$; Fig. 2). Main and interaction effects of year on fitness were nonsignificant ($P > 0.05$ for both).

To understand why nectar addition did not alter the relationship between floral larceny and seed set, we

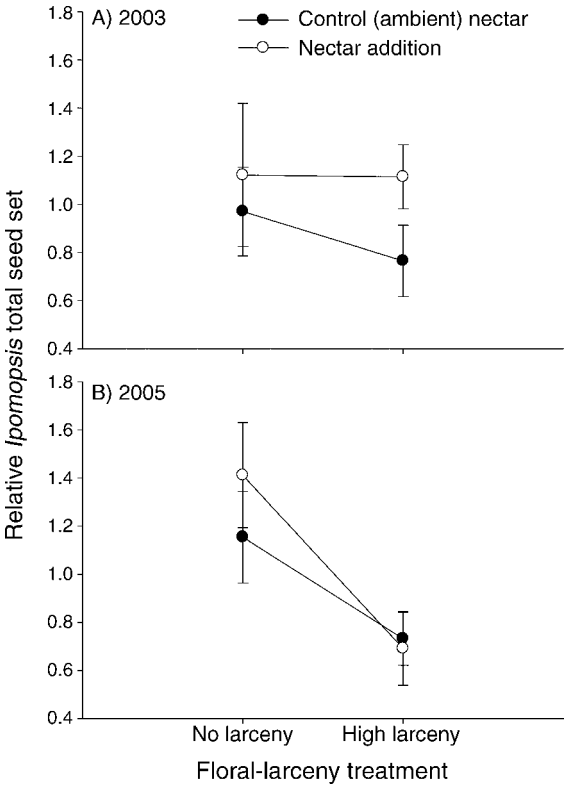

FIG. 2. Mean (±SE) relative seed set of *Ipomopsis* with no floral larceny and high experimental floral larceny as a function of nectar addition in (A) 2003 and (B) 2005. Solid symbols are plants with control (ambient) nectar; open symbols are plants in the nectar-addition treatment. Nectar addition in *Ipomopsis* did not mitigate the negative effects of floral larceny in either year.

tested two assumptions in 2003. Analysis of pollen receipt provided support for the assumption that hummingbird pollinators preferentially visited plants with increased nectar rewards. Plants in the nectar-addition treatment received 25% more pollen per flower than plants in the control treatment (mean ± SE, nectar addition = 143.89 ± 13.64 pollen grains per stigma; control = 107.14 ± 14.73 pollen grains per stigma; $t_{24} = 1.83$, $P = 0.04$). However, because pollen was not limiting to seed set in 2003 ($t_{26} = 0.38$, $P = 0.35$), these changes in hummingbird pollinator behavior and pollen deposition did not translate into differences in seed set.

Does flower production mitigate the plant-fitness costs of floral larceny?

Polemonium.—The path diagram for relative fitness of ant-damaged plants exhibited a fit to the data of 0.89 ($\chi^2 = 4.60$, df = 3, $P > 0.20$). The path analysis suggests that ant damage had a strong negative impact on seed set ($\rho = -0.54 \pm 0.18$, $t = 2.9159$, $P < 0.01$; Fig. 3A), and attractiveness to pollinators failed to compensate for ant damage. The direct effect of pollen receipt on relative fitness of ant-damaged plants was weak ($\rho = 0.16 \pm 0.19$, $P > 0.05$), perhaps because pistil loss eliminated the benefit of pollinator attractiveness for damaged flowers. In contrast, plants with larger inflorescences maintained higher seed set despite losses to ants (path from flowers per plant to seeds per plant, $\rho = 0.75 \pm 0.20$, $t = 3.74$, $P < 0.001$; Fig. 3A). The capacity of surplus flowers to compensate for ant damage reflected the relatively large magnitude of the direct positive effect of inflorescence size on seed set compared to the weak negative effect of inflorescence size on damage rate. Because ants responded only weakly to increased inflorescence size (path from flowers per plant to ant-damaged flowers, $\rho = 0.03$; Fig. 3A), the indirect negative effect of flower number on seed set via ant damage was weak (path from flowers per plant to ant-damaged flowers × path from ant-damaged flowers to seeds per plant = −0.015).

The best-fit path model for fitness of plants protected from ants exhibited a goodness of fit of 0.95 ($\chi^2 = 1.39$, df = 1, $P > 0.23$). The path model for controls (Fig. 3B) departed in three main ways from the path model for ant-damaged plants. First, plants flowering later had significantly higher relative fitness in controls ($\rho = 0.54$, $t = 1.9677$, $P < 0.05$), but not in ant-damaged plants. Second, when ants were excluded, *Polemonium* that received more pollen had higher fitness ($\rho = 0.61 \pm 0.20$, $t = 3.11$, $P < 0.001$; Fig. 3B). Third, inflorescence size had little impact on fitness in the absence of ants ($\rho = -0.19 \pm 0.27$, ns; Fig. 3B). Results suggest that larger floral-display size acts as a tolerance mechanism, but confers no advantage in the absence of floral larceny. To test this hypothesis, we conducted a nested comparison of alternative models with the path from flowers per plant to seeds per plant constrained to 0.75, as derived from the analysis of ant-damaged plants (Hayduk 1987, Mitchell 1993*b*). The test confirmed that forcing the direct effect of flower number on fitness into the path model for control plants significantly reduced the model's fit (constrained model, $\chi^2 = 9.54$, df = 2, $P = 0.009$; nested comparison of models, $\chi^2 = 8.15$, df = 1, $P < 0.005$).

Ipomopsis.—High experimental floral larceny altered some aspects of flower production (MANOVA: $\lambda = 0.10$, $F_{2,61} = 3.07$, $P = 0.05$). Plants with high larceny produced 33% more total flowers than plants with low larceny (mean ± SE, respectively, 122.34 ± 14.50 flowers and 82.63 ± 8.86 flowers; $F_{1,62} = 4.84$, $P = 0.03$). Floral-display size varied significantly among weeks ($F_{11,682} = 31.35$, $P < 0.0001$), with two peaks during the blooming season (Appendix B). During the second peak, plants with high floral larceny tended to produce more flowers than plants with low larceny (Appendix B), although this difference was not statistically significant (floral-larceny treatment × week interaction: $F_{11,682} = 1.08$, $P = 0.38$). We found no effect of floral larceny on duration of flowering (mean ± SE, high vs. low larceny, 60.00 ± 2.34 days vs. 59.91 ± 2.33 days; $F_{1,62} < 0.01$, $P = 0.98$).

We hypothesized that floral larceny would alter not only the number of flowers produced, but also the relationship between flower production and seed set. In

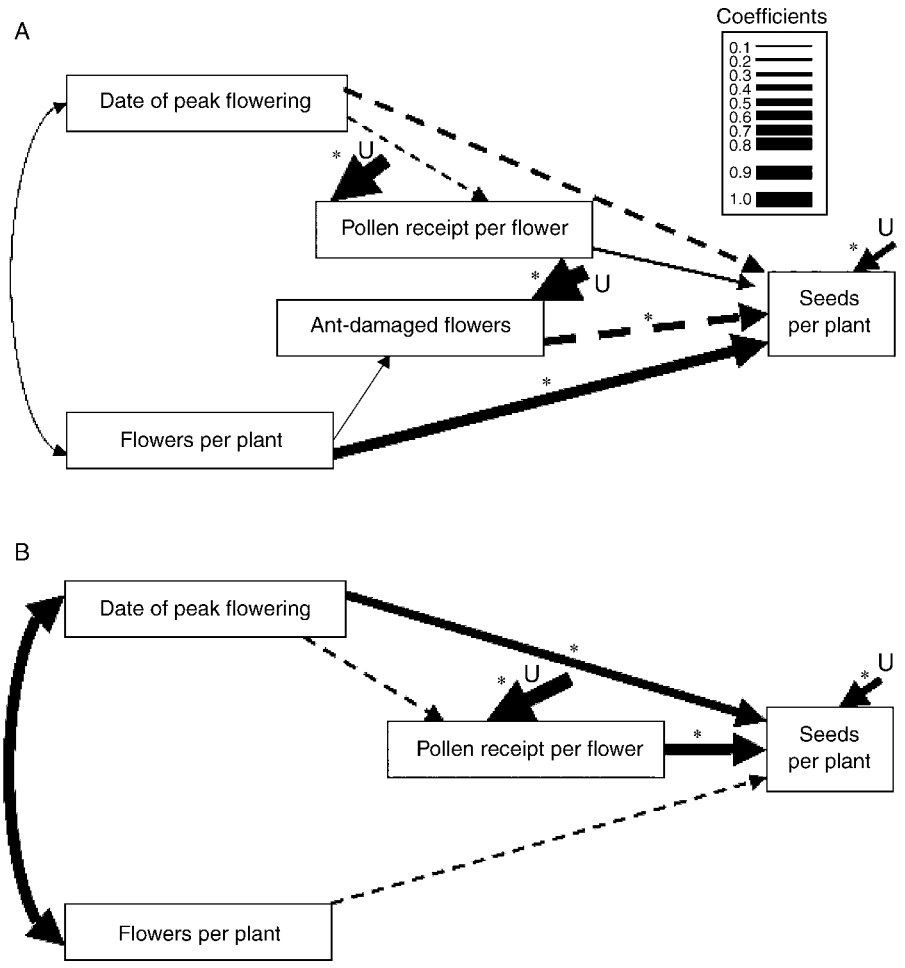

FIG. 3. Best-fit path models for relative fitness in (A) ant-damaged and (B) ant-excluded *Polemonium*. Solid arrows denote positive effects, dashed arrows show negative effects, and double-headed arrows show correlations. The width of each arrow is proportional to the magnitude of the standardized path coefficient (or correlation). Asterisks indicate effects significant at $P < 0.05$, and U indicates unexplained variance.

accord with this idea, the impact of flower production on seed set depended on larceny treatment ($F_{1,60} = 4.65$, $P = 0.04$). However, the trend was opposite to our prediction. Flower production was positively associated with seed set in both treatment groups, but the fitness benefit conferred by flower number was stronger when only 10% of flowers were damaged than when 80% were damaged (Fig. 4).

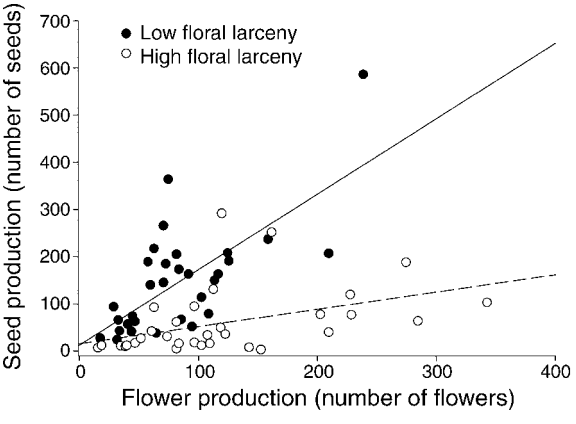

FIG. 4. Impact of *Ipomopsis* flower production on relative seed set in plants with experimental low (10% of flowers) and high (80% of flowers) floral larceny (solid and dashed lines, respectively). Increased flower production produced a higher fitness benefit for *Ipomopsis* subjected to low floral larceny.

DISCUSSION

Polemonium viscosum and *Ipomopsis aggregata* exhibit varying capacities for tolerance to floral larceny. Nectar addition did not enhance tolerance to floral larceny in either species. In *Polemonium*, the addition of nectar increased ant visitation, which largely kept pace with energetic rewards and negated any potential benefits of additional nectar on pollination service. In *Ipomopsis*, most flowers are visited by cheating bumble bees in some years (Irwin and Maloof 2002), and experiments simulating these high larceny levels suggest that

enhancement of nectar rewards would have little impact on fitness, even for plants with constitutively high levels of reward production. Both species compensated for floral larceny via prolific flower production, but the benefits were more pronounced in *Polemonium* than in *Ipomopsis*. These interspecific differences suggest that the benefits of tolerance mechanisms should depend on the abundance of floral larcenists.

Nectar and compensation for floral larceny

For reward satiation to ameliorate the pollination and fitness costs of floral larceny, losses to larcenists must be small relative to new nectar produced. A major constraint on this mode of tolerance is that rewards accumulate in individual flowers, but highly mobile pollinators may perceive reward value on a whole-plant (or patch) basis (Charnov 1976). For *Polemonium*, nectar addition proved ineffective in conferring *additional* tolerance because ant foraging kept pace with reward addition. However, interpretation of this result for plant fitness relies on two points. First, ants typically do not remove all of the nectar from *Polemonium* flowers (Fig. 1; the reasons why ants do not fully deplete flowers of nectar are unknown). Second, a previous study found that bumble bee pollinators do not discriminate among *Polemonium* flowers as a function of floral larceny (Galen and Geib 2007). Thus, results of prior research support the idea that residual nectar rewards left by ants suffice to sustain pollinator behavior: Pollination by *B. kirbyellus* does not decline under visitation by *F. n. gelidea* (Galen and Geib 2007). In *Polemonium* then, any effect of larcenists on seed set depends on collateral damage to pistils during nectar foraging. While intuitively appealing, we cannot conclude from the current study that inherent nectar production rate is high enough to account for the absence of indirect effects of ants as floral larcenists on bumble bee pollination. To test this idea, additional comparisons of bumble bee responses to varied nectar rewards in plants visited vs. unvisited by ants are needed.

In *Ipomopsis*, experimentally enriched nectar in one year increased pollen delivery to flowers, providing support for the assumption that pollinator service can be leveraged via enhanced nectar rewards. Similarly, Mitchell (1993*a*) found that *Ipomopsis* with higher nectar rewards received more hummingbird visits per flower, a pattern also found in other species (e.g., Carlson 2007). However, experiments reported in this study suggest reward levels may not mitigate the effects of floral larceny on female reproduction. The impact of floral larceny on seed set varied between years; larceny did not reduce seed set in 2003, but did in 2005. In 2003, we likely found no effect of floral larceny on seed set because plants were not pollen limited. In 2005, it is unknown if plants were pollen limited, but enhanced rewards did little to promote pollinator visitation or seed set. One explanation for why nectar rewards did not mitigate the negative effect of floral larceny in 2005 is that, with high experimental larceny, pollinators may have perceived these plants as patches of poor value, despite enriched nectar rewards in the low percentage of intact flowers.

Two caveats should be considered when interpreting our results. First, in *Ipomopsis*, we only measured the effects of nectar addition on tolerance to floral larceny through female reproduction. The effects of nectar on tolerance to floral larceny through male reproduction are unknown. However, because male reproduction is often more sensitive to changes in pollinator visitation than female reproduction (Young and Stanton 1990), plants may not tolerate damage equally through different genders (Lehtilä and Strauss 1999, but see Gronemeyer et al. 1997). A second caveat stems from experimentally adding nectar to flowers. Adding nectar to flowers masks the physiological costs of nectar production, an intrinsic factor affecting the potential cost of compensation. Water movement into nectar requires active transport through the phloem, and nectar sugar synthesis necessitates active starch loading (De la Berrera and Nobel 2004). Such intrinsic costs may constrain seed set in carbon or water-limited species (e.g., Ordano and Ornelas 2005), although for other species, there are no detectable plant-fitness costs of nectar production (Golubov et al. 2004, Leiss et al. 2004, Ornelas and Ordano 2007). The fitness costs of nectar production are unknown for *Polemonium* and *Ipomopsis*, both being species that produce relatively small amounts of nectar (typically <4 μL per flower per day). The topic of nectar production costs warrants further attention, given the fundamental importance of nectar in mediating consumer-based interaction webs (Irwin et al. 2004*a*).

Flower production and compensation for floral larceny

Polemonium and *Ipomopsis* differ in several life-history attributes that mediate possible modes of reallocation via flower production in response to floral larceny. In *Polemonium*, like other iteroparous alpine plants, flower bud meristems are produced in the summer before anthesis, and individual flowering times are brief, reducing risk of frost damage to flowers and fruits at the expense of developmental plasticity in flower number (Bechtold et al. 2002). Tolerance to larceny in *Polemonium* requires a "bank" of extra flowers that replace reproductive losses due to collateral damage by ants. In contrast, *Ipomopsis* flower once after many years of growth, producing large floral displays that persist over several weeks (Campbell 1997). This longer flowering period within a season may allow for plastic increases in flower number to compensate for poor pollination of earlier flowers. Plants with high floral larceny likely reallocate resources from seed to flower production, although the reallocation may not allow plants to fully compensate for larceny if, for example, resources or pollination limit seed production in later flowers. The two species also differ in the kind of

fitness costs inflicted by larcenists. In *Polemonium*, where ants leave residual nectar in flowers, indirect effects of ants on pollinator service are negligible, yet ants occasionally cause direct damage to pistils and pollen (Galen 1983, Galen and Butchart 2003). Conversely, perhaps because bumble bees remove most of the nectar from *Ipomopsis* flowers, floral larceny by bumble bees discourages hummingbird pollination (Irwin and Brody 1998). Despite these developmental and ecological differences, surplus flowers provide a buffer for larcenist-inflicted fitness costs in both species.

The magnitude of the benefit provided by prolific flowering likely differs between species. In *Polemonium*, ant visitation generates a benefit of large floral display that is otherwise unobserved. Conversely, in *Ipomopsis*, prolific flowering compensates for lost pollinator service mainly at low larceny intensity and less effectively under high larceny. Interestingly, a simple analysis suggests that escalating larceny pressure in *Polemonium* would also reduce the compensatory advantage of additional flowers. Consider the scenario of ant damage to 80% of *Polemonium* flowers per plant. Under this condition, the slope of the relationship between expected seed set, calculated as 20% of actual seed set, and the number of flowers per plant drops sharply indicating dramatically reduced fitness accrual with flower number (Fig. 5). This exercise suggests that the functional response of larcenists to flower availability can determine the extent to which prolific flowering contributes to tolerance. As with herbivory, allocation to new organs provides tolerance only if antagonists consume constant or fixed amounts rather than percentages of plant biomass, allowing new growth (or flowers) to escape (Coley et al. 1985). In other words, floral larceny impact depends on the balance between attack and compensation rates (Tiffin 2000).

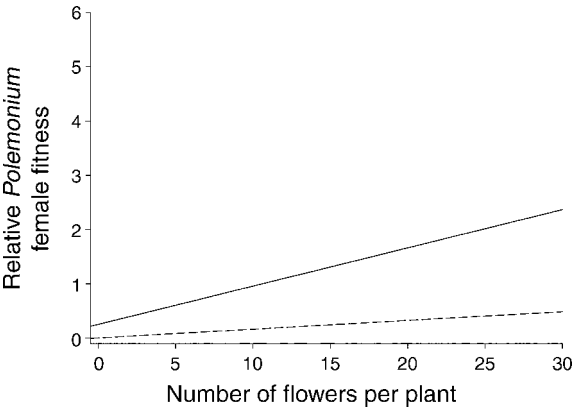

FIG. 5. Best-fit regression lines for fitness accrual with flower number in *Polemonium* under natural levels of ant damage (solid line, $R^2 = 0.12$, $F_{1,31} = 4.20$, $P < 0.05$), and a hypothetical damage rate of 80% (dashed line, seed set reduced to 20% of actual seed set per plant).

Synthesis and new directions

Our experiments focused on two mechanisms of tolerance, nectar production and flower production, in part because these invite comparisons with parallel mechanisms underlying tolerance to herbivory. However, other traits and interactions may mitigate floral-larceny impacts; we provide two examples. First, Newman and Thomson (2005) propose that enhanced pollination efficiency may mitigate the fitness costs of floral larceny in *Linaria vulgaris*. For *Polemonium,* our results suggest that this mechanism is unlikely to promote tolerance: Pollen receipt enhanced fitness only when ants were absent (Fig. 3). For *Ipomopsis* too, we find no evidence that high pollinator efficiency mitigates the costs of floral larceny; in particular, we find no difference in per-flower pollen deposition by pollinators visiting flowers with vs. without floral larceny (R. E. Irwin and C. E. Engel, *unpublished data*). Second, although floral larcenists reduce the fitness of some plant species, larceny has positive effects on female-fitness components in others due to shifts in foraging behavior and flight distances of animal pollinators (Maloof 2001, Richardson 2004, but see Irwin 2003). These examples raise the question of whether animal-pollinated plants may achieve overcompensation to floral larceny due to behavioral responses of their mutualist pollinators. Shifts to longer flight distances should enhance fitness by promoting outcrossing and compatible pollination in self-incompatible plants, and by avoiding inbreeding depression in self-compatible plants, assuming strong spatial genetic structuring of plant populations. Both of these scenarios illuminate a key feature of tolerance to floral larceny, namely a great diversity of currencies for tolerance are possible, including mutualist-pollinator service, plant resources to support the mutualist partner, and fitness benefits from the partnership. Whether such a diversity of currencies for tolerance is unique to floral larceny or also applies to tolerance to herbivory is under investigation (Strauss and Murch 2004).

In conclusion, our study suggests that the intensity of species interactions may constrain the efficacy of tolerance mechanisms in mitigating the impacts of floral larceny. For floral larceny as for herbivory, we still have much to learn about the evolutionary potential of tolerance, about genetic and ecological constraints on its effectiveness, and about selection for compensation in comparison to other modes of defense (e.g., Galen 1983, Irwin et al. 2004*b*). Nonetheless, a focus on mechanisms of tolerance may yield generality across the rich diversity of flowering plants, their antagonists, and animal pollinators (Tiffin 2000). The next steps are to understand why floral larceny intensities are so variable both within and among species and to estimate tolerance to floral larceny using clones or closely related plants across a gradient of damage levels. A reaction–norm approach to measuring tolerance will more formally allow for comparison of the strength of tolerance to floral larceny vs. herbivory (Strauss and Agrawal 1999)

and will provide a means to assess the potential for evolution of tolerance mechanisms to floral larceny.

Acknowledgments

We thank H. Baltzer, E. Bruneau, S. Dunklee, M. Erhart, J. Geib, A. McKinley, D. Leuchtman, K. and K. Ritter, R. Rizo, and B. Wilke for help in the field and lab; K. Becklin, A. I. Michels, L. Burkle, S. Elliott, P. Muller, and G. Pruett for helpful comments on the manuscript; and NSF Grants DEB-0316110 (C. Galen), DEB-0089643 (R. Irwin), and DEB-0455348 (R. Irwin) for funding.

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APPENDIX A

Repeated-measures ANOVA for nectar standing crop in *Polemonium viscosum* flowers before and after exposure to ant visitation (*Ecological Archives* E089-178-A1).

APPENDIX B

Phenological pattern of flower production in *Ipomopsis aggregata* with 10% or 80% of flowers with floral larceny (*Ecological Archives* E089-178-A2).