

Nonadditive effects of flower damage and hummingbird pollination on the fecundity of *Mimulus luteus*

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Abstract Flower herbivory and pollination have been described as interactive processes that influence each other in their effects on plant reproductive success. Few studies, however, have so far examined their joint effects in natural populations. In this paper we evaluate the influence of flower damage and pollination by the hummingbird *Oreotrochilus leucopleurus* on the fecundity of the Andean monkey flower *Mimulus luteus*. We performed a 2×2 factorial experiment, with artificial clipping of lower petals and selective exclusion of the hummingbird as main factors. In spite of the relatively low proportion (27.5%) of the variance in seed production accounted for by the full factorial model, artificial damage and hummingbird exclusion, as well as their interaction, were highly significant, indicating nonadditive effects of factors on plant fecundity. In the presence of hummingbirds, undamaged flowers had a seed production that was 1.7-fold higher than for damaged flowers, suggesting that the effect of flower damage on female reproductive success occurs probably as a consequence of hummingbird discrimination against damaged corollas. This result indicates that the impact of flower herbivory on plant fecundity was contingent on

the presence or absence of hummingbirds, suggesting that pollinators may indirectly select for undamaged and probably resistant flower phenotypes. A second interaction effect revealed that undamaged flowers produced 78.5% more seeds in the absence of rather than in the presence of *O. leucopleurus*, raising the question of the ecological mechanism involved. We suggest that the strong territorial behavior exhibited by the bee *Centris nigerrima* may confine the foraging activities of the remaining bee species to safe sites within enclosures. Overall, our results provide evidence that hummingbird pollination and flower herbivory have interdependent effects on *M. luteus* fecundity, which indicates that it will be difficult to predict their ecological and evolutionary consequences unless interactions are analyzed in an integrated form.

Keywords Chile · Andes mountain range · *Oreotrochilus leucopleurus* · Nectar guide · Flower herbivory

Introduction

The relationship between herbivory and pollination has increasingly attracted the attention of ecologists because herbivores often modify characters involved in pollination attraction, such as the number of flowers (e.g., Karban and Strauss 1993; Quesada et al. 1995), corolla size (e.g., Strauss et al. 1996; Lehtilä and Strauss 1999), and flowering time (Frazee and Marquis 1994). It is known that floral herbivory can have direct and indirect effects on plant reproductive success (Strauss 1997; Krupnick et al. 1999; Mothershead and Marquis 2000; Kelly and Dyer 2002). On the one hand,

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herbivores may directly reduce plant fitness by damaging sexual structures such as pistils, ovaries, and anthers (e.g., Schemske and Horvitz 1988; Hendrix and Trapp 1989; Bertness and Shumway 1992; English-Loeb and Karban 1992; Malo et al. 2001). On the other hand, herbivory may indirectly reduce reproductive success by degrading floral appearance, rendering flowers less attractive to pollinators (e.g., Karban and Strauss 1993; Frazee and Marquis 1994; Cunningham 1995; Strauss et al. 1996; Krupnick et al. 1999; Lehtilä and Strauss 1999). However, for floral herbivores to influence plant fitness indirectly via pollinators, at least four conditions are necessary: (1) herbivory must affect floral traits; (2) some stage of plant reproduction must be pollen-limited; (3) pollinators must discriminate against damaged flowers; and (4) pollinator discrimination between damaged and undamaged flowers must translate into variation in some component of plant fitness (see also Mothershead and Marquis 2000). Because pollinator species often differ in perceptual capacity and ability to detect flower shape, size, color, scent, and reward (see Chittka and Thomson 2001; Schaefer et al. 2004), the final outcome of floral herbivory via pollination may be contingent on the composition of the pollinator assemblage, especially to the presence of pollinator species with the perceptual ability to distinguish damaged from undamaged flowers. Unfortunately, most studies linking floral herbivory and pollination have focused on the pollinator assemblage as a whole rather than on a species basis, and as a consequence, the relative abilities of different pollinator species to propagate (or hamper) the impact of herbivory remains a topic rarely touched upon in the literature.

The observation that herbivory and pollination interact in their fitness effects has led some authors to suggest that inferences on the evolutionary trajectory of plant traits that are based on single interactions may be limited when other interactions are not explicitly taken into account (e.g., Strauss 1991; Ehrlén 1997, 2002; Herrera et al. 2002). For instance, detection of nonadditive effects in factorial experiments with pollination and herbivory as main factors has revealed that positive effects of pollination on plant fitness occur only in the absence of herbivores, and herbivores often have detrimental effects only in the presence of pollinators, which probably wipes out any selective advantage of plants exposed to the action of pollinator-mediated selection (Herrera 2000; Herrera et al. 2002; Gómez 2005). Taken together, these results suggest that it is not possible to determine the fitness impact of pollination and herbivory in isolation because their effects are often interdependent at the ecological and probably at

the evolutionary level (e.g., Armbruster 1997, 2002), rendering it difficult to make meaningful predictions of microevolutionary change across generations based on single interactions (reviewed in Strauss and Irwin 2004).

In this study, we evaluate the influence of flower damage and hummingbird pollination as determinants of plant fecundity in the Andean monkey flower *Mimulus luteus* in a high-elevation locality in the Chilean Andes. The only vertebrate pollinator at the study site is the Andean Hillstar hummingbird *Oreotrochilus leucopleurus*. Even though the hummingbird is entirely absent from some monkey flower populations in central Chile, when present, it is an important agent of phenotypic selection that discriminates flowers on the basis of corolla size and nectar guide size and shape (Medel et al. 2003). To quantify the extent to which flower damage influences pollination by *O. leucopleurus*, we imposed artificial damage on the corolla and tested for nonadditive effects between damage and hummingbird pollination on the fecundity of *M. luteus* using a factorial 2×2 experiment. More specifically, in this study we addressed the following questions: (1) does hummingbird pollination influence the fecundity of *M. luteus* regardless of flower damage? (2) What is the joint effect, if any, of flower damage and hummingbird pollination on the fecundity of this species? (3) Do hummingbirds amplify or hamper the potential impact of flower herbivory on plant reproductive success?

Methods

Natural history

This study was carried out on February 2002 and 2003 in an Andean bog at the El Yeso locality (33°37' S, 70°01' W, 2,580 m elevation) in central Chile. The Andean monkey flower, *Mimulus luteus* var. *luteus* (Phrymaceae, Beardsley and Olmstead 2002) is a hydrophilic annual or perennial plant species that grows in wetlands across Chile from sea level to an elevation of 3,650 m. Corollas of *M. luteus* are yellow, and lower petals often have a conspicuous red nectar guide that varies in size and shape both within and among populations (von Bohlen 1995; Medel et al. 2003). In the study site, flower visitors include the bees *Centris nigerrima*, *Bombus dahlbomii*, *Bombus terrestris*, and *Megachile semirufa*. The corolla of *M. luteus* does not reflect in the UV spectrum (Botto-Mahan et al. 2004), which indicates that this wavelength does not influence flower herbivory and pollinator visits. Flowers of *M. luteus* are damaged by larvae of *Mesonychium* sp.

(Apidae, Hymenoptera) and *Rachiplusia virgula* (Noctuidae, Lepidoptera). All of these larvae damage petals and flower buds, often causing flowers to abort prior to full seed development.

Flower herbivory and pollen limitation

To quantify the importance of the hummingbird *O. leucopleurus* relative to insect pollinators, we recorded the flower visitors over a total of 42 h of observation distributed between 8:00 and 20:00 h during four consecutive days in the first week of February 2002. The pollinator assemblage did not change during the flowering season of *M. luteus* (mid-January to end of February), which suggests that our four-day observation period did not underestimate pollination visits. Visitation rates were calculated as the number of visits per flower per hour. To quantify the extent of natural flower herbivory, on 29th January 2002 we tagged 200 flower buds, one bud per plant, and checked damage daily until withering. The number of damaged petals and the location of damage (upper, lateral or lower petal) were also recorded. Digital photographs of all monitored flowers were taken and their corolla and nectar guide size measured for subsequent inclusion as covariates in statistical analyses. Flower measurements were performed in UTHSCSA Image tool for Windows v. 2.0 (Wilcox et al. 2000). The necessity of pollinators for reproduction was estimated from the following crossing treatments: (1) spontaneous self-pollination, by bagging individual flower buds; (2) artificial self-pollination, with stigmas manually saturated with pollen from the same flower; (3) artificial cross-pollination, with stigmas manually saturated with pollen from plants 5 m distant from the focal flower. Each treatment consisted of 20 flowers from different plants. All capsules were collected 23–26 days after anthesis and carried to the laboratory for seed counting.

Experimental procedure

On 3rd February 2002, in the middle of the flowering season of *M. luteus*, we set up a field experiment in a two-way factorial design to dissect the effects of flower damage, hummingbird pollination, and their interaction on the reproductive success of *M. luteus*. The effect of floral damage on the seed set was evaluated on a per-flower basis by clipping lower petals with circular 0.28 cm² perforations (Fig. 1). Because corollas showing deviations from symmetry may suffer reduced flower visitation and female reproductive success (e.g., Møller 1995; Møller and Eriksson 1995; but see Siikamäki et al. 2002; Botto-Mahan et al. 2004), clippings were performed at the geometric center of the lower petal. The effect of hummingbird pollination was evaluated by precluding bird access to flowers within exclosures, while exposing another set of flowers to complete pollination by insects and hummingbirds. Exclosures consisted of closed-topped rigid polyethylene cylinders 100 cm in height and 30 cm in diameter made of 6.25 cm² dark green mesh, which allowed insects free access to enclosed flowers. We randomly assigned 200 flowers from different plants to one of the following four treatments: (1) damaged flowers and hummingbirds excluded; (2) damaged flowers and hummingbirds present; (3) undamaged flowers and hummingbird excluded, and; (4) undamaged flowers and hummingbirds present (natural situation). Only first-day flowers were used at the beginning of each experiment. During the season, most plants presented only one open flower at a time. This prevented us from replicating flowers per plant without disturbing pollinators. Consequently, all subsequent analyses are on a per-flower basis. To avoid a confounding effect of natural herbivory on flowers, we checked for the presence or absence of herbivory on petals daily. Capsules were collected 23–26 days after experiment initiation, and seeds were counted in the laboratory.

Fig. 1 Flower of *Mimulus luteus*, illustrating a corolla before (*left*) and after (*right*) experimental clipping of the lower petal. Photograph by R. Medel



Results

Flower herbivory and pollen limitation

Insects visited flowers mainly in the morning, whereas hummingbirds visited flowers at sunset, with a marked peak of visitation at 19:00 (Fig. 2). The bird *O. leucopleurus* effected a 5.8-fold higher visitation rate than insects on average, which suggests that hummingbirds are probably the most important pollinator for *M. luteus* in the study site (see also Medel et al. 2003). Even though we were unable to distinguish damage from the hymenopteran and lepidopteran larvae, evidence of floral herbivory was recorded in 40 out of 196 recovered flowers (20.4%). Damage on the lower petal was recorded in 20 out of 40 damaged flowers. The chance of flowers becoming damaged did not vary with corolla or nectar guide size (logistic regression analyses: corolla size: $\chi^2_1=1.12$, $P=0.290$; nectar guide size: $\chi^2_1=0.03$, $P=0.862$). Regarding female reproductive success, neither the presence of floral herbivory as a whole nor the number of damaged petals influenced seed production (one-way ANOVA, presence of herbivory: $F_{(1,194)}=0.58$, $P=0.448$; number of damaged petals: $F_{(2,126)}=0.57$, $P=0.567$). These results did not change substantially when corolla and nectar guide size were included as covariates. However, when the location of damage was taken into account, the flowers damaged on the lower petal produced significantly fewer seeds than flowers damaged in other petals (one-way ANOVA, $F_{(2,37)}=8.61$, $P=0.006$, Fig. 2), probably reflecting the fact that nectar guides are located almost exclusively in this petal.

The fruit set was higher in crossed than in selfed plants (spontaneous self-pollination = 8.7%, artificial self-pollination = 52.6%, artificial cross-pollination = 94.1%; G -test with Yates' correction, $G=33.01$, $P<0.001$, Table 1). Seed production was dependent on the crossing treatment involved (ANOVA, $F_{(2,56)}=7.92$, $P<0.001$) and Student–Newman–Keuls post hoc comparisons revealed that spontaneous self-pollinated flowers produced fewer seeds per fruit than flowers in the other two treatments (mean±SE, spontaneous self-pollination = 6.43 ± 4.66 , $N=23$; artificial self-pollination = 378.42 ± 99.23 , $N=19$; artificial cross-pollination = 235.47 ± 82.96 , $N=17$). Artificial self- and cross-pollination treatments did not differ in seed production ($P=0.167$), implying complete self-compatibility. Overall, these results indicate that, even in the face of complete self-compatibility, a pollen vector is required to ensure the effective pollination of *M. luteus*.

Experimental damage and hummingbird exclusion

The full factorial model accounted for 27.5% of the variation in seed production (overall model, $F_{(3,173)}=21.9$, $P<0.001$). Hummingbird and damage factors, as well as their interaction, were statistically significant in a two-way ANOVA (Table 1), indicating that individual effects cannot be interpreted separately because of their significant interaction. Interaction slices were used to assess the statistical significance of factors at different treatment levels. The interaction between flower damage and pollination is graphically illustrated in Fig. 3. Flower damage had a highly significant effect on seed production when humming-

Fig. 2 Frequency of visits to *Mimulus luteus* made by the hummingbird *Oreotrochilus leucopleurus* (open circles), and pooled insect species (closed circles). Data represent cumulative visits over 42 h of observation. The inset shows the impact of natural flower herbivory on the mean seed production (± 1 SE) of *M. luteus*. UD undamaged flowers; DLP damaged in the lower petal; DOP damaged in other petal. Numbers above error bars indicate sample size in each treatment group. Levels with different letters are statistically significant at $\alpha=0.05$ in Scheffé a posteriori contrasts

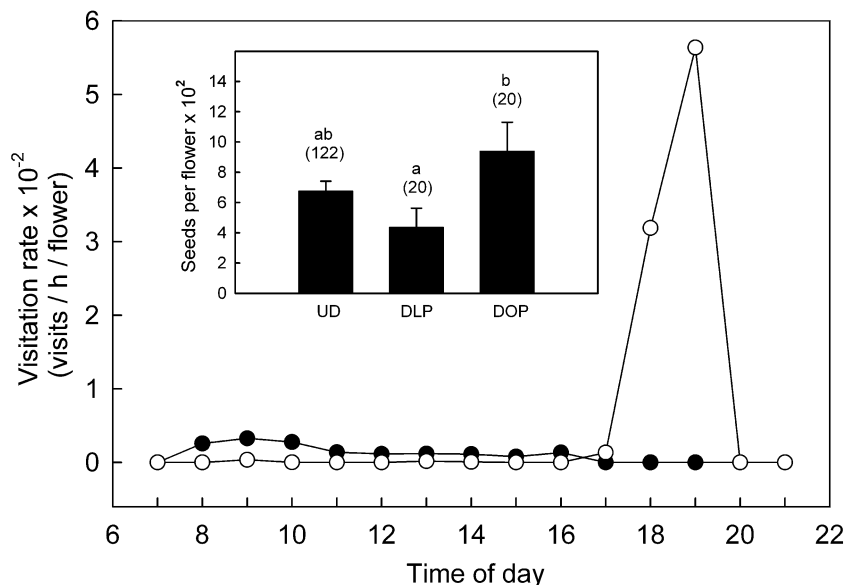


Table 1 (a) Two-way ANOVA for the effects of damage (damaged or undamaged) and hummingbird (present or excluded) on seed production. Data were transformed as log(seed production +1) to meet the assumptions of ANOVA. (b) Summary of interaction slices for the effects of hummingbirds and flower damage on seed production in *M. luteus*

Source	df	MS	F	P
(a) ANOVA results				
Damage (<i>D</i>)	1	12.15	21.53	<0.001
Hummingbird (<i>H</i>)	1	7.25	12.84	<0.001
<i>D</i> × <i>H</i>	1	17.03	30.18	<0.001
Residual	174	0.56	–	–
Source	df	SS	F	P
(b) Interaction slices				
Damage, hummingbirds present	1, 174	32.52	62.76	<0.001
Damage, hummingbirds excluded	1, 174	0.20	0.38	0.538
Hummingbird, damage present	1, 174	20.27	39.13	<0.001
Hummingbird, damage absent	1, 174	1.77	3.42	0.066

For each classification variable, slices perform a simultaneous comparison among all of the levels within the second classification variable. See Fig. 3 for a graphical representation

birds were present. In the absence of the hummingbird, however, floral damage was irrelevant for seed production. These results suggest that *O. leucopleurus* reduced flower visitation when faced with corollas damaged in the lower petal. Similarly, hummingbirds were important for seed production in the presence of damage. Interestingly, damaged flowers exposed to hummingbirds had a significant 71.6% reduction in seed production in comparison to damaged flowers with hummingbirds excluded (Fig. 3). Finally, undamaged flowers in the presence of the hummingbird exhibited borderline significantly higher seed production than in their absence, confirming that *O. leucopleurus* was an important pollen vector for *M. luteus*.

Discussion

Even though natural flower herbivory as a whole had no significant effect on the seed production of *M. luteus*, flowers damaged on the lower petal produced fewer seeds than flowers damaged in other petals. These results suggest that the location of damage may be a critical factor for plant reproductive success, especially if damage alters the signal that is sensed by pollinators (see review in Schaefer et al. 2004). Avoidance of damaged flowers has been reported in a wide range of pollinator species, including bats (e.g., Cunningham 1995), butterflies (e.g., Murawski 1987), bees (e.g., Karban and Strauss 1993; Strauss et al. 1996; Krupnick

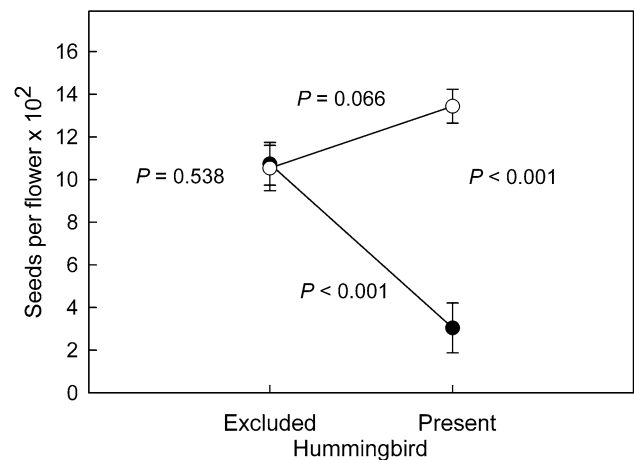


Fig. 3 Interaction graph for the effects of hummingbird exclusion and artificial flower damage on the mean seed production of *Mimulus luteus*. Circles indicate mean seed production (± 1 SE) with flower damage (closed circles) or flower undamaged (open circles)

et al. 1999), flies (e.g., Lohman 1996; Strauss et al. 1996), and hummingbirds (e.g., Gass and Montgomerie 1981; Krupnick et al. 1999; Canela and Sazima 2003). Because experimental clipping was performed on the petal that bears the nectar guide, it is quite possible that hummingbirds do not evaluate only flower herbivory but also nectar guide damage, especially if guides represent honest signals for pollen or nectar reward (see reviews in Waser 1983; Waser and Price 1985). For instance, our correlative results indicate that natural herbivory in the lower petal significantly reduced seed production in comparison to herbivory in other petals, which suggests that nectar guide damage influences the final decision made by hummingbirds in their foraging activities. However, traits that attract pollinators might at the same time attract other animals that destructively feed on flowers. For example, trait-mediated conflicts have been previously described in pollination–seed predation (e.g., Silander 1978; Brody 1992) and herbivory–pollination (e.g., Galen and Cuba 2001; Leege and Wolfe 2002; Irwin et al. 2003) relationships. In this study, the presence of flower herbivory did not show a significant functional relationship either with corolla or nectar guide size, which suggests that pollination and herbivory probably do not conflict on the basis of floral characters in this species.

Results from the factorial experiment revealed that the influence of flower damage and hummingbird pollination on the fecundity of *M. luteus* was contingent on the presence or absence of each other. For instance, the presence of hummingbirds had only a borderline positive influence on seed production ($P=0.066$) in the absence of experimental herbivory. Damage, in turn, had a negative effect on seed production only in the

presence of hummingbirds ($P < 0.001$), suggesting that *O. leucopleurus* avoids flowers with damaged corollas. This strong effect disagrees, in part, with observations on natural herbivory, where flowers damaged in the lower petal had a similar reproductive success to undamaged flowers (Fig. 2). This discrepancy may be explained, at least in part, by the fact that, unlike natural damage where herbivory does not always occur at the geometric center of the landing petal, artificial clipping always damaged the nectar guides, probably affecting the foraging decisions made by pollinators to a higher extent.

We detected a strong (78.5%) decrease in the seed production of damaged flowers in the presence of hummingbirds in comparison to the situation with hummingbirds excluded ($P < 0.001$, Fig. 3). This counterintuitive result can be explained, at least in part, by two mechanisms that are not mutually exclusive. First, it is possible that hummingbirds not only avoid visiting damaged flowers but also prevent bees from accessing patches of *M. luteus*. There is ample evidence for the dominant role of hummingbirds under a range of ecological conditions (e.g., Feinsinger 1976; Ewald and Carpenter 1978; Hixon et al. 1983; Sandlin 2000), including situations of hummingbird–insect competition for nectar reward where hummingbirds often expulse insects and even other hummingbirds from their foraging territories (Primack and Howe 1975; Gill et al. 1982; Laverty and Plowright 1985; Stoaks 2000). Even though *O. leucopleurus* was observed expulsing bees and wasps in the study site, the low temporal overlap between hummingbirds and insects (Fig. 2) suggests that this mechanism is not sufficient to account for the strong reduction in the seed production of damaged plants. Second, it is possible that the high seed production observed in fenced and damaged plants reflects an increased pollination rate by bees that are normally expulsed from flower patches by other territorial bee species. This hypothesis was partially supported by the observation that males of *Centris nigerrima* patrolled well-defined flower patches, often pursuing and expulsing individuals that trespass their territories. For instance, we recorded expulsions in 25 out of 30 intraspecific intrusions (83.3%), and in 9 out of 10 interspecific intrusions (90.0%). Taken together, these data indicate that *C. nigerrima* males showed a strong territorial behavior in 34 out of 40 intrusions (1,279 min of observation in a patch of 423 flowers of *M. luteus* during 24th January to 1st February 2006) (see also Raw 1975; Alcock et al. 1977). Whether the foraging activities of bees are restricted to places outside the influence of *Centris* males, however, needs to be evaluated

in future studies and should be considered to be only a tentative explanation at present.

Results from the factorial experiment are consistent with other studies designed to test nonadditive effects (Herrera 2000; Herrera et al. 2002; Gómez 2005). Common to all of these studies is the conclusion that between-individual variation in plant fecundity cannot be adequately described from additive single-interaction studies, because pollination and herbivory are interdependent at the ecological and probably at the evolutionary level (e.g., Armbruster 1997, 2002; Strauss and Irwin 2004). The system *M. luteus*–pollination–herbivory may represent an appropriate model for examining not only the role of pollinators in magnifying or mitigating the impact of flower herbivory on plant fitness but also the potential indirect role of pollinators on the evolution of plant defense against flower herbivory. Because natural flower herbivory had no significant impact on the seed production of *M. luteus*, the preference of hummingbirds for undamaged flowers may indirectly select for defense mechanisms that otherwise would not be selected by flower herbivores. In this way, the evolution of plant resistance or tolerance against flower herbivory may be constrained, or even driven, by indirect selection imposed by pollinators if sufficient genetic variation for plant defense exists (see also Fineblum and Rausher 1997). Even though many studies have reported that pollinators avoid visiting damaged flowers (e.g., Murawski 1987; Karban and Strauss 1993; Cunningham 1995; Irwin 2000), eventually multiplying the negative effect of herbivores, the potential indirect effects of pollinators in defensive trait evolution needs to be assessed in future studies, especially in situations characterized by low fitness-impact of herbivory and high avoidance of pollinators for damaged flowers.

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