

Testing non-additive effects of nectar-robbing ants and hummingbird pollination on the reproductive success of a parasitic plant

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Abstract Nectar robbing may have an indirect negative effect on plant reproduction by discouraging legitimate pollinator species from visiting robbed flowers. In this study, we set up a 2×2 factorial design with nectar-robbing ants and hummingbird pollination to test for non-additive effects on fruit set, seed mass, and seed germination of the leafless mistletoe *Tristerix aphyllus* (Loranthaceae). Even though ants caused conspicuous damage at the base of the floral tubes, nectar availability was reduced by only 8 % in the presence of ants. The green-backed firecrown *Sephanoides sephaniodes* was insensitive to the presence of ants. Rather, the bird responded to flower number and the presence or the absence of damage, but not to the extent of damage within inflorescences. As hummingbirds were largely insensitive to variation in nectar robbing, the interaction ant \times hummingbird had no effect on plant-reproductive success. Thus, the factorial experiment did not

provide evidence for indirect negative effects of nectar robbing on plant reproduction. These results suggest that indirect effects of nectar robbers on pollinator behaviour may occur under a more restricted set of conditions than those previously considered. We suggest that the low amount of nectar removed by nectar-robbing ants was insufficient for hummingbirds to avoid robbed flowers, which restricted the potential for non-additive effects.

Keywords Chile · Flower damage · Fruit set · Germination · Indirect effects · Mistletoe · *Sephanoides* · *Tristerix*

Introduction

Nectar robbers are animals that access floral nectar by biting or piercing holes in the sides of flowers without contacting the anthers and stigma, thereby failing in effective pollen transfer (Inouye 1980). Nectar robbing is a widespread phenomenon among flowering plants, especially in species which have narrow flower tubes and nectar chambers (see review in Irwin et al. 2010). Nectar robbing is carried out by species belonging to different taxonomic groups, including birds, bees, ants, wasps, and butterflies (Faegri and van der Pijl 1979; Inouye 1980). The impact of nectar robbers on plant fitness ranges from positive to negative (reviewed in Maloof and Inouye 2000; Irwin et al. 2001). Nectar robbers will have a positive

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indirect effect on plant reproduction when pollinators reduce the number of flowers visited per inflorescence and reduce geitonogamy (pollination with pollen from flowers in the same inflorescence). Similarly, plants may be benefitted when robbers deplete nectar and pollinators are forced to increase their foraging area, resulting in larger distances of pollen transport (e.g., Hernández and Toledo 1979; Zimmerman and Cook 1985; Irwin and Brody 1999, 2000). Negative effects of nectar robbing on plant reproduction occur when robbers consume primary reproductive tissues such as pistils, anthers, or ovules, thereby reducing directly the gametes available for reproduction (e.g., McDade and Kinsman 1980) or when the consumption of secondary tissues such as petals or sepals thus decreasing the flower attraction to legitimate pollinators, altering pollination service, and plant-reproductive success (e.g., Roubik 1982). Neutral effects occur when the physical damages imposed by nectar robbers on flowers are evident, which, however, have no consequence for plant reproduction (Malooof 2001; Richardson 2004; Kjonaas and Rengifo 2006).

By performing floral damage, decreasing the nectar standing crop, and sometimes changing sugar concentration, nectar robbers often reduce substantially the chance of pollinator visitation to flowers and inflorescences. However, most studies assume that failure of pollination is caused by the flower damage inflicted by nectar robbers. This assumption is not necessarily justified, as nectar robbing and pollination may represent independent rather than interactive processes. In other words, nectar robbing may influence plant-reproductive success through ecological processes unrelated to changes in flower attraction. For example, Roubik (1982) reported that nectar-robbing bees of *Pavonia dasypetala* (Malvaceae) aggressively defended their feeding sites and attacked only the pollinator of the plant, the hummingbird *Phaethornis superciliosus*. By excluding pollinators from feeding sites, nectar-robbing bees reduced substantially the seed production of robbed flowers without changing flower attraction. While several studies have quantified the importance of nectar robbing for plant-reproductive success (e.g., Navarro 2000; Burkle et al. 2007; Zhang et al. 2009), no study has yet examined in a factorial design the presence of interactive effects of nectar robbers and legitimate visitors, a prerequisite for negative indirect effects of nectar robbing on plant reproduction. In this study, we

examine non-additive effects of floral damage by nectar-robbing ants on hummingbird pollination and the potential indirect consequences of nectar robbing for plant-reproductive success.

Tristerix aphyllus (Loranthaceae) is a leafless mistletoe, and its flowers are extensively damaged by ants. Even though ant-induced nectar robbing has been widely reported in other systems (e.g., Norment 1988; Galen 1983; Herrera et al. 1984; Galen and Cuba 2001; Romero 2002; Galen and Butchart 2003; Lach 2005), its effect on pollinator behavior, to our knowledge, has not been assessed experimentally. Consequently, the aims of this study were (1) to examine potential effects of nectar-robbing ants on the behavior of the green-backed firecrown hummingbird *Sephanoides sephaniodes*, the main pollinator of the mistletoe *T. aphyllus*; and (2) to examine the occurrence of non-additive effects of nectar robbing and pollination on the reproductive success of the parasitic plant. To this end, we characterize the damage performed by ant species on flowers, examine pollinator behavior in relation to the presence and extent of flower damage, and quantify interactive effects of nectar robbing and pollination on the fruit set, seed weight, and germination of *T. aphyllus*.

Materials and methods

Study site and natural history

This study was conducted during June–October 2003 in Las Chinchillas National Reserve (31°30' S, 71°06' W, Aucó, Region of Coquimbo, Chile), located ~300 km northeast of Santiago. The climate is a semiarid Mediterranean type with most rainfall concentrated in the winter season. The mean annual precipitation is 167 mm with ample variation between years, and frequent droughts alternate with unusual years of high precipitation that apparently co-occur with El Niño Southern Oscillation events (Jaksic 2001). The vegetation is thorny; the most common shrub species are *Flourensia thurifera* (Asteraceae), *Bahia ambrosioides* (Asteraceae), and *Porlieria chilensis* (Zygophyllaceae). Cactus species are represented by the columnar *Echinopsis chiloensis* and *Eulychnia acida*, and the globular *Maihueniopsis ovata* and *Eriosyce aurata*. The two columnar cactus species are parasitized by *T. aphyllus* in 36 and 16 %

on the average, respectively (Medel et al. 2002). To avoid potential confounding effects of working with different host species, all observations and experiments were performed on the cactus *E. chiloensis* as this species is the most abundant host in the study site and shows the highest prevalence of the parasitic plant (Medel et al. 2002). Since cacti are often being infected by several mistletoes, and a single parasitic plant may protrude repeatedly from the same cactus column forming different inflorescence units, we restricted our study to cactus harboring a single mistletoe inflorescence to avoid confounding effects and pseudoreplication (Fig. 1a).

Tristerix aphyllus infects only Cactaceae species in north-central Chile (Kuijt 1969). The vegetative portion exists as an endophyte within the host tissues, and the reproductive portion emerges from the host

stems (Mauseth et al. 1984, 1985; Fig. 1b). The inflorescences of *T. aphyllus* have a variable number of tubular flowers (between 200 and 3,000). Mean flower length (SE) is 48.15 mm (0.16) ($N = 989$), flowers have a lower ovary, only one ovule, one style, and four yellow stamens exerted from the floral tube. The floral tube is formed by four red tepals that are fused in the proximal portion of the flower to form a 4-mm length nectar chamber immediately above the ovary. Nectar production ranges from 0.3 to 71.3 μL during 17 h, and flowers are pollinated mainly by the migratory hummingbird *S. sephaniodes* (Trochilidae) (Medel et al. 2002). During the pollination season, the bird visits most of the *T. aphyllus* population, often foraging on several flowers of the same inflorescence in the same visit (Medel et al. 2002). Even though *T. aphyllus* is self-compatible, self-pollinated plants had

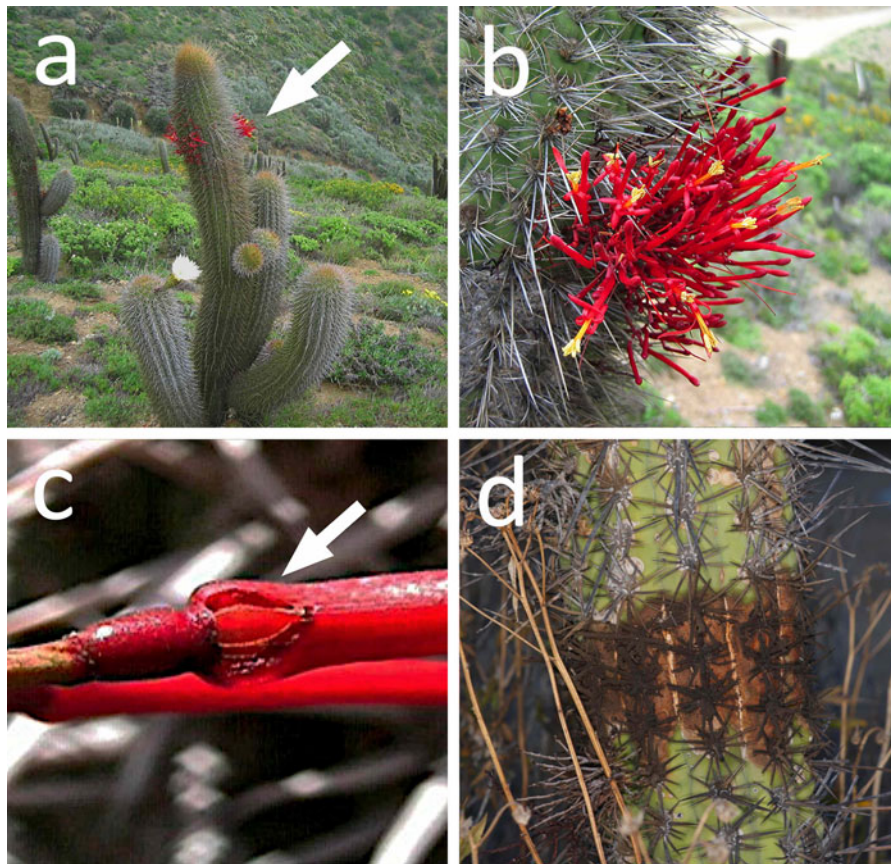


Fig. 1 **a** Mistletoe–cactus system, showing the emergence of the reproductive portion of *T. aphyllus* from the main cactus stem. **b** Inflorescence of *T. aphyllus* protruding from the spiny surface of the cactus *E. chiloensis*. **c** Damage made by nectar-

robbing ants on the nectar chamber of flowers of *T. aphyllus*. **d** Cactus stem with Tanglefoot applied to prevent the ant access to mistletoe inflorescences

a 25 % lower fruit production than outcrossed plants indicating that hummingbirds play an important role in gamete transport (González et al. 2007). Regarding nectar robbing, three native ant species have been identified as potential nectar robbers, namely *Camponotus morosus* (worker, 11–14-mm length), *Solenopsis gayi* (worker, 3–4-mm length), and *Conomyrma goetschi* (worker, 5–6-mm length). Even though ants rarely damage other portions of the flower, most damage is located in the nectar chamber, where ants pierce floral tissues at the base of the tepals to form holes of variable sizes to access nectar (Fig. 1c). Except for *C. goetschi* which could enter legitimately into the flower without contacting the reproductive organs, all the ant species gain access to the nectar through the holes made from outside.

Ant prevalence, floral damage, and pollinator behavior

To assess the pattern of ant prevalence on inflorescences and the extent of floral damage, we recorded the ant species present on 125 inflorescences and the presence or the absence of robbed flowers. The location of damage on individual flowers was examined in 19 inflorescences. To investigate the effect of ants on pollinator behavior, we performed focal observations on 27 inflorescences with ants present and 58 inflorescences with ants excluded. Ants were excluded by applying Tanglefoot™, a non-drying sticky coating that forms a barrier against walking insects, at the base of the parasitized cactus branch in such a way as to prevent the free access of ants to inflorescences (Fig. 1d). Tanglefoot was applied at an appropriate distance to avoid potential interference with hummingbird behavior. Bird behavior was measured by recording the number of visits and the time spent on inflorescences when hummingbirds show the maximal activity at the study site (7:30–8:30 h, and 18:00–19:30 h, Smith-Ramírez 1999). We performed focal observations in the morning (30 min observation) and afternoon (30 min observation). Data for each inflorescence were pooled to obtain 1-h observation per day. Each inflorescence was observed only during 1 day. Observations were performed during 5 consecutive days since June 9, 2003. Bouts were considered as a valid visit when the hummingbird introduced its beak in the flower tube. Comparisons of hummingbird behaviors in the presence and the

absence of ants were performed by one-way ANCOVA using the number of open flowers (damaged and undamaged pooled) as covariate. In a different group of plants ($N = 118$) with no ants, we recorded the number of robbed and unrobbed flowers to estimate the effects of damage on the duration and the number of visits of hummingbirds on inflorescences. We used generalized linear models (GLMs) to estimate the significance of effects assuming a reciprocal link and exponential distribution for the time spent by birds feeding on inflorescences, and a log link and Poisson distribution for the number of visits to inflorescences.

Effects of nectar robbing on *T. aphyllus* fecundity

To measure the indirect effect of ants on the reproductive success of *T. aphyllus*, we chose 80 mistletoes parasitizing different host individuals. Ants were present in all the inflorescences at the beginning of the experiment, and the inflorescences had at least 200 flowers each. We established a 2×2 factorial design, with ants and hummingbirds as main factors. Inflorescences were randomly assigned to one of the following four treatments ($N = 20$ inflorescence per treatment): (1) ants and hummingbirds present ($A+$, $H+$); (2) ants present and hummingbirds excluded ($A+$, $H-$); (3) ants excluded and hummingbirds present ($A-$, $H+$); and (4) ants and hummingbirds excluded ($A-$, $H-$). Ant exclusion was performed by physically removing the ants present in inflorescences and applying Tanglefoot at the base of the parasitized cactus branch. Hummingbirds were excluded by covering the inflorescences with translucent tulle nets (mesh size = 1.2 mm). Net enclosures were loosely tied to the cactus branch with wire, leaving at least 1 cm of open space in the net margins, which ensured that ants in ($A+$) treatments found no obstacle to move freely along the cactus branch and mistletoe inflorescence. Inflorescences of the control situation were left intact, that is without tulle and Tanglefoot application. Ants in ($A+$) treatments remained active at least ca. 1 month from initiated the experiment, suggesting that tulle nets did not influence the presence of ants over such duration. After assignment of treatments, the nectar volume of 1–10 first-day flowers per inflorescence was measured with capillary tubes. Nectar measurements were performed during the first 10 days after initiating the experiment. Nectar volume values

per flower were averaged on a per inflorescence basis for subsequent analyses. One hundred flower buds per inflorescence were tagged to evaluate fruit set. Three months later, at the end of the fruiting season, we estimated the fruit set (% of flowers setting fruit). Because 17 inflorescences suffered physical damage attributable to the action of frugivorous birds, we estimated the fruit set only in cases where no evidence of damaged was detected ($N = 63$). Four inflorescences were completely destroyed by birds, which permitted seed weight estimation in 76 inflorescences. We collected 10–13 fruits per inflorescence. The fruit pericarp was manually removed, and the naked seeds were weighted and placed in Petri dishes with damp filter paper for assessment of germination success (4–13 seeds per plant). Seed germination could be assessed for 75 inflorescences. Dishes were watered twice a day for 10 days. Data were analyzed using GLMs. For nectar volume and seed weight, we assumed a reciprocal link and exponential distribution. Fruit set and germination were examined using a logit link and binomial distribution. The presence of significant interaction terms indicates that ant nectar robbing and pollination interact to affect the plant-reproductive trait; that is, the trait response was non-additive. If the interaction term was not significant, then plant reproduction responded additively to nectar robbing and pollination.

Results

Ant prevalence and floral damage

Ants were present in 82.4 % of the inflorescences ($N = 125$). All plants had flowers damaged by nectar robbers; the percentage of robbed flowers per inflorescence ranged from 30 to 70 %. Floral damage occurred at the base of the corolla tubes in 93 out of 310 robbed flowers from 19 inflorescences (Fig. 1c). The remaining 217 damaged flowers presented holes above the nectar chamber, near to the tip of the flower. Damage to the ovary was never detected and excised stamens were observed only in 5 of 114 robbed flowers. Most damage consisted of elliptic and irregular holes (mean \pm SE, 3.8 ± 0.23 mm length; 2.3 ± 0.14 mm width). *Conomyrma goestchi* was the ant species with the highest prevalence (79.6 %), followed by *C. morosus* (35.7 %), and *S. gayi*

(12.7 %). *Conomyrma goestchi* and *C. morosus* were found together in 24 % of inflorescences; *C. goestchi* and *S. gayi* in 11.2 %; *C. morosus* and *S. gayi* in 7.2 %; and the three species in 5.6 % of the inflorescences.

Effects of floral damage on pollinator behavior

The time spent (seconds) by the hummingbird *S. sephaniodes* on inflorescences was not affected by the presence of ants (mean \pm SE, +A: 15.40 ± 3.43 ; -A: 16.74 ± 23.53 , ANCOVA, $F_{1,82} = 0.01$, $df = 1$, $P = 0.918$). Similarly, the number of visits of hummingbirds to inflorescences was not affected by nectar-robbing ants (mean \pm SE; +A: 1.11 ± 0.13 ; -A: 1.24 ± 0.12 , ANCOVA, $F_{1,82} = 0.345$, $df = 1$, $P = 0.558$). The number of open flowers was important for the time spent on each visit ($F_{1,82} = 15.342$, $df = 1$, $P < 0.001$) and borderline significant for the time spent on inflorescences ($F_{1,82} = 3.447$, $df = 1$, $P = 0.066$). GLM coefficients revealed that the presence of damage in inflorescences reduced the attraction of hummingbirds to plants (Table 1), but the extent of damage did not reduce the duration and the number of visits of hummingbirds to plants. Rather, both the number of the damaged and the undamaged flowers increased indistinctly the foraging activity of hummingbirds on inflorescences (Table 1).

Effects of ants and hummingbirds on nectar volume and plant fecundity

No evidences for non-additive effects of hummingbirds and ants were detected for any of the dependent variables examined (Table 2), indicating that additive effects, if any, characterize this system. The only borderline significant effect was that of hummingbirds on the mean nectar volume per inflorescence (Table 2). As expected, the inflorescences open to hummingbirds showed lower nectar volume per flower than those with hummingbirds excluded (mean \pm SE; +H: 2.83 ± 0.35 μ L, -H: 4.33 ± 0.35 μ L). The presence of ants, in turn, reduced nectar availability by a non-significant 8 % compared to the situation when ants were excluded (mean \pm SE; +A: 3.43 ± 0.34 μ L, -A: 3.73 ± 0.39 μ L, $F_{1,76} = 0.38$, $P = 0.538$). In general, ant nectar robbing was irrelevant for fruit set, seed weight and germination (Table 2).

Table 1 Results from GLMs for effects of floral and inflorescence damage (0 = absence of damage, 1 = presence of damage) on the time and number of visits of the hummingbird *S. sephaniodes* to *T. aphyllus*

Response/effect	Estimate (SE)	χ^2	<i>P</i>
Time on inflorescence			
Number of flowers damaged	0.045 (0.007)	39.1	<0.001
Number of flowers undamaged	0.028 (0.001)	336.9	<0.001
Damage to inflorescence (0–1)	–0.408 (0.074)	32.1	<0.001
Visits to inflorescence			
Number of flowers damaged	0.033 (0.009)	11.8	<0.001
Number of flowers undamaged	0.030 (0.002)	205.2	<0.001
Damage to inflorescence (0–1)	–0.213 (0.095)	5.1	0.024

No inflorescence had ants when hummingbird behavior was recorded. *N* = 118 inflorescences in both cases

Table 2 Summary of GLM effects of hummingbird pollination (*H*), ant nectar robbing (*A*), and their interaction (*H* × *A*) on nectar volume and plant reproductive traits

Response/effect	Estimate	χ^2	<i>P</i>
Nectar volume (<i>N</i> = 80)			
<i>H</i>	–0.064	3.82	0.051
<i>A</i>	–0.021	0.39	0.533
<i>H</i> × <i>A</i>	0.023	0.48	0.487
Fruit set (<i>N</i> = 63)			
<i>H</i>	–0.400	1.73	0.189
<i>A</i>	–0.102	0.11	0.742
<i>H</i> × <i>A</i>	–0.077	0.06	0.803
Seed weight (<i>N</i> = 76)			
<i>H</i>	0.060	0.00	0.944
<i>A</i>	–0.045	0.00	0.958
<i>H</i> × <i>A</i>	0.072	0.00	0.932
Germination (<i>N</i> = 75)			
<i>H</i>	–0.400	1.43	0.231
<i>A</i>	–0.093	0.07	0.784
<i>H</i> × <i>A</i>	–0.149	0.19	0.660

N indicates sample size (number of plants). Analyses of seed weight and germination considered the mean values per plant. We weighted, on average, 9.3 seeds per plant (range 4–13 seeds) and the same number of seeds was used for the germination experiment

Discussion

Our results indicate that the duration and the number of hummingbird visits to inflorescences increased with floral display (i.e., with the number of flowers per inflorescence) and decreased with the presence of damage on inflorescences. This result is consistent

with patterns observed in diverse pollination systems where floral display tends to increase pollinator visitation rate (e.g., Montalvo and Ackerman 1987; Rodríguez-Robles et al. 1992; Fenster et al. 2006; Dudash et al. 2011). However, when flower number was separated into robbed and unrobbed flowers, hummingbird behavior was largely insensitive to flower damage. This result was surprising because pollinators are often assumed to avoid robbed and damaged flowers to maximize the net energy intake and minimize foraging time (e.g., Roubik 1982; Irwin and Brody 1998; Irwin 2000). For instance, it is known that pollinators often avoid robbed flowers when floral damage changes petal display and inflorescence appearance (e.g., Karban and Strauss 1993; Lohman et al. 1996; Krupnick et al. 1999; Carduel and Koptur 2010; Danderson and Molano-Flores 2010), flower production and phenology (e.g., Frazee and Marquis 1994; McCall and Irwin 2006), or when damage occurs on petals involved in pollinator attraction (e.g., Pohl et al. 2006; Botto-Mahan et al. 2011).

The reduction of nectar-standing crop may decrease the number of visits relative to intact flowers (Irwin and Brody 1998). However, if nectar robbers do not remove enough nectar to make the differences large enough to be detected by pollinators, as observed in this study, variation in nectar levels may have a marginal effect on hummingbird foraging decisions (Burkle et al. 2007). In this study, nectar-robbing ants reduced nectar availability by 8 %, suggesting that lack of sufficient reduction precludes hummingbird avoidance behavior. The observation that nectar availability, probably one of the most informative

cues for hummingbirds, did not change substantially after ant robbery (Table 2) suggests that nectar variation is a necessary condition for the occurrence of a significant interaction between ant nectar robbing and pollination. Only one study has, to our knowledge, examined the effect of nectar availability on the hummingbird response to robbed/unrobbed flowers. Irwin (2000) examined experimentally the cues used by broad-tailed hummingbirds (*Selasphorus platycercus*) and rufous hummingbirds (*Selasphorus rufus*) to avoid robbed flowers of *Ipomopsis aggregata*. Her results indicate that hummingbirds make their decision based on nectar availability, but not on the presence or the location of flower damage. Whether *S. sephaniodes* behaves in a similar way to *Selasphorus* species when faced with comparable situations is unknown at present. However, it has been described that *S. sephaniodes* has cognitive abilities that permit individuals to learn and remember the location of the most profitable nectar sources (González-Gómez and Vásquez 2006), which suggests that nectar availability plays an important role in the foraging decisions of this species. It is likely that flower damage does not provide an informative and reliable cue for hummingbirds unless accompanied by a significant reduction in nectar availability.

Whatever the cue used by hummingbirds to make their foraging decisions, ant \times hummingbird interaction effects seem to be playing a minor role in this system, as nectar-robbing ants had no important effects on nectar availability or plant-reproductive success. For instance, the presence of nectar-robbing ants on inflorescences did not influence the conversion of flowers to fruits (fruit set), seed weight, or germination success of *T. aphyllus* (Table 2). Even though ants have been traditionally considered the prototype of nectar robbers or nectar thieves (Faegri and van der Pijl 1979; Wyatt 1980), the amount of nectar removed by ants in this system (8 %) is relatively low in comparison with other robber taxa such as bees, birds, and mites. For example, short-tongued bumblebees have been shown to remove 50–80 % of the nectar-standing crop (Morris 1996; Maloof 2001; Castro et al. 2008); birds reduce 44 % of the nectar standing crop (González-Gómez and Valdivia 2005, but see Arizmendi et al. 1996); and flower mites reduce the nectar standing crop up to 50 % (Colwell 1995; Lara and Ornelas 2001). It is likely that robbers that leave behind a high fraction of nectar have

weaker effects on plant reproduction than robbers that remove a large fraction of the nectar available (McDade and Kinsman 1980). If so, nectar-robbing ants may have a low potential to induce indirect effects on plant-reproductive success by discouraging legitimate pollinators.

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