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Nectar 'theft' by hummingbird flower mites and its consequences for seed set in *Moussonia deppeana*

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Summary

1. Mites (Acari: Mesostigmata: Ascidae) that live and feed in the flowers of about 100 plant species are transported in the nares of hummingbirds (Trochilidae). Mites may compete with hummingbirds for nectar secreted by the host plants, and this could affect the dynamics and reproductive outcomes of the mutualism between plants and their pollinating hummingbirds.

2. Here we combined field observations and experimental manipulations to assess the role of hummingbird flower mites (*Tropicoseius* sp. nov.) on nectar secretion and reproductive output of protandrous *Moussonia deppeana* (Schlecht. & Cham.) Hanst. (Gesneriaceae) during their flowering period in a cloud forest remnant.

3. During the 4 days that the flowers of *M. deppeana* last, flowers were visited exclusively by hummingbirds (*Lampornis amethystinus*). Bud production per inflorescence peaked in December. There were few open flowers per inflorescence in November, but numbers increased as the flowering season progressed (December and January).

4. The availability of each flower phase differed over the flowering season. Staminate-phase flowers were more abundant over the flowering season than pistillate-phase flowers. These differences were statistically significant over time.

5. Nectar availability was reduced by up to 50% in the presence of hummingbird flower mites. Over the 4 days of observation, significantly more nectar was secreted to flowers from which mites were excluded than to flowers with no mite exclusion. The same effect was observed during flowering, but mites consumed a greater percentage of the total nectar secreted in December.

6. Significantly more nectar was secreted during the staminate phase than in the pistillate phase, independent of time and treatment.

7. A manual pollination experiment suggested that mites act like secondary pollinators in this self-compatible, non-autogamous plant, at least in flowers that were not pollinated manually and had no access to pollinating hummingbirds.

8. Although seed production was not reduced significantly by flower mites, our results suggest that the presence of floral mites can affect pollen transmission, as the amount of nectar available to hummingbirds was reduced drastically. This can directly affect hummingbird foraging patterns and reduce the fitness of the host plants.

Key-words: Hummingbirds, México, nectar secretion, pollination biology, protandry

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Introduction

Birds acting as pollinators are important in the maintenance of pollen flow and in promoting outcrossing and genetic variability among plant populations (Stiles 1981). Many plant species of the New World depend on hummingbirds (Trochilidae) for pollination, and these birds, in turn, depend on the nectar of these plants for food. Flowers pollinated by hummingbirds can typically support a variety of non-pollinating, 'illegitimate' visitors such as bees, ants, passerine species, other hummingbirds, and even bacteria (Arizmendi, Domínguez & Dirzo 1996; Colwell *et al.* 1974; Inouye 1983; Irwin & Brody 1998; McDade & Kinsman 1980; Ornelas 1994; Roubik 1982; Traveset, Willson & Sabag 1998). These visitors may 'steal' nectar. The most common nectar thieves in many of these flowers are the hummingbird flower mites in the family Ascidae (Colwell 1973).

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Hummingbird flower mites share a forced affiliation with the flowers of a variety of plant species pollinated exclusively by hummingbirds. Mites feed on pollen and nectar over several days until they are dispersed as 'stowaways' (Colwell 1985) in the beaks and nares of hummingbirds (Paciorek *et al.* 1995). During their life cycle (7–12 days), mites can also move within an inflorescence by walking to newly opened flowers. Once they mate, flower mites deposit eggs in the flower and the cycle repeats (Colwell 1985). Mite species (Acari: Mesostigmata: Ascidae) in the genera *Rhinoseius* Baker & Yunker, *Proctolaelaps* Berlese, *Tropicoseius* Baker & Yunker, and *Lasioseius* Berlese, have been collected from a variety of floral visitors including hummingbirds, sunbirds, bumblebees and butterflies (Baker & Yunker 1964; Lindquist & Evans 1965; Naeem, Dobkin & O'Connor 1985; Ryke 1964; Treat 1975). *Proctolaelaps* and *Lasioseius* have been recorded in more than 50 hummingbird species and over 100 plant species from approximately 20 families (Colwell 1985). However, *Rhinoseius* and *Tropicoseius* are the only genera whose species are known exclusively from hummingbirds or flowers visited by them (Colwell 1979, 1983; Dobkin 1985; Naskrecki & Colwell 1998).

The interaction between hummingbirds, flower mites and their host plants has been well studied (Colwell 1973, 1979, 1986; Dobkin 1984, 1985, 1987, 1990; Heyneman *et al.* 1991; Naskrecki & Colwell 1998). However, the effect of mites on the hummingbirds and their plants has not yet been explored thoroughly. Some investigations have suggested that nectar consumption by mites reduces the availability of nectar to hummingbirds and potentially reduces the reproductive success of the host plant (Paciorek *et al.* 1995). Colwell (1995) found that the flower mite *Proctolaelaps kirmsei* consumed 40% of the nectar secreted by *Hamelia patens* (Rubiaceae) flowers, suggesting an antagonistic role of the mites towards plants. The impact of pollen consumption by mites (Paciorek *et al.* 1995) and of their voracious exploitation of nectar from flowers of their host plants (Colwell 1995) must be evaluated in terms of mites as important potential competitors with hummingbirds, and of the reproductive success of the host plant. It is important to consider that mite densities in host plants can vary temporally and spatially, and may negatively affect (direct or indirectly) the plant–hummingbird interaction. Dobkin (1984, 1987, 1990) suggested that flower mites can provide compensatory benefits to their hosts by acting as secondary pollinators, but this has never been tested experimentally.

Organisms that produce negative effects on plants can drive many ecological and evolutionary processes in natural populations (Real 1996). Some studies have demonstrated that the action of these antagonistic organisms affects the population dynamics of their hosts as well as the community structure (Augspurger 1988; Alexander 1992; Dobson & May 1996; Garnett & Holmes 1996; Gilbert & Hubbell 1996; Lively 1996; Real 1996; Simms 1996). However, the effects of potential antagonists such as flower mites have not been sufficiently explored in the plant–hummingbird interaction. Here we evaluated the effects that hummingbird flower mites (*Tropicoseius*) have on nectar secretion and reproductive success (seed set) of the protandrous shrub *Moussonia deppeana* (Gesneriaceae).

Materials and methods

STUDY AREA

Field work was carried out from November 1997 through February 1998 in a remnant of cloud forest (55 ha), in the Parque Ecológico Francisco Xavier Clavijero near the city of Xalapa, Veracruz, México (19°30′ N, 96°57′ W; at 1280 m a.s.l.). Mean annual precipitation is 1500 mm and mean annual temperature is 18 °C. The climate is mild and humid throughout the year, with a dry, cold season from November to March (Williams-Linera 1997). Floristic details of the area are given by (Castillo-Campos 1991) and (Williams-Linera 1993).

STUDY SPECIES

Moussonia deppeana (Schlecht. & Cham.) Hanst. (Gesneriaceae) is an abundant, 1–3 m high sub-shrub in shaded areas of the forest remnants. Flowers with tubular, red corollas (corolla length, mean ± SE = 32·28 ± 2·07 mm; $n = 60$), are pollinated mainly by hummingbirds (Wiehler 1982). We observed Amethyst-throated Hummingbird (*Lampornis amethystinus*) visiting flowers of this plant and acting as a trapliner. *Moussonia deppeana* flowers have separate male and female phases (protandry) of diurnal anthesis and always last for 4 days. The male period of flowering lasts 2 days (staminate phase), followed by a 2-day female phase (pistillate phase) (Wiehler 1983; C. Lara, personal observation). Axillary inflorescences have pronounced peduncles with compound gesneriaceous cymes (Wiehler 1975). The flowering period lasts from November to February. Fruits are dry, bivalved capsules with loculicidal dehiscence (Wiehler 1975). Seeds are small and numerous. The undescribed hummingbird flower mites in *M. deppeana* are almost certainly of the genus *Tropicoseius* Baker & Yunker (Colwell 1979; Martínez-Burgoa 1998; R. K. Colwell, personal communication).

FIELD PROCEDURES

Flowering phenology

The flowering phenology was followed in detail in 20 plants tagged in October 1997. Five inflorescences per plant were randomly chosen to count bud and flower numbers and to determine the reproductive stage of the flowers in each inflorescence. Inflorescences were censused monthly throughout the flowering period (November 1997 to February 1998). Inter-plant

variation in the bud and flower production was tested using a two-way ANOVA (Zar 1984).

Effects of mites on nectar secretion

In November 1997 we randomly selected four buds about to open from each of 10 plants of *Moussonia deppeana* ($n = 40$ flowers), and tagged the buds with plastic rings. To measure the effect of mites on the nectar secretion we applied the following treatments: (1) mites and hummingbirds were excluded by applying Tanglefoot (sticky resin; The Tanglefoot Co., Grand Rapids, MI, USA) in each pedicel of 20 flowers, then flowers were bagged with mosquito-net bags; (2) only hummingbirds were excluded from a further 20 flowers bagged with mosquito-net bags (mites could move freely among flowers of the same inflorescence). Nectar secretion was measured the following day at 3 h intervals (0700, 1000, 1300, 1600 and 1900 h) following standard procedures (Kearns & Inouye 1993). Nectar volume per flower was estimated by using calibrated micropipettes (5 µl) and a ruler, and nectar concentration (brix) with a hand-refractometer (American Optical 10431). Nectar secretion was measured in the same flower for the 4 days the flower lasted. The same experiment was repeated in December ($n = 40$ flowers) and January ($n = 40$ flowers). Nectar secretion among plants with and without mites over the 4 days of the experiment was analysed using repeated-measures ANOVA (Zar 1984). In the model, the mite treatment (exclusion of mites and hummingbirds versus exclusion of hummingbirds only) was treated as a fixed effect; month was nested within treatment as a random effect; and flower age was the repeated factor. All main effects were tested over their appropriate interaction factor. A paired *t*-test was used to examine the differences between flower phases on nectar secretion. All statistical analyses were done using general linear modelling with STATVIEW and SUPERANOVA (Abacus Concepts, Inc. 1989, 1996).

Effects of mites on seed set

Five inflorescences were chosen randomly from each of 20 plants in January 1998. A bud about to open was chosen at random from each inflorescence ($n = 100$ flowers). Each plant was subjected to the following mite-exclusion treatments: (1) Tanglefoot was applied on each pedicel ($n = 20$ flowers); (2) Tanglefoot was applied on each pedicel and at the base of the inflorescence ($n = 20$); (3) Tanglefoot was applied only at the base of each inflorescence ($n = 20$); (4) no Tanglefoot was applied ($n = 20$). After Tanglefoot application all buds were bagged with mosquito-net bags to exclude hummingbirds and mites being dispersed by them. Mite exclusion allowed us to evaluate how different degrees of exclusion (Tanglefoot on the pedicel versus on the inflorescence base) affect seed set.

Once the flowers opened and reached the pistillate phase (early morning of the third day) we cross-pollinated them manually with a paint brush following Kearns & Inouye (1993) and a single individual as pollen donor. The remaining 20 flowers (treatment 5) were not pollinated manually but were bagged to exclude hummingbirds and mites being dispersed by them. Tanglefoot was not applied to these flowers so that the role of mites as pollinators (as a test of self-compatibility) could be determined. In 1999 we carried out an additional pollination control with plants in the same population to show that *M. deppeana* is not autogamous. Twenty buds were chosen randomly from inflorescences distributed among five plants. Each open flower was protected from mites and hummingbirds by applying Tanglefoot to the pedicel and with no manual pollination (as a test of autogamy; treatment 6). All flowers remained bagged until fruit maturation.

Fruit capsules from experimental flowers were later collected. Because the fruits of this species produce many seeds, direct counting is impractical. The weight of the collected fruits was correlated with total seed mass from a fruit (all seeds included) and then a linear regression calculated. To calibrate this, we measured the length of seeds of a sample from two fruit sizes (large fruits, mean $\pm$ SE = 0·197 $\pm$ 0·002 mg, $n = 30$; small fruits, mean $\pm$ SE = 0·142 $\pm$ 0·002 mg, $n = 30$) to determine the importance of seed length in the relationship. The interplant variation in fruit weight among treatments was tested using one-way ANOVA (Zar 1984).

Results

FLOWERING PHENOLOGY

Bud production per inflorescence started in November (mean $\pm$ SE = 2·81 $\pm$ 0·24 buds), peaked in December (13·8 $\pm$ 0·25 buds), then decreased in January (10·9 $\pm$ 0·14 buds) and February (3·55 $\pm$ 0·11 buds). Time differences were statistically significant ($F_{3,2796} = 539{\cdot}46$, $P < 0{\cdot}0001$). Few open flowers per inflorescence were present in November (2·55 $\pm$ 0·074 flowers). Numbers increased significantly as the flowering season progressed (December, 7·74 $\pm$ 0·15 flowers; January, 8·01 $\pm$ 0·13 flowers), diminishing in February (1·92 $\pm$ 0·88 flowers). Time differences were statistically significant ($F_{3,2796} = 766{\cdot}88$, $P < 0{\cdot}0001$).

The availability of each flower phase differed over the flowering season. Staminate flowers were more abundant than pistillate flowers (mean number of staminate flowers per inflorescence, 4·8 $\pm$ 0·24, $n = 400$; mean number of pistillate flowers, 2·3 $\pm$ 0·19, $n = 400$), and these differences were statistically significant through time ($F_{3,792} = 23{\cdot}67$, $P < 0{\cdot}0001$). However, *post hoc* contrasts showed significant differences in the number of pistillate and staminate flowers only in January (Fig. 1).

EFFECTS OF MITES ON NECTAR SECRETION

Mites had a significant effect on nectar secretion of *M. deppeana* flowers (Table 1). Over the 4 days of

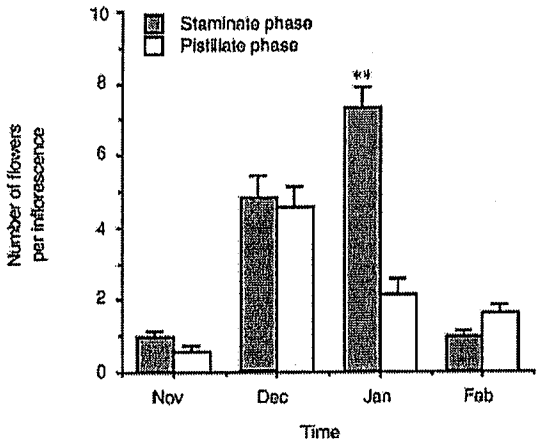

Fig. 1. Mean number of staminate and pistillate flowers per inflorescence (mean ± SE) in *Moussonia deppeana* over the 1997–99 flowering season. Note that in January staminate flowers are more abundant than pistillate flowers. **, $P < 0{\cdot}001$.

observation, significantly more nectar was secreted in flowers in the mite-exclusion treatment than in flowers with no mite exclusion (Table 2). The same results were observed over time, as shown in Fig. 2 (month as random effect; Table 1). However, mites consumed a greater percentage of the total nectar in December (Table 2). The proportion of nectar consumed by mites per flower was 50% in November, 56% in December, and 53% in January. *Post hoc* contrasts showed that significantly more nectar was secreted in November, independent of treatment (Fig. 2). As the experiment progressed, nectar secretion declined so that the effect of the repeated factor (flower age) was also significant in the overall model (Table 1). More nectar was secreted during the staminate phase (mean ± SE = $1{\cdot}76 \pm 0{\cdot}22$ µl) than in the pistillate phase ($1{\cdot}18 \pm 0{\cdot}17$ µl), and these differences were statistically significant, independent of time and treatment ($t = 2{\cdot}79$, d.f. = 11, $P < 0{\cdot}05$).

EFFECTS OF MITES ON SEED SET

Lengths of seeds from small (mean ± SE = $0{\cdot}497 \pm 0{\cdot}04$ mm, $n = 50$) and large fruits ($0{\cdot}503 \pm 0{\cdot}04$ mm, $n = 50$) were not significantly different ($F_{1,98} = 0{\cdot}76$, $P > 0{\cdot}05$). The linear regression of fruit weight on total seed mass was positive ($R^2 = 0{\cdot}92$, $F_{1,98} = 1138{\cdot}94$, $P < 0{\cdot}0001$). This means that seed number increases linearly with fruit weight. The exclusion of mites had no effect on seed production in the hand-pollinated treatments 1–4. Although fruit weight varied significantly among treatments ($F_{5,114} = 94{\cdot}76$, $P < 0{\cdot}0001$), treatments 5 and 6 explained the variation among treatments (Bonferroni–Dunn test, $P < 0{\cdot}0001$; Fig. 3). Only 15% of flowers that were protected from mites and hummingbirds and had no hand pollination (treatment 5) produced seeds. However, less seed was produced in these flowers than in flowers with mites and without hand pollination (Bonferroni–Dunn

Table 1. Repeated-measures ANOVA examining variation in nectar secretion among plants with and without mites over the 4 days of the experiment. Mite treatment (exclusion of mites and hummingbirds versus exclusion of hummingbirds only) was treated as a fixed effect; month nested within treatment as a random effect; and flower age as the repeated factor. Nectar secretion was examined as a function of treatment and calculated as the volume secreted at each 3 h interval over the 4 days. All main effects were tested over their appropriate interaction factor

Source	Sum of squares	d.f.	Mean square	*F*	*P*
Treatment	490·222	1	490·222	153·697	0·0001
Month	212·894	2	106·447	33·374	0·0001
Flower age	432·181	3	144·060	45·167	0·0001
Treatment × month	27·227	2	13·613	4·286	0·0146
Treatment × flower age	49·893	3	22·915	7·184	0·0001
Month × flower age	49·893	6	8·316	2·607	0·0170
Treatment × month × flower age	24·126	4	4·021	1·261	0·2742

Table 2. Effects of mites on nectar secretion (µl) of *Moussonia deppeana* flowers (mean ± SE) by month. $n = 20$ in each treatment

		Staminate phase		Pistillate phase	
Month	Treatment	Day 1	Day 2	Day 3	Day 4
November	Mites excluded	2·02 ± 0·14	3·50 ± 0·24	2·40 ± 0·14	2·04 ± 0·07
	Mites not excluded	1·01 ± 0·08	2·01 ± 0·17	1·24 ± 0·13	0·92 ± 0·11
December	Mites excluded	1·28 ± 0·09	2·68 ± 0·17	1·33 ± 0·07	0·92 ± 0·11
	Mites not excluded	1·00 ± 0·75	1·03 ± 0·73	1·05 ± 0·72	0·39 ± 0·04
January	Mites excluded	1·70 ± 0·13	2·45 ± 0·15	1·70 ± 0·10	1·12 ± 0·91
	Mites not excluded	1·35 ± 0·10	1·20 ± 0·07	0·69 ± 0·49	0·41 ± 0·57

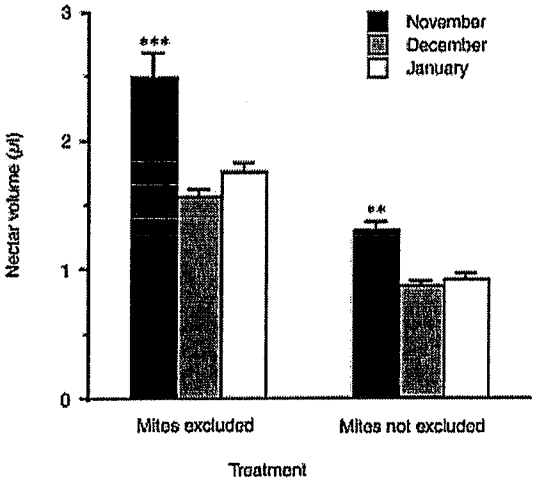

Fig. 2. Total effect of mites on the nectar secretion (mean ± SE) in *Moussonia deppeana*. **, $P < 0{\cdot}001$; ***, $P < 0{\cdot}0001$.

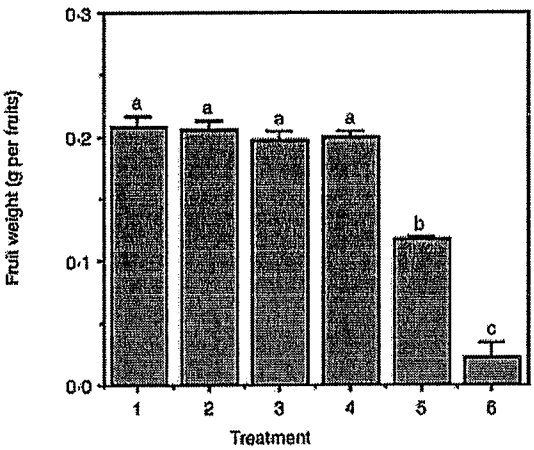

Fig. 3. The effect of mites on seed set (mean ± SE) in flowers subjected to the following mite-exclusion treatments: (1) Tanglefoot applied on each pedicel and manually pollinated ($n = 20$ flowers); (2) Tanglefoot applied on each pedicel and at the base of each inflorescence and manually pollinated ($n = 20$); (3) Tanglefoot applied only at the base of each inflorescence and manually pollinated ($n = 20$); (4) no Tanglefoot applied but manually pollinated ($n = 20$); (5) no manual pollination and no Tanglefoot ($n = 20$); (6) no manual pollination but Tanglefoot applied on each pedicel. All inflorescences were bagged for all treatments.

test, $P < 0{\cdot}0001$; Fig. 3). This suggests that mites act like secondary pollinators and that *M. deppeana* is a self-compatible, non-autogamous plant.

Discussion

At natural densities, flower mites significantly affect nectar secretion of *M. deppeana*. The magnitude of the effect suggests that *Tropicoseius* flower mites are important consumers of nectar and may be antagonistic to the plant–hummingbird interaction, as previously suggested by Colwell (1995). Hummingbird-pollinated plants in the humid tropics typically open one or two flowers daily (Colwell & Naeem 1994). On average, *M. deppeana* opens more flowers per inflorescence as the flowering period progresses, allowing mites to move freely among flowers within the same inflorescence. Also, the population of mites may become larger as the number of open flowers increases throughout the flowering season (Colwell & Naeem 1994). This would explain the variation in nectar consumption by mites as the season progressed. Mite numbers were not quantified directly in this study. However, an average of 16·5 mites per flower in November, 9·2 in December and 11·8 in January was estimated, based on data for the nectar consumption rate by adult mites (Colwell 1995) and on our data for nectar depletion in flowers with mites (Fig. 2).

Visitation patterns and foraging behaviour of hummingbirds can be affected directly by mite activities, particularly at the flowering peak of *M. deppeana*. A fitness cost to *M. deppeana* arising from consumption by mites may be shorter hummingbird visits per flower. Field studies suggest that hummingbirds visit flowers only a few times, therefore reducing the probability of pollen removal and transfer during each visit (Cruden, Hermann & Peterson 1983; Rathcke 1992; Zimmerman 1988). However, most studies have not considered how the gender of the flower influences pollinator behaviour. In protandrous *M. deppeana*, hummingbirds are expected to prefer flowers offering a richer nectar reward (staminate phase). Staminate flowers typically secrete more nectar than pistillate flowers (Devlin & Stephenson 1985; this study), possibly as a result of intrasexual selection (Bawa 1980; Bullock & Bawa 1981). In addition, the production of more of staminate flowers during the flowering season may increase pollen donation. This is consistent with predictions generated by the male-competition component of sexual selection theory. Devlin & Stephenson (1985) showed that hummingbirds are sensitive to variations in nectar reward. Hummingbirds adjust their foraging behaviour by visiting staminate flowers of protandrous *Lobelia cardinalis* from the middle to the top of inflorescences that mature acropetally. It is necessary to determine whether the durations of staminate and pistillate phases, and the asymmetries in their attractiveness and temporal availabilities, are controlled by pollinator foraging in *M. deppeana*, as documented in other protandrous plants (Devlin & Stephenson 1985; Koptur *et al.* 1990; Richardson & Stephenson 1989).

Another fitness cost among plants subjected to a constant removal of nectar is the negative effect on their total energy budget (Pleasants & Chaplin 1983; Southwick 1984). Pyke (1991) demonstrated that artificially removing nectar of hand-pollinated flowers of *Blandfordia nobilis* (Liliaceae) reduced seed number. This is contradicted by the fact that *M. deppeana* flowers subjected to nectar consumption by mites produced the same number of seeds as flowers from which nectar was not removed by mites.

Our data show for the first time that mites may be significant pollen vectors within inflorescences; flowers containing mites and that were not hand-pollinated produced only half as many seeds as cross-pollinated flowers. This suggests that flowers of *M. deppeana* are self-compatible, as are other protandrous plants (Devlin & Stephenson 1985, 1987; Richardson & Stephenson 1989), and that floral mites may aid in selfing.

Flower mites that consume pollen may impose a male fitness cost to the host plant, reducing the availability of pollen for transfer by hummingbirds from staminate to pistillate flowers. However, a decrease in nectar availability per flower may force hummingbirds to visit more *M. deppeana* flowers, increasing plant fitness through more frequent outcrossing and a wider distribution of pollen (Colwell 1995; McDade & Kinsman 1980). These alternatives require explicit testing.

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