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Effects of nectar theft by flower mites on hummingbird behavior and the reproductive success of their host plant, *Moussonia deppeana* (Gesneriaceae)

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Hummingbird flower mites are transported in the nares of hummingbirds and may compete with them by "robbing" nectar secreted by the host plants. We have shown that *Tropicoseius* sp. flower mites consume almost half the nectar secreted by the long-lived, protandrous flowers of *Moussonia deppeana* (Gesneriaceae) pollinated by *Lampornis amethystinus* (Trochilidae). In this paper, we ask whether mimicking nectar consumption of flower mites alters some aspects of hummingbird foraging patterns, and, if so, how this affects host plant seed production. We observed hummingbirds foraging on (a) plants in which nectar was removed from the flowers and then filled with a sugar solution to half the volume of nectar simulating nectar consumption by flower mites, and (b) plants where nectar was removed and then filled with the sugar solution up to normal nectar volumes. Flower mites were excluded from both groups of plants to control for mite activity. Hummingbirds made fewer but longer visits to plants and revisited more the flowers with nectar removal than those without the treatment. We then conducted a pollination experiment on pistillate flowers using a stuffed *L. amethystinus* hummingbird to evaluate the effect of pollination intensity (number of bill insertions into one flower) on seed production. Flowers with more insertions produced significantly more seeds than those flowers that received fewer insertions. We conclude that the simulation of nectar consumption by hummingbird flower mites can influence the behavior of the pollinator, and this may positively affect seed production.

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Hummingbirds can act as mutualists with plants by transporting pollen grains among flowers (Stiles 1981, Feinsinger 1987), but they may also act as antagonists by carrying flower mites (Colwell 1973, Lara and Ornelas 2001a) and other infectious organisms to new host plants (Lara 2001). The antagonistic role of hummingbirds as vectors of plant pathogens contrasts with their more widely known role as nectar robbers (Colwell et al. 1974, McDade and Kinsman 1980, Ornelas 1994, Navarro 1999, Lara and Ornelas 2001b) because the transmission of such pathogens by floral visitors searching for nectar rewards may end up, besides depletion of nectar rewards (Colwell 1995, Lara and Ornelas 2001a), in sexually transmitted diseases (Jennersten 1983, Roy 1993, 1994, Lara 2001) and pollen consumption (Paciorek et al. 1995). Therefore, the supposedly mutually beneficial interaction between plants and hummingbirds can be defeated by the transmission of antagonistic organisms along with pollen grains.

Nectar of hummingbird-pollinated flowers is regularly robbed by a variety of nonpollinating, "illegitimate" visitors such as bees, ants, passerine species, and hummingbirds (Colwell et al. 1974, McDade and Kinsman 1980, Roubik 1982, Inouye 1983, Ornelas

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1994, Arizmendi et al. 1996, Traveset et al. 1998, Irwin and Brody 1999, Navarro 1999, Lara and Ornelas 2001b). The most common nectar "thieves" in many hummingbird flowers are hummingbird flower mites (Acari: Mesostigmata: Ascidae) (Lara and Ornelas 2001a). These mites feed on pollen and nectar from flowers of a great variety of plant species exclusively pollinated by hummingbirds (Colwell 1973, 1979, Dobkin 1984, 1985, 1987, Heyneman et al. 1991, Naskrecki and Colwell 1998). To disperse to newly opened flowers, mites typically climb onto the bill of a visiting hummingbird and ride in the bird's nares to another inflorescence of the proper host plant species (Colwell 1985, Dobkin 1990), so that the relationship of flower mites with hummingbird hosts is strictly phoretic (Colwell 1973, 1979, 1985, Naeem et al. 1985, Dobkin 1990). However, the consequences for the plants and their pollinators of hummingbird flower mite transmission among host plants have not yet been explored thoroughly. Two studies have documented that nectar consumption by mites reduces nectar availability to hummingbirds (Colwell 1995, Lara and Ornelas 2001a) and potentially reduces the reproductive success of the host plant (Paciorek et al. 1995, Lara and Ornelas 2001a). Lara and Ornelas (2001a) showed that nectar availability in hummingbird-pollinated flowers of *Moussonia deppeana* (Gesneriaceae) is reduced up to 50% in the presence of hummingbird flower mites (*Tropicoseius* sp. nov.) but seed production was not reduced significantly.

Hummingbird foraging is influenced by flower color (Stiles 1976), flower morphology (Montgomerie 1984, Temeles 1996), inflorescence design (Hainsworth et al. 1983, Gass and Sutherland 1985), and nectar characteristics (Hainsworth and Wolf 1976, Stiles 1976, Gass and Roberts 1992, Roberts 1992, Navarro 1999). Lara and Ornelas (2001a) suggested that the action of flower mites might influence hummingbird foraging. To our knowledge, this has not yet been investigated. Here, we use an experimental and observational approach to examine whether amethyst-throated hummingbird (*Lampornis amethystinus*) respond behaviorally (the number of flowers visited per foraging bout, number of probes per flower, and flower-handling time) to changes in nectar availability of *M. deppeana* flowers simulating the presence of flower mites. Then, we evaluate whether these behavioral responses influence host-plant seed production by indirectly affecting pollen transmission.

Methods

Study site

The fieldwork was carried out in a remnant of cloud forest (55 ha), in the Parque Ecológico Francisco Xavier Clavijero near Xalapa, Veracruz, Mexico (19° 30′ N, 96° 57′ W; at 1280 m a.s.l.). Floristic details and a full description of the study area are given in Castillo-Campos (1991), Williams-Linera (1993, 1997), and Lara and Ornelas (2001a).

Study species

Moussonia deppeana (Schlecht. and Cham.) Hanst. (Gesneriaceae) is an abundant, 1–3 m tall sub-shrub distributed in shaded areas of forests from southern Mexico to Honduras (Wiehler 1982). This species flowers from November to February. The axillary inflorescences have pronounced peduncles with compound cymes of four flowers each (Wiehler 1975). On average, eight flowers are open on a plant at one time (Lara and Ornelas 2001a). The orange-red, tubular flowers (corolla length, mean $\pm$ SE = 32.28 $\pm$ 2.07 mm, $N = 60$; Lara and Ornelas 2001a) have separate male and female phases (protandry) of diurnal anthesis and last invariably four days. Each flower passes through a two-day male period (staminate phase), followed by a two-day female phase (pistillate phase). Self-pollination is not possible within a flower (Lara and Ornelas 2001a); however, there are many flowers open on plants at once and hummingbirds visiting multiple flowers on a plant and flower mites moving as pedestrians among flowers on a plant may result in geitonogamy (within-plant pollen transfer). We do not know how geitonogamy influences seed production in this plant after hummingbird visitation. However, by carrying pollen grains among flowers within inflorescences, flower mites promote selfing but reduce seed production to 50% (Lara and Ornelas 2001a). Staminate phase flowers produce on average more nectar per day (1.65 μL/flower) than pistillate phase flowers (1.27 μL/flower) (Lara and Ornelas 2001a), both with a 19–20% sugar concentration (C. Lara unpubl.). Undescribed hummingbird flower mites of the genus *Tropicoseius* Baker and Yunker (Colwell 1979) can infect flowers heavily (Lara and Ornelas 2001a). Fruits are dry, bivalved capsules with loculicidal dehiscence (Wiehler 1975). Seeds are small (seed length, mean $\pm$ SE = 0.5 $\pm$ 0.003 mm, $N = 100$; C. Lara unpubl.) and numerous (451.4 $\pm$ 0.7 seeds per capsule, $N = 60$; C. Lara unpubl.).

Lampornis amethystinus Swainson, is a traplining hummingbird, endemic to the highlands of Central Mexico and Middle America. It is distributed from southern Nayarit and southern Tamaulipas States to El Salvador and Central Honduras (Howell and Webb 1995). In our study site, amethyst-throated hummingbirds feed from flowers of *Palicourea padifolia* (Rubiaceae), *Lobelia laxiflora* (Lobeliaceae) and bromeliads (Contreras and Ornelas 1999, Lara and Ornelas 2001a, C. Lara pers. obs.). During winter, these hummingbirds pollinate and mostly rely on flowers of *M. deppeana* for nectar (Lara and Ornelas 2001a). In our study site,

there are ca 300 individuals of *M. deppeana*. If hummingbirds find *M. deppeana* unrewarding, they can switch to other alternative hosts to foraging. *Lobelia laxiflora* (Lobeliaceae) flowers during the same period (November–March), and it is visited and pollinated by *L. amethystinus* and *Amazilia cyanocephala*; however, few individuals are found in our study site. *Tillandsia deppeana* (Bromeliaceae) also flowers during the same period (January–May), but it is visited and pollinated by other hummingbird species (*Campylopterus curvipennis*, *A. yucatanensis*, and *A. cyanocephala*), bees, and butterflies (C. Lara and J. F. Ornelas unpubl.). We believe *M. deppeana* is the most preferred host for this hummingbird species.

Nectar availability and foraging

The nectar volume encountered by hummingbirds in *M. deppeana* can be significantly reduced by prior consumption by flower mites. This may strongly influence subsequent foraging responses of legitimate pollinators. Possible behavioral responses of pollinators correlated with nectar consumption by flower mites include modifications in the number of flowers visited, time spent per flower, number of probes per flowers, and other behavioral adjustments such as the distance they need to travel to fill their energetic demands. We hypothesized that the capabilities of hummingbird flower mites to remove nectar may strongly influence the subsequent behavior of the legitimate pollinators to meet their short-term energy demands. Experimental manipulation of nectar consumption by flower mites is impractical because flower mites cannot be easily handled. Instead, a mite-exclusion experiment was conducted in November and December 1998. We excluded flower mites from flowers and then mimicked the ecological conditions by artificially reducing nectar volumes to half as flower mites do in nature, and compared the responses of pollinators with those that visited flowers with full nectar crops. By excluding the mites and experimentally manipulating nectar volume, we could test the direct effects of nectar volume manipulations on hummingbird behavior without any counfounding direct or indirect effects of mites.

We excluded flower mites from 10 randomly selected flowering plants by applying tanglefoot (The Tanglefoot Co.) to each pedicel of buds and bagging them with bridal netting. We then extracted the nectar accumulated by 0800 from eight flowers (mean number of open flowers on a plant) in one focal plant (four of each flower phase) using 5-μL callibrated micropipettes and replaced it with a 20% (by mass) sugar solution (Lara and Ornelas 2001b) of half the volume accumulated by the time of the manipulation (staminate phase = 3.8 μL/flower, pistillate phase = 2.1 μL/flower), and according to the reported nectar volumes for this species from 0800 to 1000 (Lara and Ornelas 2001a). This procedure allowed us to simulate the action of flower mites before observing the first hummingbird arrival. We then recorded the following information: (1) number of flowers visited, (2) flower phase (staminate vs pistillate), (3) duration of each visit per flower (seconds), and (4) number of probes to each flower visited. Duration of visits was measured using a stopwatch to record time on each flower. Once the hummingbird left the focal plant, we refilled the flowers with the same volume and sugar solution. This procedure was performed before the next hummingbird visit. Consequently, the observed hummingbird behavior would represent responses to nectar depletion by flower mites, rather than generalized responses to nectar removal during a preceding hummingbird visit, or removal by other species of nectar robbers. That is, our nectar removal design should affect the behavior of the first hummingbird to visit an inflorescence. Once that visit has occurred, subsequent birds encountered the same experimental conditions. We continued this type of manipulation on the same plant until noon, except that volumes of sugar solution were adjusted after 1000 to what a hummingbird would find from 1000 to 1200 in flowers with no prior visits (staminate phase = 3.2 μL/flower, pistillate phase = 1.9 μL/flower). Typically, we gathered data for 1 to 9 (5 as average) hummingbird visits per plant per day. The following day we repeated the same procedure but with a plant from our control group, and the third day with a plant from the experimental group, and so on until we observed all 10 plants. We applied the nectar-removal treatment on five plants ($N = 40$ flowers). The same protocol was used on five additional plants that served as controls; for each focal plant we removed the nectar from eight flowers ($N = 40$ flowers), as described above, and then refilled the flowers with the sugar solution corresponding to the average nectar volume at the time of the observation, mimicking the absence of flower mites, and controlling previous hummingbird visitation. Once we finished our first run of observations, we repeated the procedure starting with the first plant, so each plant was used twice. Our observations on the same plant were considered as independent since we used different flowers each time and these were conducted ten days apart. The remaining open flowers were removed from each of the plants the day of observation to minimize differences among plants in conspicuosness and attractiveness to pollinators.

ANOVAs with a nested design were used to evaluate the effects of nectar removal and flower phase on the number of flowers visited per foraging bout and number of probes to individual flowers of *M. deppeana*. Between-plant variation was assessed with nectar treatment as the main factor and plants nested within treatment. Within-plant variation was also included in the model with flower phase as a fixed factor and

number of flowers and number of probes as the dependent variables. Along with the main effects, flower phase × nectar treatment, and flower phase × plants (nectar treatment) interactions were included in the model. Number of flowers visited per foraging bout and number of probes were square root transformed before the analysis to normalize data (Zar 1999), but untransformed data are reported. Numbers of flowers visited per foraging bout and numbers of probes per flower are likely intercorrelated response variables. Therefore, we first did a nested MANOVA incorporating these two response variables. Using a MANOVA followed by univariate ANOVAs, as described above, will reduce the probability of inflating the Type I error rate.

Because flower-handling time varied among flowers, it was necessary to control for these differences in the analysis, as handling time might affect the number of flowers visited per plant and the number of probes to a given flower. We analyzed the relationship between number of flowers visited and number of probes to flowers of *M. deppeana* and $\log_{10}$ transformed flower-handling time per flower using ANCOVA (Zar 1999) with handling time (seconds) as the covariate. In the model, nectar removal treatment was a fixed factor, flower-handling time was the covariate, and number of flowers visited and number of probes served as the dependent variables. Because we used repeatedly the same plants (between-plant variation), the plant factor was nested within treatment. Along with the main effects (treatment and flower-handling time), flower handling time × nectar removal treatment and flower handling time × plants (nectar removal treatment) interactions were also included in the model. Data were square root or $\log_{10}$ transformed as needed before analysis.

Pollination intensity and seed production

We investigated how nectar loss by flower mites affects hummingbird behavior, and, consequently, how hummingbird responses affect the female component of plant fitness. A pollination experiment was conducted in January and February 2000 to evaluate the effect of number of probes on number of seeds produced by flowers of *M. deppeana*. Twenty flowering plants were selected randomly along the main trail of our study site. From each plant, we chose five buds that were ready to open and excluded flower mites as explained above. Once they opened, flowers were bagged with bridal netting for two days (staminate phase). Hummingbird pollination was conducted on 10 plants with 3-d flowers ($N = 50$) and 10 additional plants with 4-d flowers ($N = 50$) (flower age) by using a stuffed *L. amethystinus* hummingbird as pollen vector. Pollinations were accomplished by probing the hummingbird's bill into the corolla of a donor staminate flower with dehisced anthers and then into the corolla of a receptive recipient (pistillate phase) flower as described by Gronemeyer et al. (1997). We mimicked hummingbird behavior in flowers as closely as possible. Pollen loads carried by the stuffed bird were not representative of those carried by live birds because pollen from a specific donor flower may persist on hummingbirds for many flowers (Feinsinger and Busby 1987), so that a bird carries pollen from many flowers. Consequently, the quantity and quality (single versus mixed genotypes) of pollen were different from what is typical under natural conditions. Instead, we used staminate flowers as pollen donors only from one plant to minimize possible genetic effects and to simplify our experimental design.

We charged the bird with the pollen from only one flower before probing a female-phase flower. Female-phase flowers received from one to five bill insertions each preceded by individual probes to staminate flowers depending on the assigned pollination intensity treatment. Probe treatments were nested within plants (i.e., each plant had flowers with each of the treatments) as a way to control for both maternal and paternal plant effects. Because most pollen adhered to the hummingbird's forehead, we could remove all remaining pollen grains with a paintbrush before performing the next cross. After crosses were performed, flowers remained bagged for three weeks until fruit ripening. Given the abundant seeds per fruit in this species, we used total seed weight as an estimate of female reproductive success as shown by Lara and Ornelas (2001a). Variation in seed production (total seed weight) between groups of flowers (flower age) as a function of pollination intensity was assessed with a two-way ANOVA (Zar 1999). Total seed weight was $\log_{10}$ transformed before analysis.

All statistical analyses were run using General Linear Modeling with StatView and SuperANOVA (Abacus Concepts 1989, 1996).

Results

Nectar availability and foraging

Plants with half the normal nectar received fewer hummingbird visits (mean $\pm$ SE $= 5.2 \pm 0.38$, $N = 10$) than plants without nectar removal (mean $\pm$ SE $= 6.5 \pm 0.72$, $N = 10$), but this difference was not significant (one-way ANOVA, $F_{1,10} = 2.53$, $P > 0.05$). However, mimicking nectar consumption of flower mites in *M. deppeana* flowers altered some aspects of *L. amethystinus* foraging.

Number of flowers visited per bout and number of probes per flower were positively correlated ($r^2 = 0.56$). Therefore, we first run a nested MANOVA incorporating these two response variables to explicitly account for the correlation among the dependent variables. The

overall MANOVA tests indicated that the changes in foraging behavior due to treatment and flower phase were significant at the 0.0001 significance level. Treatment effect on the two dependent variables (number of flowers visited per foraging bout and number of probes per flower) was significant (Wilks' lambda, $F_{2,86} = 175$, $P = 0.0001$). Flower phase had also a significant effect on the two dependent variables (Wilks' lambda, $F_{2,86} = 10.4$, $P = 0.0001$). In contrast, the plant (treatment) effect and flower phase × treatment and flower phase × plant (treatment) interactions were not significant at the 0.05 significance levels. Because the MANOVA was significant, we then followed with the univariate ANOVAs.

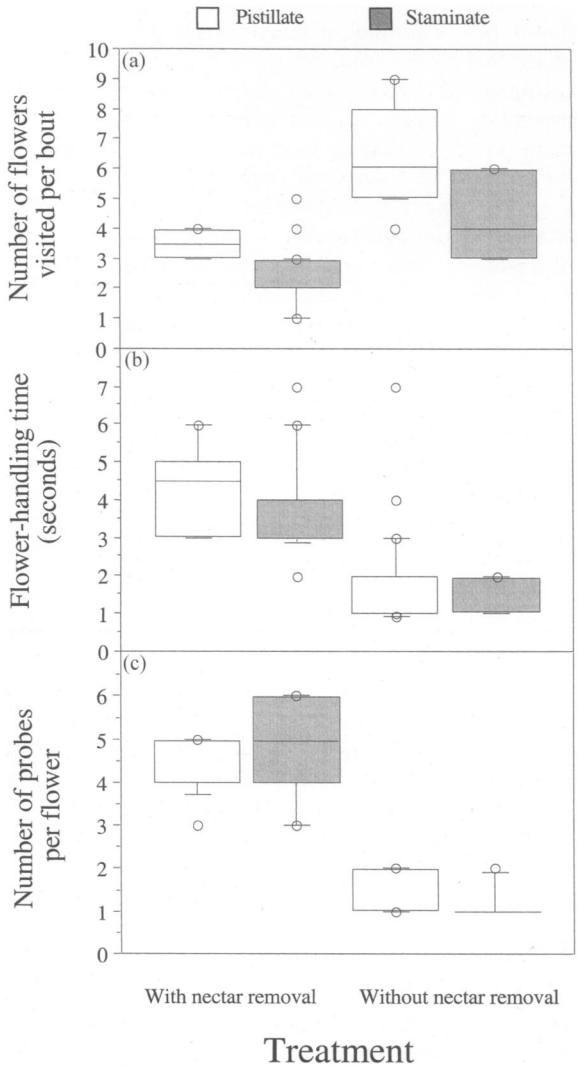

Fig. 1. Foraging behavior of *Lampornis amethystinus* on plants of *Moussonia deppeana* with and without nectar removal measured as (a) number of flowers visited per foraging bout, (b) flower-handling time, and (c) number of probes per flower. Box plots show the 10th, 25th, 50th (median), 75th, and 90th percentiles. Values above the 90th and below the 10th percentile are plotted as open circles.

Hummingbirds visited fewer flowers per foraging bout on plants with reduced nectar than the control plants ($F_{1,87} = 59.1$, $P < 0.0001$; Fig. 1), and female-phase flowers were more visited than male-phase flowers, independently of nectar removal treatment ($F_{1,87} = 19.9$, $P < 0.0001$). None of the interactions were significant (Table 1). Hummingbirds visited flowers with nectar removal significantly longer than the control flowers, independently of flower phase (Fig. 1), but the number of flowers visited by *L. amethystinus* did not vary with handling time (Table 2). The handling time × treatment interactions were not significant, so we removed them from the model. Once we did this, nectar removal treatment was significant ($F_{1,96} = 131$, $P < 0.0001$). The non-significant P-value for flower-handling time ($F_{1,96} = 2.31$, $P = 0.13$) indicates that this variable was not useful in predicting hummingbird behavior. Differences in hummingbird behavior may depend on the visitation sequence of staminate and pistillate flowers within a bout because of the differences in nectar production between phases. Therefore, we explored this further to see whether the occurrence of more visits to a given plant was the result of first visiting a less-rewarding pistillate flower. We found that hummingbirds that started a foraging bout with a pistillate flower visited more flowers (6.3 ± 0.2, $N = 59$) than those that started with a staminate flower (2.8 ± 0.2, $N = 58$), and this difference was statistically significant (one-way ANOVA, $F_{1,115} = 160$, $P < 0.0001$). Accordingly, hummingbirds spent significantly less time per flower if they started with a pistillate flower (2.27 ± 0.15) than they did with a staminate flower (3.62 ± 0.19; one-way ANOVA, $F_{1,115} = 30.6$, $P < 0.0001$), and made fewer probes to individual flowers (1.5 ± 0.1) than they did if they started with staminate flowers (4.0 ± 0.2; one-way ANOVA, $F_{1,115} = 95.5$, $P < 0.0001$).

Flowers with half the normal volume received more probes by hummingbirds than the control flowers ($F_{1,87} = 302$, $P < 0.0001$), independently of flower phase ($F_{1,87} = 0.82$, $P = 0.36$; Fig. 1). Again, none of the interactions were significant (Table 1), and the number of probes did not covary with handling time (Table 2). Nectar removal treatment was significant ($F_{1,96} = 305$, $P < 0.0001$) after removing the non-significant handling time × treatment interactions from the model (Table 2). Non-significant results for flower-handling time ($F_{1,96} = 0.003$, $P = 0.98$) also indicate that this variable was not useful in predicting hummingbird behavior. However, differences in nectar availability among experimental flowers could explain the observed differences in probing behavior. We explored this further and found that hummingbirds visited the same number of flowers on plants observed from 0800 to 1000 (mean ± SE = 4.8 ± 0.3) and plants observed from 1000 to 1200 (mean ± SE = 4.8 ± 0.3; one-way ANOVA, $F_{1,115} =$

Table 1. ANOVA results for hummingbird foraging in (a) the number of flowers visited per bout and (b) number of probes per flower by *Lampornis amethystinus* on flowers of *Moussonia deppeana* with and without nectar removal.

Source of variation	df	MS	*F*	*P*
a)				
Between-plant variation				
Treatment	1	4.432	59.143	0.0001
Plant (Treatment)	18	0.118	1.578	0.0838
Within-plant variation				
Flower phase	1	1.493	19.926	0.0001
Flower phase × Treatment	1	0.017	0.230	0.6328
Flower phase × Plant (Treatment)	8	0.010	0.131	0.9977
Residual	87	0.075		
b)				
Between-plant variation				
Treatment	1	12.203	301.584	0.0001
Plant (Treatment)	18	0.060	1.494	0.1116
Within-plant variation				
Flower phase	1	0.033	0.823	0.3669
Flower phase × Treatment	1	0.001	0.013	0.9083
Flower phase × Plant (Treatment)	8	0.044	1.094	0.3749
Residual	87	0.040		

Table 2. ANCOVA results for the regression of (a) mean number of flowers visited per bout and (b) mean number of probes per flower by *Lampornis amethystinus* against flower-handling time on flowers of *Moussonia deppeana* with and without nectar removal.

Source of variation	df	MS	*F*	*P*
a)				
Treatment	1	1.786	23.160	0.0001
Plant (Treatment)	18	0.201	2.613	0.0019
Flower handling time	1	0.419	5.430	0.0224
Flower handling time × Treatment	1	0.227	2.940	0.0904
Flower handling time × Plant (Treatment)	18	0.111	1.445	0.1354
Residual	77	0.077		
b)				
Treatment	1	0.388	9.215	0.0033
Plant (Treatment)	18	0.034	0.810	0.6834
Flower handling time	1	0.000	0.007	0.9345
Flower handling time × Treatment	1	0.052	1.239	0.2691
Flower handling time × Plant (Treatment)	18	0.038	0.898	0.5826
Residual	77	0.042		

1.11, $P = 0.29$). Nonetheless, the number of probes per flower (and flower-handling time) significantly increased on plants visited during the second observation period (number of probes per flower, $F_{1,115} = 6.16$, $P = 0.014$; flower-handling time, $F_{1,115} = 4.49$, $P = 0.036$). Hummingbirds made 2.3 ± 0.2 probes per flower on plants observed from 0800 to 1000 and 3.1 ± 0.2 from 1000 to 1200; as a consequence, flower-handling time was higher on the latter group of flowers (2.67 ± 0.19 and 3.19 ± 0.19 s, respectively).

Pollination intensity and seed production

Results of pollination with the stuffed hummingbird showed that seed production on *M. deppeana* increases with the number of probes to individual flowers ($F_{4,90} = 66.1$, $P < 0.0001$), but seed mass did not vary with flower age ($F_{1,90} = 0.17$, $P = 0.67$). The interaction between number of probes and flower age was not significant ($F_{4,90} = 1.27$, $P = 0.28$). Post-hoc mean comparisons (Games-Howell post-hoc procedure) showed that flowers with more bill insertions (≥ 3) set significantly more seeds ($P < 0.0001$) than those with fewer insertions (≤ 2) (Fig. 2).

Discussion

Maloof and Inouye (2000) summarized the behavioral responses of pollinators caused by nectar robbers. Such responses may influence plant fitness and can have substantial ecological consequences (Miller and Travis 1996). Hummingbird flower mites may influence plant fitness directly by aiding in selfing (Lara and Ornelas 2001a; see Methods) and indirectly by changing the behavior of the legitimate pollinator. Here, we show that the capabilities of hummingbird flower mites to

remove nectar may strongly influence the subsequent behavior of the legitimate pollinators.

Hummingbird responses to reduced nectar volumes

It has been shown that pollinators diminish the frequency and the duration of visits to flowers with less nectar, and that these changes in behavior negatively affect plant fitness (Schmid-Hempel 1985, Thomson 1988, Irwin and Brody 1999, 2000, Plowright et al. 1999, Robertson et al. 1999). In our study, hummingbirds reduced the number of flowers visited per foraging bout under diminished conditions of nectar volume. This suggests that *Tropicoseius* flower mites may play a negative role on the plant–hummingbird interaction by altering the behavior of the main pollinator as previously suggested (Colwell 1995, Paciorek et al. 1995, Lara and Ornelas 2001a). Female-phase flowers were more visited than male-phase flowers. This result was unexpected given that less nectar is produced during the female phase (Lara and Ornelas 2001a). Differences in hummingbird behavior may depend on the visitation sequence of staminate and pistillate flowers within a bout. We found that the outcome of the first visit to a flower influences subsequent hummingbird decisions to maximizing nectar extraction. However, hummingbirds spent more time on flowers with nectar removal than they did on the control flowers, independently of flower phase (Fig. 1), and flower handling time was not useful in predicting hummingbird behavior. Therefore, we interpreted the observed differences among hummingbirds as responses to differences among flowers in nectar availability.

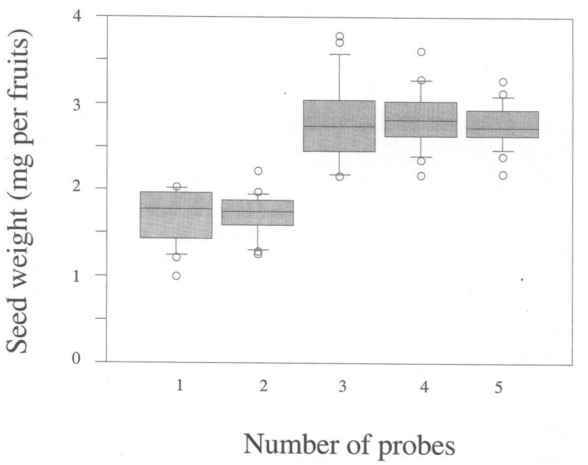

Fig. 2. Effect of pollination intensity measured as number of probes to pistillate flowers of *M. deppeana* on seed production. Box plots show the 10th, 25th, 50th (median), 75th, and 90th percentiles. Values above the 90th and below the 10th percentile are plotted as open circles.

Flowers with half the normal volume received more probes by hummingbirds than the control flowers, independently of flower phase. This was also an unexpected result. The number of probes did not covary with handling time indicating that this variable was not useful in predicting this behavior. Differences in nectar availability during the two periods of observation might partially explain this result. Hummingbirds visited both groups of plants with the same frequency; however, the number of probes per flower (and flower-handling time) significantly increased on plants visited during the second period of observation. Although our experiment was not designed to tease apart this factor, nectar variation among flowers may increase flower revisitation (Heinrich 1979, Zimmerman 1988). An alternative, non-mutually exclusive explanation for the unusual increase in the number of probes to the same flower after encountering low-nectar flowers is that hummingbirds stimulate further nectar secretion by increasing the number of probes. This might be something important to test in the future.

Nectar volumes were replenished after each hummingbird foraging bout. There is a chance that hummingbirds might be able to figure out that we were filling the flowers with "nectar" so that our plants and flowers were visited much more than usual. In the Rocky Mountains, R. E. Irwin (pers. comm.) did an experiment where she replenished nectar volumes after broad-tailed hummingbird (*Selasphorus platycercus*) visits and found that the birds would wait for her to replenish the volumes and then would fly back to the rewarding plants for more nectar. We believe this is unlikely for amethyst-throated hummingbird visits because (1) plants had natural levels of hummingbird visitation (3.1 ± 0.5 flowers per foraging bout; 1.9 ± 0.2 probes per flower; C. Lara and J. F. Ornelas unpubl.; see Fig. 1), and (2) we observed each of them on separate days minimizing the possibility of hummingbirds learning and memorizing our experimental protocol.

Among-flower variation in nectar volume may increase or reduce the number of visits to the plant (Feinsinger et al. 1985), but this is not independent from the pollinator's ability to discriminate against flowers with a low nectar volume (Hainsworth et al. 1983, Montgomerie 1984, Gass and Sutherland 1985, Real and Caraco 1986, Rathcke 1992). We have shown that hummingbirds respond to changes in nectar availability of flowers where nectar consumption by hummingbird flower mites was mimicked; however, whether these birds can discriminate against those flowers heavily infected with flower mites awaits to be investigated. Hummingbirds can determine the nectar status of flowers of some species visually prior to visiting (Gass and Montgomerie 1981) and discriminate against robbed flowers (Irwin and Brody 1998); however, our data show that hummingbirds do not identify

plants with nectar removal before visiting them. This is not surprising given that many researchers have found that birds must test flowers or plants before knowing their reward status. Yet, it is perplexing why birds keep revisiting flowers in the low-nectar treatment. One possible explanation for this result is that it is less energetically costly to revisit flowers on low-nectar plants than flying to a new plant that may have even lower nectar rewards. Further research is needed on plant strategies of scheduling nectar presentation. This can give some light on how hummingbird behavior (i.e., probing intensity) influences nectar production and pollen and mite transmission, and, as a consequence, the male and female components of plant reproductive fitness.

Effects of mites on flower reproduction

Nectar volume variation among flowers has been used to test ideas about hummingbird foraging behavior (e.g., Feinsinger 1978, 1983); however, the interplay between nectar production patterns, pollinator behavior, and host plant reproductive success has been rarely examined (Rathcke 1992). We found that the female reproductive success of *M. deppeana* increased with increasing pollination intensity, suggesting pollen limitation. Our pollination methodology ignored the whole-plant context of plant mating. In particular, the actual fitness consequences of low nectar availability in individual flowers that depend on pollen export and import from the affected flowers, but also on the overall attractiveness of the entire plant and the tendency for pollinator movement among flowers on the plant. By having plants with the same number of flowers in each reproductive phase, we minimized possible differences in the overall attractiveness of the entire plant.

Here, we were only interested in the female fitness consequences of pollen import due to low nectar availability in pistillate flowers. Nectar variation among flowers and territorial behavior may increase flower revisitation (Heinrich 1979, Zimmerman 1988), but restrict hummingbird movements among flowers. A reduction in the foraging area may limit pollen transfer (Levin and Kerster 1969, Zimmerman 1988), and this can be detrimental to male fitness component of plants (Price and Waser 1979, 1982, Waser and Price 1983). An increase in flower revisitation to more-rewarding staminate flowers surely ends up in increasing pollen export. In contrast, flower revisitation to pistillate flowers should maximize pollen import at later hours. We know that plant fitness depends on both pollen export and import from the affected flowers, but an increase in flower revisitation for pistillate flowers at later hours may represent an advantage if they receive pollen loads with more mixed genotypes. As stated, we do not know how geitonogamy influences seed production in this plant after hummingbird visitation, but because the plant has been shown to be self-compatible (Lara and Ornelas 2001a), inbreeding depression is suspected. We know, however, that flower mites can promote geitonogamous crosses (within-plant pollen transfer) that end up in fewer seeds compared with those produced after xenogamous crosses (Lara and Ornelas 2001a). Further experimentation is needed to determine its potential ultimate effects on plant reproductive success by measuring both pollinator and mite behavior, and seed production. In addition, further evaluation of the male component of plant fitness should consider the possible detrimental effect of pollen consumption by flower mites (Paciorek et al. 1995).

Lastly, nectar removal can be energetically costly to some plants (Pleasants and Chaplin 1983, Southwick 1984, Navarro 1999). Pyke (1991) showed that seed production in *Blandfordia nobilis* (Liliaceae) was reduced after removing nectar from plants pollinated manually. Navarro (1999) showed that experimental nectar removal increased the total volume of nectar produced by each flower of *Macleania bullata* (Ericaceae) without affecting sugar concentration. The additional nectar secretion entailed an energetic cost that reduced fruit set. The interpretation of our results can be confounded if host plants replaced the nectar we removed (and replaced with a sugar solution), with additional nectar secretion. This alternative requires explicit testing.

Effects of mites on hummingbird foraging and energetics

Numerous studies with solitary bees, bumblebees and other bees, and hummingbirds have shown that flower-handling time varies negatively with nectar volume. Confronted with large nectar volumes, pollinators spend more time per flower (Hodges and Wolf 1981, Thomson 1982, Zimmerman 1983, Montgomerie 1984, Galen and Plowright 1985, Gass and Sutherland 1985, Neff and Simpson 1990, Rathcke 1992, Ohashi and Yahara 1999), and those that encounter little nectar visit fewer flowers per plant (Pyke 1978a, b, Hartling and Plowright 1979, Heinrich 1979, Hainsworth et al. 1983, Pleasants and Zimmerman 1983, Galen and Plowright 1985, Hodges 1985, Kato 1988, Cresswell 1990, Neff and Simpson 1990). Although longer visits to extract more nectar is simply a consequence of a fixed extraction rate, it may promote pollen flow, outcrossing, and an increase in female reproductive success (McDade 1983, Schemske and Pautler 1984, Hodges 1985, Stanton et al. 1986, Bertin 1988, Cruzan 1989, Young and Stanton 1990, Jennersten and Nilsson 1993). However, if illegitimate, nonpollinating floral visitors and/or extrinsic environmental conditions (nectar reabsorption and water evaporation) reduce nectar availability, then a direct, negative effect on the energy

spent by the pollinator should be observed. Flower mites only reduce by half the normal nectar volume (C. Lara and J. F. Ornelas unpubl.) compared to traditional nectar robbers, which usually reduce the standing crop of nectar to zero (R. E. Irwin pers. comm.). This difference may explain why birds do not discriminate against low-nectar plants of *M. deppeana*.

We conclude that high rates of nectar consumption by flower mites in *M. deppeana* affect hummingbird foraging and these behavioral responses have positive consequences on the host plant reproductive success. Further studies need to evaluate how nectar and pollen consumption by flower mites affects both male and female fitness components of protandrous plants at different temporal and spatial scales.

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