

# Flower mites and nectar production in six hummingbird-pollinated plants with contrasting flower longevities

Carlos Lara and Juan Francisco Ornelas

**Abstract:** Hummingbird flower mites and hummingbirds may compete intensely for the nectar secreted by their host plants. Here, we present the results from field experiments in which flower mites were excluded from flowers of six hummingbird-pollinated plants with contrasting flower longevities. Nectar measurements were taken on flowers from which mites were excluded and those without mite exclusion over their lifespans. The exclusion of mites had a significant positive effect on the amount of nectar available in plants with long-lived flowers. In contrast, nectar availability in short-lived flowers was not significantly reduced after mite exclusion. The significance of the mite-exclusion treatment was independent of floral morph and flower age. Results also suggest that the magnitude of the mite-exclusion treatment depends on the volume of nectar produced by the flower throughout its lifetime. The treatment effect was detected when nectar consumption, presumably by flower mites, exceeded 13% of the nectar produced by the flowers; nectar availability was not significantly reduced when nectar volume was  $< 7 \mu\text{L}$  per flower. It appears that flower mites consume proportionately more nectar in long-lived flowers than in short-lived flowers. Parasitic hummingbird flower mites seem to be preferentially taking advantage of plant-pollinator interactions in which flowers last several days and produce large volumes of nectar. The consequences of this finding concerning plant-hummingbird-mite interactions await further investigation. As a working hypothesis, we propose that nectar production has increased over evolutionary time not only by the selective pressures imposed by the pollinators, but also to compensate for the reduction they suffer after exploitation by nectar robbers and thieves such as flower mites.

*Key words:* Ascidae, flower longevity, hummingbird pollination, multiple-species interactions, mutualism exploitation, nectar theft.

**Résumé :** Les acariens des oiseaux-mouches et les oiseaux-mouches floricoles sont en forte compétition pour le nectar secrété par leurs plantes hôtes. Les auteurs présentent les résultats d'expériences conduites sur le terrain dans lesquelles les acariens floricoles ont été exclus des fleurs de six plantes pollinisées par des oiseaux-mouches, ces fleurs ayant diverses longévités. Ils ont mesuré le nectar sur des fleurs dont les acariens ont été exclus et des fleurs sans exclusion, au cours de leurs durées de vie. L'exclusion des acariens affecte positivement la quantité de nectar disponible sur les plantes ayant des fleurs longévives. Au contraire, chez les plantes ayant des fleurs à courte durée de vie, l'exclusion des acariens n'a pas d'effet significatif. L'importance du traitement par exclusion des acariens est indépendante de la forme de la fleur et de l'âge de la fleur. Les résultats suggèrent également que l'importance du traitement par exclusion des acariens dépend du volume de nectar produit par la fleur, au cours de sa durée de vie. On détecte l'effet du traitement lorsque la consommation du nectar, probablement par les acariens floricoles, dépasse 13 % du nectar produit par les fleurs; la disponibilité n'est pas significativement réduite lorsque le volume du nectar est  $< 7 \mu\text{L}$  par fleur. Il semble que les acariens floricoles consomment proportionnellement plus de nectar chez les fleurs longévives que chez les fleurs à courte durée de vie. Les acariens floricoles parasites des oiseaux-mouches semblent tirer surtout avantage des interactions pollinisateur/plante chez lesquelles les fleurs durent plusieurs jours et produisent de grandes quantités de nectar. Les conséquences de ces observations sur les interactions plantes – oiseaux-mouches – acariens nécessitent plus de recherches. Comme hypothèse de travail, les auteurs proposent que la production de nectar aurait augmenté au cours de l'évolution, non seulement sous l'effet de la pression sélective imposées par les pollinisateurs, mais aussi afin de compenser pour la réduction subie sous l'effet des voleurs de nectar et charpateurs tels que les acariens floricoles.

*Mots clés :* Ascidae, longévité des fleurs, pollinisation par les oiseaux-mouches, interactions multi-spécifiques, exploitation mutuelle, voleur de nectar.

[Traduit par la Rédaction]

Received 17 April 2002. Published on the NRC Research Press Web site at <http://canjbot.nrc.ca> on 10 December 2002.

**C. Lara<sup>1</sup> and J.F. Ornelas.<sup>2</sup>** Departamento de Ecología y Comportamiento Animal, Instituto de Ecología, A.C., Km 2.5 antigua carretera a Coatepec, Apartado Postal 63, Xalapa, Veracruz 91070, Mexico.

<sup>1</sup>Present address: Laboratorio de Ecología del Comportamiento, Centro de Investigaciones Fisiológicas (CIF), Universidad Autónoma de Tlaxcala, Carretera Tlaxcala-Puebla, Km 1.5 s/n Tlaxcala, Tlaxcala 90070, Mexico.

<sup>2</sup>Corresponding author (e-mail: [ornelasj@ecologia.edu.mx](mailto:ornelasj@ecologia.edu.mx)).

## Introduction

Plant-pollinator mutualisms are often “exploited” by species that gather the reward offered to pollinators but do not provide a return benefit to either mutualist partner (Bronstein 2001). Flowers that are best pollinated by hummingbirds are illegitimately exploited by bees, bumblebees, ants, passerine birds, and hummingbirds themselves (Inouye 1983; Maloof and Inouye 2000; Irwin et al. 2001; Lara and Ornelas 2001a, and references therein). However, the most commonly observed nectar thieves (*sensu* Inouye 1980) are hummingbird flower mites (Acari: Mesostigmata: Ascidae) (Dobkin 1984; Colwell 2000), which get into the flowers as pedestrians from nearby flowers or disembark “legitimately” from the hummingbird bills directly into the flowers. Both sexes are transported between inflorescences via the nasal cavities of hummingbirds (Colwell 1985) and most individuals probably spend their entire life (about 2 weeks) on their natal inflorescence (Colwell 2000). Typically, each local mite-breeding group is founded by a few adult mites disembarking from hummingbirds into the first flowers of an inflorescence (Colwell 1995). The group quickly grows to dozens or hundreds of mites, depending on mite and host species (Colwell 1986a, 1986b; Colwell and Naeem 1994). These numbers are sufficient to threaten the entire nectar production of an inflorescence.

Hummingbird flower mites prefer the nectar of their own characteristic host species to the nectar of the hosts of other hummingbird flower mite species in the same assemblage (Heyneman et al. 1991). Some floral traits of host plants are important for the development, growth, and dynamics of flower mite populations. For instance, the number of flower mites within an inflorescence is positively correlated with corolla length and nectar production (Colwell and Naeem 1994). Although commonly observed among hummingbird-pollinated flowers, the ecological impact of nectar thieves has been mostly ignored (Maloof and Inouye 2000; Irwin et al. 2001). Nectar thieves can directly affect plant fitness by depleting nectar and excluding pollinators from flowers and they can indirectly affect fitness by forcing pollinators to modify their foraging behavior. The ecological significance of nectar “theft” by hummingbird-flower mites is not known.

The interaction between flower mites, hummingbirds, and their host plants has been studied extensively for almost 30 years (Colwell 1973, 1979, 1995; Dobkin 1985, 1987, 1990; Heyneman et al. 1991), but some aspects still warrant consideration. The role flower mites play in plant-hummingbird interactions has been defined as parasitic, symbiotic, or mutualistic (Proctor and Owens 2000). Nectar consumption by flower mites qualifies them as significant plant parasites (Colwell 1995; but see Dobkin 1984), especially considering their voracious consumption of pollen (Paciorek et al. 1995). The high rate of nectar consumption also implicates these mites as important competitors with hummingbirds (Colwell 1995; Lara and Ornelas 2001b). In fact, the role of these mites as competitors for nectar represents a far more costly negative interaction, from the point of view of hummingbird energetics, than this exploitation of the birds for transport (Colwell 2000).

Although the exploitation of nectar by flower mites in hummingbird-pollinated flowers was thought to be negli-

ble (Dobkin 1984), two recent studies have shown experimentally that mites and hummingbirds may compete intensely for nectar. The flower mite *Proctolaelaps kirmsei* can consume up to 41% of nectar produced by flowers of *Hamelia patens* (Rubiaceae) (Colwell 1995). We showed that nectar availability in flowers of *Moussonia deppeana* (Gesneriaceae) was reduced by up to 56% when *Tropicoseius* sp.nov. flower mites were not excluded from them (Lara and Ornelas 2001b). In the same study, we showed with a manual-pollination experiment that the presence of mites had no negative effects on seed production. However, the reduction in nectar availability altered the foraging behavior of the legitimate pollinators in a way that may positively affect seed production (Lara and Ornelas 2002). Yet, the generality of these results has not been explored thoroughly.

The plant-hummingbird-mite interactions may have been overlooked in the literature because the outcomes are subtle and complex, and depend on: (i) whether or not flower mites are abundant (density-dependent), (ii) their temporal and spatial distribution, (iii) whether or not hummingbirds are able to discriminate against flowers heavily infested with flower mites (frequency-dependent), (iv) the nature of the floral display (e.g., number of flowers per plant, inflorescence number), (v) volume, sugar concentration, and “taste” of nectar, and (vi) the availability and spatial distribution of other floral resources in the environment to hummingbirds and mites. Here, we present the results from field experiments designed to exclude mites from flowers of six hummingbird-pollinated plants. The main goal of our study is to determine how flower longevity and amount of nectar produced influence nectar consumption by natural populations of flower mites.

## Materials and methods

### Study sites and plant species

Fieldwork was carried out from March 1999 through September 2000 in three sites of central Veracruz, Mexico. We chose six of the most common hummingbird-pollinated plants, which contrast in corolla length (from 14 to 60 mm), breeding system (from selfing to outbreeding; protandry, distyly), and flower longevity (from 1- to 6-day lifespans). All of these plant species were infested with flower mites. The presence of natural populations of mites in plants was verified by collection *in situ*. Basic information on the reproductive ecology of these plants was collected during this period.

### Site 1

Parque Ecológico Francisco Xavier Clavijero (19°30'N, 96°57'W; at 1280 m altitude) is a protected remnant of cloud forest (55 ha), 2.5 km from the city of Xalapa, Veracruz, Mexico. Mean annual precipitation is 1500 mm and mean annual temperature is 18°C. The climate is mild and humid throughout most of the year with a dry and cold season from November to March. The canopy is dominated by tree species such as *Carpinus carolineana* (Betulaceae), *Cinnamomum effusum*, *Ocotea* sp. (Lauraceae), *Liquidambar styraciflua* (Hamamelidaceae), *Quercus germana*, *Quercus xalapensis* (Fagaceae), and *Oreopanax xalapensis* (Araliaceae). Floristic

details of the area are given by Castillo-Campos (1991) and Williams-Linera and Tolome (1996).

*Tillandsia deppeana* Steudel (Bromeliaceae) is an endemic epiphyte commonly found in pine and tropical deciduous forests from Tamaulipas to Oaxaca, Mexico (Smith and Downs 1977). This semelparous, rosette-like bromeliad (0.8-m high) is characterized by its reddish, pinnated inflorescences. Flowers with blue tubular corollas are open for one day (García-Franco and Rico-Gray 1991) (Fig. 1a). Out-crossed flowers produce more seeds, but selfing and geitonogamy are possible (García-Franco and Rico-Gray 1991). Flowering occurs from January to May at Clavijero. Each plant produces 70–230 flowers and opens 3–4 flowers per day (García-Franco et al. 2001). It is visited and pollinated by hummingbirds (*Campylopterus curvipennis*, *Amazilia yucatanensis*, and *Amazilia cyanocephala*), bees, and butterflies. It hosts *Tropicoseius peregrinator* and, at our study site, *Tropicoseius erro* (Fig. 1d) flower mites (García-Franco et al. 2001).

*Palicourea padifolia* (Roem. and Schult.) C. M. Taylor and Lorence (Rubiaceae) is a self-incompatible, distylous, 2–7 m high shrub (Contreras and Ornelas 1999). It is abundant in disturbed areas of cloud forests from southern Mexico to Panama (Taylor 1989). It can be recognized by reddish-purple, pyramidal inflorescences, opposite-branched panicles with yellow, 1-day flowers occurring in cymose clusters of the terminal inflorescence (Taylor 1989) (Fig. 1b). Long-styled flowers have shorter corollas than short-styled flowers (Contreras and Ornelas 1999). This species typically flowers at Clavijero from March until August, and the flowering peak is reached between May and mid-June (Contreras and Ornelas 1999). Individual plants produce 30–50 inflorescences each year and each inflorescence opens approximately three flowers per day (C. González, J. F. Ornelas, and L. Jiménez, data not included). Flowers are visited by 11 species of hummingbirds, solitary bees, and butterflies (Contreras and Ornelas 1999). Non-territorial, short-billed hummingbirds are thought to be the main pollinators (J. F. Ornelas, data not included). It is almost certainly a host plant of *Tropicoseius peregrinator* flower mites (Naskrecki and Colwell 1998) (Fig. 1e).

*Lobelia laxiflora* H. B. K. (Lobeliaceae) is a perennial, 1.3-m high shrub commonly growing in humid, disturbed, open areas and widely distributed from Arizona, U.S.A. to Colombia (McVaugh 1942). This shrub has red-orange, tubular, protandrous flowers that change in color from red-orange to pale pink-yellowish (Fig. 1c). Flowers last 5 days (2 days as staminate phase and 3 days as pistillate phase). The flowering period at Clavijero is from November to March. Each inflorescence opens two to five flowers per day. Flowers are visited and pollinated by hummingbirds (*Lampornis amethystinus*, *Amazilia cyanocephala*), bees, and butterflies. It is a host plant of *Tropicoseius chiriquensis* (Fig. 1f) in El Cielo, Tamaulipas and western Mexico, and almost certainly in Veracruz (Naskrecki and Colwell 1998).

### Site 2

Chavarrillo (19°24'N, 96°48'W; at 1000 m altitude) is an unprotected oak woodland located 30 km south of Xalapa, Veracruz, Mexico. Mean annual precipitation is 1110 mm and mean annual temperature is 24.5°C. The climate is mild

and humid throughout most of the year, with a dry and cold season from October to May. This area has been heavily deforested; however, in remnants, species such as *Quercus peduncularis* and *Quercus oleoides* (Fagaceae), and *Brahea dulcis* (Arecaceae) dominate the canopy. In the understory, cycads (*Zamia loddigesii* and *Dioon edule*) (Zamiaceae) and *Acacia* sp. (Fabaceae) are common. A detailed description of this area is given by Castillo-Campos (1985).

*Hamelia patens* Jacq. (Rubiaceae) is a small, semi-woody, 3-m high bush indigenous to many tropical areas in Central and South America (Elias 1976). The plant produces hermaphroditic, homogamous (self-pollination is possible), bright reddish-orange, 1-day flowers (Fig. 2a). Their flowering period at Chavarrillo is from February to August. Individuals bear several dozen flowering inflorescences at a time. Each inflorescence opens about three flowers per day; flowers are visited regularly by hummingbirds (*Anthracothorax prevostii*, *Amazilia tzacatl*, and *Amazilia beryllina*), as well as occasionally by stingless bees (*Trigona* spp.), wasps, and butterflies. The mite *Proctolaelaps kirmsei* (Fig. 2d) is a common inhabitant of its flowers from Veracruz, Mexico, to South America (Colwell 1995).

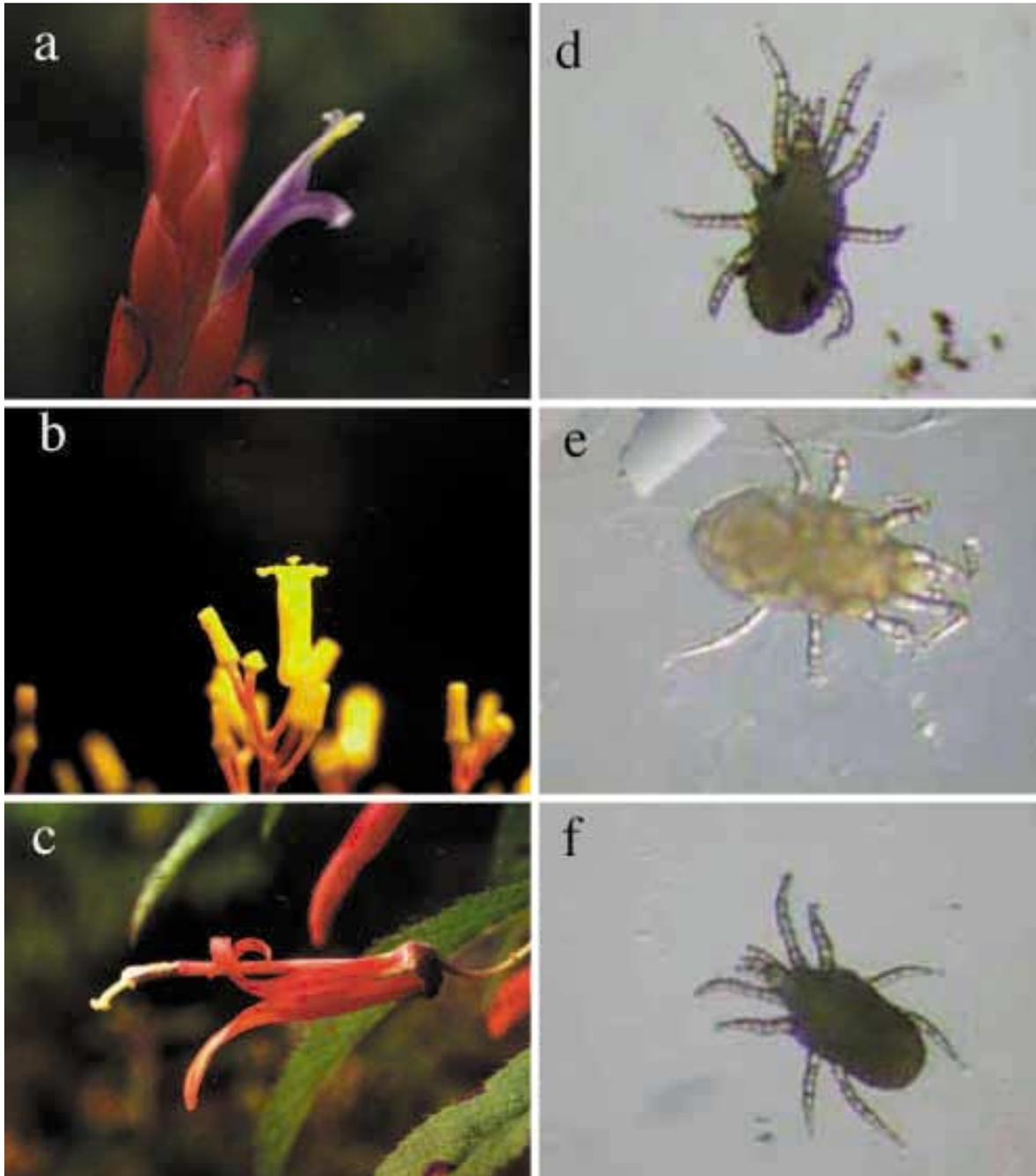
*Bouvardia ternifolia* (Cav.) Schltld. (Rubiaceae) is a self-incompatible, distylous herb (1–1.5 m high) widely distributed in open areas of woodlands from Arizona, U.S.A. through southern Mexico (Faivre 2000). Flowers have corollas fused as a tube and grouped in terminal cymes (Fig. 2b). Long-styled flowers have shorter corollas than short-styled flowers (Faivre 2000). Flowers last 4–5 days and change color from scarlet to pale red or pink by the third day. This plant typically flowers at Chavarrillo from July to November. Hummingbirds (*Amazilia tzacatl* and *Amazilia beryllina*) are the main pollinators. *Tropicoseius* sp. flower mites (Fig. 2e) live in their flowers (Naskrecki and Colwell 1998).

### Site 3

La Mancha (19°36'N, 96°22'W; at < 50 m altitude) is a protected remnant (70 ha) of mostly tropical deciduous forest and sand dunes 30 km northeast of Cardel in coastal Veracruz, Mexico. Mean annual precipitation is 1300 mm and mean annual temperature is 22.9°C. The climate is warm and subhumid throughout the year with a rainy season from June to September. Scrubby species include *Caesalpinia crista*, *Diphysa robinoides*, *Acacia* sp. (Fabaceae), *Opuntia stricta* (Cactaceae), *Hibiscus tiliaceus* (Malvaceae), *Turnera ulmifolia* (Turneraceae), and *Randia latevirens* (Rubiaceae). Floristic details of the area are given by Novelo (1978).

*Lobelia cardinalis* L. (Lobeliaceae) is a perennial, self-compatible, protandrous shrub (1–1.5 m high) that grows in shaded to open wet sites from southern Canada to Colombia (McVaugh 1942; Devlin and Stephenson 1985). At La Mancha, it produces spikes of brilliant, scarlet-red flowers on branching stems (Fig. 2c) above green or deep bronze-purple foliage from late June to mid-August. The rosettes elongate and eventually produce a single terminal racemose inflorescence of 2 to more than 50 flowers. The inflorescence develops acropetally and the tubular flowers last 6 days at our study site (4 days as male phase and 2 days as female phase). Consequently, in mid-flowering season, a typical raceme has developing fruits, female-phase flowers,

**Fig. 1.** Hummingbird-pollinated flowers at Clavijero, (a) *Tillandsia deppeana* (Bromeliaceae), (b) *Palicourea padifolia* (Rubiaceae), and (c) *Lobelia laxiflora* (Lobeliaceae), and their corresponding flower mites (d) *Tropicoseius erro*, (e) *Tropicoseius peregrinator*, and (f) *Tropicoseius chiriquensis*.



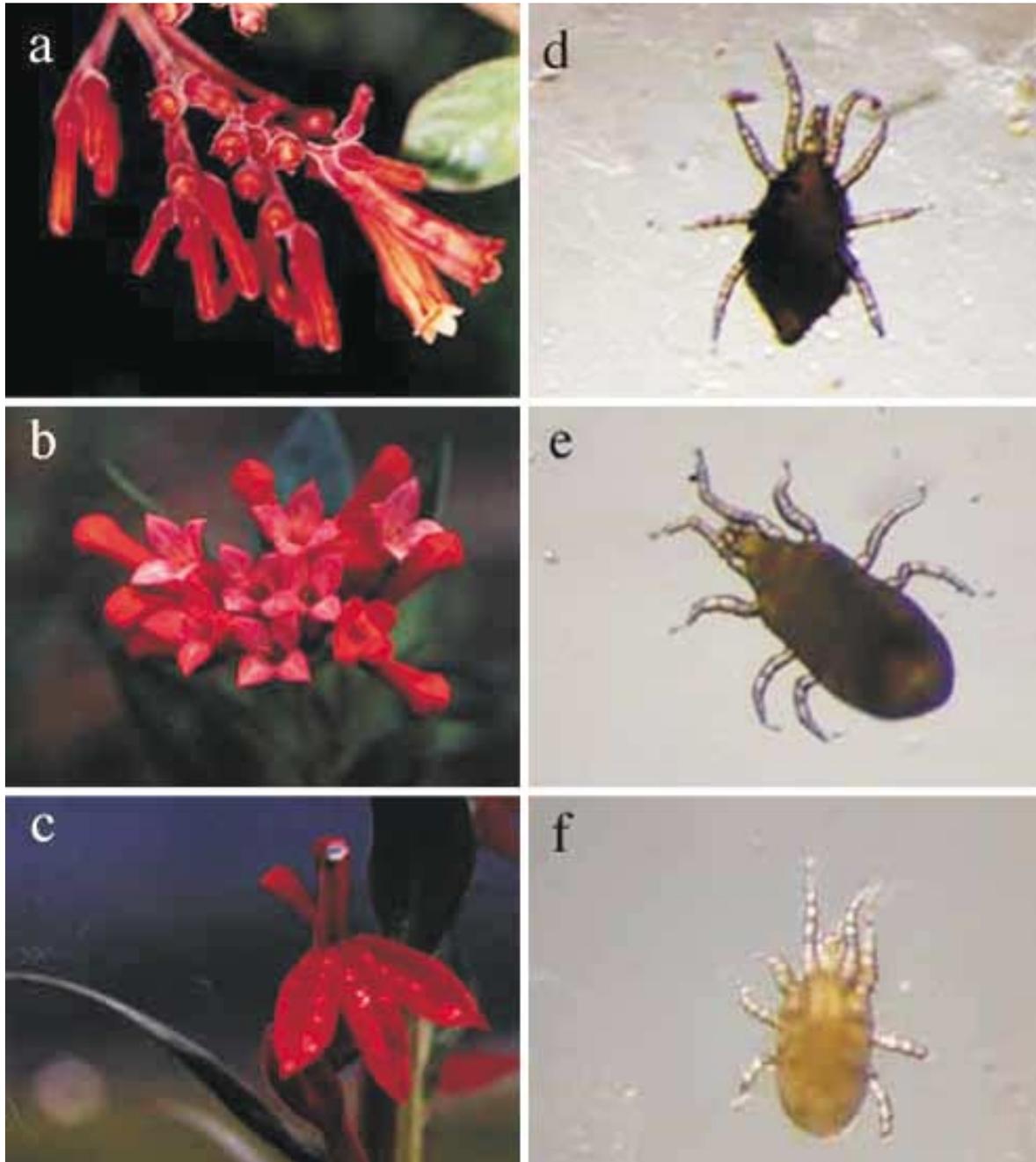
male-phase flowers, and flower buds distributed in sequence from the basal to the terminal portion of the inflorescence. Flowers are pollinated by hummingbirds (*Amazilia yucatanensis* and *Amazilia tzacatl*). Hummingbird flower mites (*Tropicoseius* sp.) (Fig. 2f) inhabit their flowers (Naskrecki and Colwell 1998).

#### Experimental protocol

For each plant species, we randomly chose 10 individuals from which we also randomly selected four buds ready to open ( $n = 40$  flowers per plant species). We chose 10 indi-

viduals from each floral morph of *P. padifolia* and *B. ternifolia* because short-styled flowers have longer corollas than long-styled flowers ( $n = 40$  flowers per floral morph). To measure the effect of mite exclusion on nectar production we applied two different treatments. In the first treatment, mites and hummingbirds were excluded. This was accomplished by applying Tanglefoot® (The Tanglefoot Co., Grand Rapids, Mich.) onto each pedicel of 20 flowers and then bagging them with mosquito-net bags (mesh size,  $1.2 \times 1.2$  mm). In the second treatment, only hummingbirds were excluded. Twenty flowers were bagged with mosquito-net

**Fig. 2.** Hummingbird-pollinated flowers at Chavarrillo and La Mancha. (a) *Hamelia patens*, (b) *Bouvardia ternifolia* (Rubiaceae), and (c) *Lobelia cardinalis* (Lobeliaceae), and their corresponding flower mites (d) *Proctolaelaps kirmsei*, (e) *Tropicoseius* sp., and (f) *Tropicoseius* sp.



bags (mites could move freely as pedestrians among flowers of the same inflorescence (Lara and Ornelas 2001b). Flower mites can leave flowers that become physiologically unsuitable and move in response to resource supply (Dobkin 1985, 1990). All study species open fewer than five flowers per inflorescence per day, except *B. ternifolia* which opens 1–15 flowers (Table 1). As flower mite manipulation is impractical under field conditions, we assumed that mite numbers would stay the same over the experiment. Additional Tanglefoot<sup>®</sup> was applied at the base of the *P. padifolia* and *H. patens* inflorescences to minimize possible effects from

the nature of the floral display (inflorescence number), and to reduce the possibility of mites violating our experimental exclusion design and (or) migrating to unmanipulated inflorescences during our repeated sampling of experimental flowers.

Nectar production was measured at 3-h intervals (at 07:00, 10:00, 13:00, 16:00 and 19:00) the day following exclusion in both groups of plants according to standard procedures (Kearns and Inouye 1993). Nectar was extracted repeatedly using 5  $\mu$ L-calibrated micropipettes from individual flowers over their lifetimes (non-destructive method). Repeated re-

removal of nectar may stimulate the production of additional nectar (Castellanos et al. 2002, and references therein); since we were limited by daily flower availability (*Tillandsia deppeana*), we did not account for this in our experimental design. Instead, we applied the same methodology to all plants. In a previous report, we showed that the greatest impact of mite exclusion occurred in the middle of the flowering period (i.e., peak of flower abundance), suggesting that the magnitude of the mite-exclusion treatment increases as mite population increases (Lara and Ornelas 2001b). Based on this outcome, nectar measurements were made at the middle of the flowering season of each plant species. Nectar measurements were made in May 1999 (*P. padifolia*), and March (*Lobelia laxiflora*), April (*T. deppeana*), May (*H. patens*), June (*Lobelia cardinalis*), and July (*B. ternifolia*) of 2000. Non-manipulated flowers were sampled for mites to see whether or not mites were common enough to be an important factor.

### Statistical analysis

Nectar production by flowers of plants excluded and not excluded from mites over the time of the experiment (1–6 days) was analyzed using repeated-measures ANOVA (Zar 1984). In the model, the mite treatment (exclusion of both mites and hummingbirds versus exclusion of hummingbirds only) was treated as a fixed effect; floral morph (*P. padifolia* and *B. ternifolia*) and flower age (*L. laxiflora*, *L. cardinalis*, *B. ternifolia*) were also treated as fixed factors. Nectar volumes produced over time (each 3-h interval) in long- (*B. ternifolia*, *L. laxiflora*, and *L. cardinalis*) and short-lived flowers (*P. padifolia*, *T. deppeana*, and *H. patens*) were the repeated measures. Data were  $\log_{10}(x + 1)$  transformed before the analysis to fulfill the requirements of parametric analysis (Zar 1984) but untransformed data are reported. All statistical analyses were done using general linear modeling with StatView and SuperANOVA (Abacus Concepts 1989, 1996).

## Results

Table 1 summarizes the information gathered during our fieldwork on the reproductive ecology of all six plant species studied. Differences among species include corolla length (range of 14 to 53 mm), flower longevity (from 1 to 6 days), mean number of open flowers per plant (from 4 to 244 flowers), and mean nectar volume (from 1 to 18  $\mu\text{L}$ /flower per day). For completeness, we have added *Moussonia deppeana* (Gesneriaceae), the only species for which there are existing published data (Lara and Ornelas 2001b).

### Nectar production by long-lived flowers

The exclusion of mites had a statistically significant impact on nectar production in protandrous flowers of *L. laxiflora* and *L. cardinalis*, independent of flower age and time of day (Table 2). Flowers from which mites were excluded had more nectar than those without mite exclusion (Figs. 3a–3b). Mites may have consumed much of the available nectar (13–25%). The exclusion of mites from long-lived, distylous flowers of *B. ternifolia* resulted in similar patterns; flowers from which mites were excluded produced significantly more nectar than those exposed to flower mites

(Table 2). There was a significant flower age  $\times$  treatment interaction (Fig. 3c), but the flower age  $\times$  floral morph  $\times$  treatment interaction was not significant (Table 2). Mites may have consumed 22% of the available nectar.

### Nectar production by short-lived flowers

No statistically significant differences in nectar availability were found between flowers from which mites were excluded and those without the exclusion in *T. deppeana*, *H. patens*, and *P. padifolia* (Table 3; Figs. 4a–4c). Nectar availability varied significantly over time in *T. deppeana* and *H. patens*, but the time of day  $\times$  treatment interactions were not significant (Table 3). Post hoc mean comparisons indicate that flowers of *H. patens* from which mites were excluded produced significantly more nectar at 10:00 than those without the exclusion at the same time of day (Games–Howell procedure,  $F_{[1, 38]} = 7.06$ ,  $p = 0.011$ ). Nectar availability also varied significantly over time in *P. padifolia*, but the time of day  $\times$  floral morph  $\times$  treatment interaction was not significant (Table 3).

## Discussion

The significant effect of nectar consumption by flower mites on three of the six plant species evaluated in this study coincides with the results of the only two previous studies (Colwell 1995; Lara and Ornelas 2001b); the exclusion of flower mites reduced the amount of nectar (volume) produced by a single flower by 2% to 56%. However, the magnitude of this effect varied among species. Nectar consumption, presumably by mites, was significantly higher among flowers that lasted several days (*L. laxiflora*, *L. cardinalis*, and *B. ternifolia*) and did not differ from that of controls. In contrast, no statistical differences were found among groups of plants with flowers that last for a single day (*T. deppeana*, *H. patens*, and *P. padifolia*). Our results also suggest that the magnitude of nectar consumption by flower mites depends on the volume produced by the flower throughout its lifetime. The relative impact of our mite-exclusion treatment was more evident in flowers that produced larger volumes of nectar. If the volume of nectar produced by an individual flower was  $< 6 \mu\text{L}$ , no significant differences among flowers were detected (except in *B. ternifolia*). One-day flowers of *H. patens* produced  $< 7 \mu\text{L}$  every 3-h interval, except at 10:00, when nectar production was highest (12  $\mu\text{L}$ ) and mites had the strongest impact. It is possible that we failed to detect the effect of the mite-exclusion treatment in *H. patens* because of geographic variation in nectar production and composition of mite communities between localities. Nevertheless, our results on nectar production in *H. patens* are congruent with those of Colwell (1995) for a population in Costa Rica. Colwell estimated the effect of flower mites by measuring nectar standing crop between 07:30 and 09:00 and found a significant effect of flower mites (41% of nectar consumed by mites). We measured nectar production at 3-h intervals and only found a significant reduction in nectar volume at 10:00 (40%). Nevertheless, the heterogeneity among the host plant – hummingbird – flower mite assemblages studied, according to several factors, could have affected our results.

**Table 1.** Morphological, phenological, and reproductive differences among host plant species best pollinated by hummingbirds in

Species	Family	Flower color	Mean corolla length $\pm$ SD (mm)	Flower longevity (days)	No. open flowers per plant	No. open flowers per inflorescence	Mean nectar production $\pm$ SD ( $\mu$ L/flower)
<i>Palicourea padifolia</i>	Rubiaceae	Yellow	(LS) 14.14 $\pm$ 1.3 ( <i>n</i> =677)	1	208 $\pm$ 39 ( <i>n</i> =15)	2.5 $\pm$ 2.7 ( <i>n</i> =89)	(LS) 2.23 $\pm$ 0.19 ( <i>n</i> =40)
			(SS) 16.90 $\pm$ 1.0 ( <i>n</i> =743)	1	244 $\pm$ 47 ( <i>n</i> =15)	1.9 $\pm$ 2.2 ( <i>n</i> =89)	(SS) 1.34 $\pm$ 0.09 ( <i>n</i> =40)
<i>Hamelia patens</i>	Rubiaceae	Red	20.33 $\pm$ 1.0 ( <i>n</i> =40)	1	30–100	1–5	6.06 $\pm$ 0.76 ( <i>n</i> =40)
<i>Bouvardia ternifolia</i>	Rubiaceae	Red	(LS) 20.90 $\pm$ 3.0 ( <i>n</i> =40)	4–5	2–50	1–15	(LS) 3.36 $\pm$ 0.07 ( <i>n</i> =40)
			(SS) 23.76 $\pm$ 3.1 ( <i>n</i> =40)	4–5			(SS) 2.89 $\pm$ 0.06 ( <i>n</i> =40)
<i>Lobelia laxiflora</i>	Lobeliaceae	Red	42.10 $\pm$ 8.5 ( <i>n</i> =30)	5	2–40	2–5	(S) 15.20 $\pm$ 0.58 ( <i>n</i> =40)
<i>Lobelia cardinalis</i>	Lobeliaceae	Red	53.00 $\pm$ 12.2 ( <i>n</i> =60)	6	2–50	2–5	(P) 11.77 $\pm$ 0.58 ( <i>n</i> =40)
							(S) 17.49 $\pm$ 0.30 ( <i>n</i> =40)
<i>Tillandsia deppeana</i>	Bromeliaceae	Blue	37.36 $\pm$ 2.2 ( <i>n</i> =35)	1	1–4	2–3	(P) 6.71 $\pm$ 0.27 ( <i>n</i> =40)
<i>Moussonia deppeana</i>	Gesneriaceae	Red	32.28 $\pm$ 2.0 ( <i>n</i> =60)	4	4–50	4	(S) 1.76 $\pm$ 0.21 ( <i>n</i> =20)
							(P) 1.18 $\pm$ 0.20 ( <i>n</i> =20)

Note: LS, long-styled; SS, short-styled; P, pistillate phase; S, staminate phase. Data for *Moussonia deppeana* from Lara and Ornelas (2001b). \*\*\**p* < 0.001 (see Results).

### The nature of the floral display

The number of open flowers per inflorescence could determine how flower mites move around flowers, but the magnitude of the flower mite effects appears to be independent of inflorescence design and number of open flowers per inflorescence (Colwell 1995). Mites had no significant effect on nectar production of *H. patens* and *P. padifolia*, each of which produces ca. 30–100 flowers per inflorescence over their lifetime (Colwell 1995; Contreras and Ornelas 1999). One could argue that the previous impact of mites already present on the inflorescence determined the effects of mites and the distribution of nectar and mites among flowers that opened the day of the experiment (Colwell 1995).

Flowering time and spatial resource distribution (flower patch size and distribution of plants) are important ecological components in host plant – hummingbird – mite interactions (Dobkin 1984, 1985; Lara and Ornelas 2001b). Although these aspects of the ecology of the system were beyond the scope of our study, it would be interesting to know whether a few plants in isolation would be more successful in avoiding mites or achieving pollination than more aggregated plants. This idea is plausible because free-ranging foragers like hummingbirds probably base their foraging decisions on patches, not on individual flowers. We have only observed territorial defense by *Amazilia* hummingbirds to individuals plants of *P. padifolia* and *H. patens*, both with a surplus of flowers (Table 1). Hummingbirds did not establish feeding territories in the remaining study species, which are more sparsely distributed and open fewer flowers per day. When plants are normally quite

sparse, there may be a payoff for producing more nectar, whatever the circumstances, and for having fewer flowers that last for more than a day, and also for selfing and apomixis.

### Mite density

Flower mite numbers may vary dramatically both in time and between localities. It is possible that flower mites violated our exclusion design and migrated to unmanipulated flowers after we repeatedly-sampled experimental flowers. But mites could have also increased in numbers among long-lived flowers; eggs take 2–3 days to eclose (Colwell 1995) and adult females could not disperse, as both groups of flowers were excluded from hummingbirds. Also, Colwell (1995) showed that the variation in nectar consumption by flower mites in *H. patens* was not explained by mite density. Nevertheless, Lara and Ornelas (2001b) have shown that flower mites consume the greatest percentage of the total nectar in mid-flowering time, suggesting that the intensity of nectar consumption covaries with population growth and mite density. Because we conducted our nectar measurements at peaks of flowering, we believe that neither population growth nor mite density are not important factors in explaining the observed pattern.

### Flower longevity

We have shown that the exclusion of mites positively impacts nectar production among plants with long-lived flowers (> 4 days). These plants bore long-tubed flowers and produced relatively larger volumes of nectar (> 7  $\mu$ L). Hummingbird-pollinated plants inhabiting the neotropical wet

Veracruz, Mexico, and the effects of flower mites on nectar production.

Flowering time	Breeding system	Floral visitors	Flower mites	Flower protection	Plant distribution	Mite density per flower	Nectar removed (%)	Effect of mites on nectar production
Mar–Aug	Distyly, self-incompatible	Hummingbirds, solitary bees, butterflies	<i>Tropicoseius</i>	No	Scattered individuals	(LS) 1 (SS) 2	(LS) 2 (SS) 11	Neutral
Feb–Aug	Outcrossed, self-compatible	Hummingbirds, solitary bees, butterflies, ants, wasps	<i>Proctolaelaps</i>	No	Scattered individuals	27	33	Neutral
Jul–Nov	Distyly, self-incompatible	Hummingbirds, bees, butterflies	<i>Tropicoseius</i>	No	Small clumps	(LS) 12 (SS) 5	(LS) 22 (SS) 15	Negative***
Nov–Mar	Protandry, geitonogamy	Hummingbirds	<i>Tropicoseius</i>	No	Small clumps	51	25	Negative***
Jun–Aug	Protandry, geitonogamy	Hummingbirds	<i>Tropicoseius</i>	No	Scattered individuals	21	13	Negative***
Jan–May	Outcrossed, geitonogamy	Hummingbirds	<i>Tropicoseius</i>	Bract, bract liquid	Isolated individuals	4	10	Neutral
Oct–Mar	Protandry, self-compatible	Hummingbirds	<i>Tropicoseius</i>	No	Scattered individuals	16	50–56	Negative***

lowlands typically bore 1-day flowers (Stiles 1975; Feinsinger et al. 1982). By contrast, flower longevity seemed longer among larger, hummingbird-pollinated flowers of herbs and shrubs at mid-elevations (Primack 1985; Stratton 1989). Stratton (1989) also identified taxonomic constraints at the family level and observed that the ecological patterns in flower longevity probably have resulted from historical selection that may or may not correlate with the current ecological predictions of flower longevity. Flower mites may prefer hummingbird-pollinated plants with flowers that last several days. A new generation of mites may be formed when flowers last several days (Colwell and Naem 1994), whereas they have to move daily from flowers that last for a single day (Dobkin 1990; Colwell and Naem 1994). Flower longevity may play an important role in the reproduction of flower mites (Colwell and Naem 1994) because eggs are laid communally at the base of the floral tube and stay floating on nectar until they hatch. Likewise, there is apparently synchronization between egg incubation and the length of time the flowers last (Colwell and Naem 1994). This observation suggests that flower mites may be tracking host plants that have increased flower longevity over evolutionary time to achieve outcrossing.

The longevity of individual flowers affects the total number of flowers open at any one time on the plant. It also determines the probability and the number of times that a flower can be visited depending on the foraging behavior of the pollinator (e.g., Primack 1985; Stratton 1989), with consequent implications for the level of outcrossing and the effectiveness of the overall floral display in attracting and rewarding pollinators. The flower must be physiologically maintained; long-lived flowers may represent a greater en-

ergy cost to the plant than those that last for a single day (see Primack 1985 for a review). It has been suggested that flowers of outbreeders have been selected to remain open longer and thereby increase the probability of visitation by pollinators (Primack 1985); however, the probability of visitation by antagonistic floral visitors (e.g., nectar robbers) and infection by flower mites and fungi should also increase (Lara 2001). If flower mites exert selective pressures on these 1-day flower plants, then plants could escape from selection exerted by flower mites by producing many 1-day flowers, as previously suggested by Dobkin (1987). Roubik (1982) argued that short-lived flowers are the result of selection to minimize loss of nectar to robbers. He and collaborators also showed that pollinators forced to visit more flowers affect greater seed set (Roubik et al. 1985). We have previously shown a positive outcome in terms of seed set as a result of flower mites acting as secondary pollinators for *Moussonia deppeana*, a protandrous gesneriad with long-lived flowers (Lara and Ornelas 2001b; see also Dobkin 1984). Plants with long-lived flowers that produce relatively large amounts of nectar and have low visitation rates would particularly benefit by resisting low levels of mite infection.

Although these ecological conditions are plausible in our study systems, seed production was not increased when mites were excluded in the *Moussonia* study (Lara and Ornelas 2001b). In the same study, we showed that 15% of the flowers excluded from hummingbirds and with no hand pollination produced only half as many seeds as cross-pollinated flowers. It was concluded that flowers of *M. deppeana* are self-compatible and that flower mites may aid in selfing (Lara and Ornelas 2001b; see also Dobkin 1984). Seed production could not be measured for the spe-

**Table 2.** Summary of repeated-measures ANOVAs on the effects of flower mites on nectar production in long-lived flowers of *Lobelia laxiflora*, *L. cardinalis*, and *Bouvardia ternifolia*.

Source of variation	df	MS	F	p
<b><i>Lobelia laxiflora</i></b>				
Between-plant variation				
Treatment	1	4.515	45.046	<0.001
Flower age	4	4.020	40.108	<0.001
Treatment × flower age	4	0.023	0.235	0.918
Within-plant variation				
Time of day	4	14.161	284.167	<0.001
Time of day × treatment	4	0.149	3.007	0.017
Time of day × flower age	16	0.301	6.047	<0.001
Time of day × treatment × flower age	16	0.014	0.285	0.997
Residual	760	0.049		
<b><i>Lobelia cardinalis</i></b>				
Between-plant variation				
Treatment	1	0.817	44.822	<0.001
Flower age	5	12.153	666.547	<0.001
Treatment × flower age	5	0.021	1.181	0.319
Within-plant variation				
Time of day	4	14.389	1755.666	<0.001
Time of day × treatment	4	0.010	1.248	0.288
Time of day × flower age	20	0.590	72.026	<0.001
Time of day × flower age × treatment	20	0.006	0.749	0.775
Residual	912	0.008		
<b><i>Bouvardia ternifolia</i></b>				
Between-plant variation				
Treatment	1	1.391	57.075	<0.001
Floral morph	1	0.831	34.118	<0.001
Treatment × floral morph	1	0.184	7.568	0.006
Flower age	4	1.962	80.516	<0.001
Flower age × treatment	4	0.227	9.319	<0.001
Flower age × floral morph	4	0.089	3.646	0.006
Flower age × floral morph × treatment	4	0.021	0.873	0.480
Within-plant variation				
Time of day	4	25.064	1940.038	<0.001
Time of day × treatment	4	0.094	7.319	<0.001
Time of day × floral morph	4	0.038	2.946	0.019
Time of day × floral morph × treatment	4	0.009	0.703	0.591
Time of day × flower age	16	0.135	10.475	<0.001
Time of day × flower age × treatment	16	0.046	3.585	<0.001
Time of day × flower age × floral morph	16	0.016	1.266	0.211
Time of day × flower age × floral morph × treatment	16	0.005	0.386	0.986
Residual	1520	0.013		

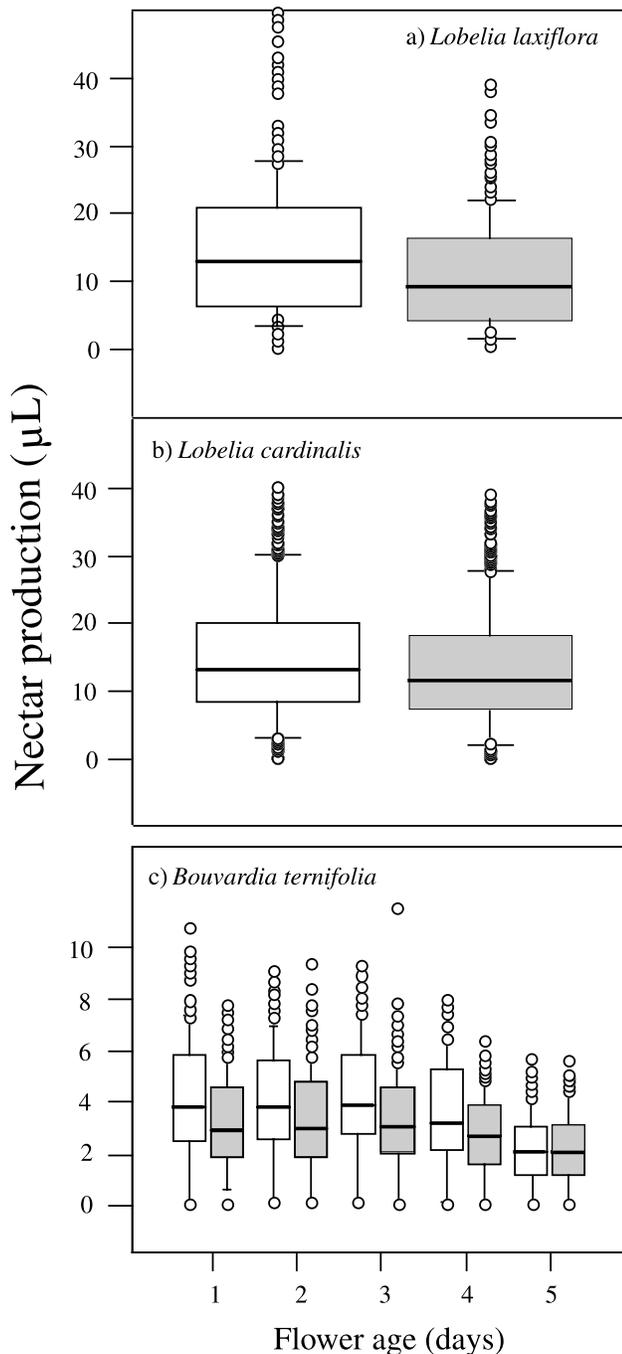
**Note:** Mite treatment (exclusion of both mites and hummingbirds versus exclusion of hummingbirds only), flower morph (only for *B. ternifolia*), and flower phase (*L. laxiflora* and *L. cardinalis*) were treated as fixed effects and the volume of nectar secreted ( $\log_{10}$  transformed) was the repeated factor. Nectar secretion was measured five times a day (3-h intervals) over flower lifespans.

cies we report here because the flowers were repeatedly manipulated for nectar extraction.

Given that flower mites compete with hummingbirds for nectar, the effect of nectar consumption by flower mites may affect hummingbird foraging behavior (Lara and Ornelas 2002; see also McDade and Kinsman 1980; Roubik 1982). Hummingbird flower mites can remove all the nectar secreted by a flower within a day. If some nectar is left to maintain the energy demands of the pollinators, the latter

may remain constant to the plant. We have documented that hummingbirds change their foraging behavior after visiting flowers from which 50% of the nectar was experimentally removed (simulating nectar consumption by flower mites). Such behavioral changes favored the female reproductive success of the host plant (Lara and Ornelas 2002). In this case, the outcome of the interaction would be positive from the plant's perspective, but negative to the hummingbirds because they have to spend more energy in gathering the re-

**Fig. 3.** Effects of mite exclusion on nectar secretion ( $\mu\text{L}$ ) by long-lived flowers of (a) *Lobelia laxiflora*, (b) *Lobelia cardinalis*, and (c) *Bouvardia ternifolia*. Because the treatment  $\times$  flower age interaction was not significant in *L. laxiflora* and *L. cardinalis*, only the treatment effect (pooling across ages) is presented. The flower age  $\times$  floral morph  $\times$  treatment interaction was not significant in *B. ternifolia* (see Table 2 for statistical details), so only the flower age  $\times$  treatment interaction is shown.  $n = 20$  flowers in each treatment. Open bars = without mites, shaded bars = with mites. Box plots show the distribution of values for individual flowers within each species: thick horizontal bar indicates median (50th percentile), box indicates 25th and 75th percentiles, error bar indicates 10th and 90th percentiles, and open circles indicate values beyond 10th and 90th percentiles.



ward to satisfy their energy demands. Plants with long-lived flowers that we have studied so far mostly grow isolated from conspecifics and we have observed no hummingbirds defending them as territories. These observations, along with the fact that the flowers are either protandrous or distylous, lead us to think that outcrossing (and (or) geitonogamy) should be promoted among plants infested with flower mites. In contrast, plants with short-lived flowers (*H. patens* and *P. padifolia*) are visited by a wider assemblage of pollinating and nonpollinating species including hummingbirds, butterflies, solitary bees, and ants (Colwell 1995; Contreras and Ornelas 1999). As previously suggested (Roubik 1982; Dobkin 1987), the reduction in flower longevity ("one-dayness") along with a surplus of flowers (Roubik et al. 1985), may enhance outcrossing by increasing resource patchiness and (or) flower visitation rates (see also Carpenter 1979; McDade and Kinsman 1980); however, it could also be a response to nectar robbers and thieves, over evolutionary time. The effect of the mite-exclusion treatment was not detected in 1-day *T. deppeana* flowers. This result is intriguing because this semelparous epiphytic bromeliad grows isolated, produces relatively few flowers, opens 2–3 flowers per day (Table 1), and it is not defended by hummingbirds as a floral patch. The functional significance of bracts, apparently protecting the long flowers, and the bract liquid in *T. deppeana* is unknown (García-Franco and Rico Gray 1991); we do not know if this kept the mites away from our control plants.

#### Mite feeding habits and nectar consumption by other floral inhabitants

It is possible that the observed differences among species in nectar availability resulted because mite species simply have different feeding habits or consumption rates. Dobkin (1984) estimated 12  $\mu\text{L}$  per day of nectar consumption by *Rhinoseius* mites, which is ca. 20% of the average daily volume of nectar secreted by a single, 1-day, *Heliconia* flower. Colwell (1995) estimated 6.3  $\mu\text{L}$  per day of nectar consumption by *Proctolaelaps* mites, which is ca. 41% of the nectar secreted by single, 1-day, *Hamelia* flowers. In our study, nectar consumption, presumably by flower mites, ranged from 33 to 55% among long-lived flowers and from 2 to 33% among short-lived flowers (Table 1). Because only *Tropicoseius* mites inhabited our study plants (except *H. patens*), we believe that the observed differences in nectar availability among long-lived flowers are not likely explained by differences in consumption rates among species of flower mites.

Other floral inhabitants such as thrips and non-hummingbird mites may have contributed to the observed reduction in nectar availability. Flower thrips and non-hummingbird mites (dispersed by bees and butterflies) are known to feed on floral tissue and consume pollen from flowers affecting pollination of mainly trees and vines in the tropics (Sakai 2001); whether they consume nectar the way hummingbird-flower mites do, remains to be investigated.

#### Plant responses to repeated nectar removals

Our results suggest that hummingbird-flower mites reduced the standing crop of nectar, but whether or not plants compensated for nectar loss cannot be directly addressed

**Table 3.** Summary of repeated-measures ANOVAs on the effects of flower mite exclusion on nectar production in short-lived flowers of *Tillandsia deppeana*, *Hamelia patens*, and *Palicourea padifolia*.

Source of variation	df	MS	F	p
<b><i>Tillandsia deppeana</i></b>				
Between-plant variation				
Treatment	1	0.115	1.318	0.257
Within-plant variation				
Time of day	4	0.696	14.395	<0.01
Time of day × treatment	4	0.076	1.573	0.183
Residual	180	0.048		
<b><i>Hamelia patens</i></b>				
Between-plant variation				
Treatment	1	0.211	1.158	0.289
Within-plant variation				
Time of day	4	4.448	39.771	<0.001
Time of day × treatment	4	0.195	1.747	0.143
Residual	152	0.112		
<b><i>Palicourea padifolia</i></b>				
Between-plant variation				
Treatment	1	0.130	0.184	0.669
Floral morph	1	0.514	7.414	0.008
Treatment × floral morph	1	0.056	0.811	0.371
Within-plant variation				
Time of day	4	2.464	48.867	<0.001
Time of day × treatment	4	0.053	1.060	0.376
Time of day × floral morph	4	0.254	5.032	<0.001
Time of day × floral morph × treatment	4	0.047	0.927	0.448
Residual	304	0.050		

**Note:** Mite treatment (exclusion of both mites and hummingbirds versus exclusion of hummingbirds only) and floral morph (only in *P. padifolia*) were treated as fixed effects and the volume of nectar secreted ( $\log_{10}$  transformed) was the repeated factor. Nectar secretion was measured five times a day (3-h intervals).

with our data. Plants with flowers that last several days may respond by continuously secreting nectar; when robbed or thieved they could either reabsorb nectar or produce less nectar per day. Because flower mites do not damage the flower (no apparent physical damage to floral tissue) the way nectar robbers do, there is no conceivable feedback. Continuous nectar production by long-lived flowers occurred at the same rate in all our study plants but decreased by the fifth day in all cases. Despite this, the treatment effect was constant over their lifespans (Table 2; see also Lara and Ornelas 2001b). Our results suggest that nectar production occurred continuously even in the absence of pollination (removal and deposition of pollen by hummingbirds). Increased nectar production may have been stimulated by continuous extraction resulting in an underestimation of nectar availability. This is particularly important for the plants with short-lived flowers. That is, we may have failed to detect the effect of the mite-exclusion treatment because plants secreted additional nectar to compensate for the loss of nectar attributed to flower mites. This explanation is feasible only if plants are able to “sense” the presence of flower mites and, as a feedback response, they increased nectar secretion. It is highly likely that the plants sense the physical presence of the mites; however, we were draining the flowers the same way in both types of exclusion, and the effect of the mite-exclusion treatment was constant over time in most

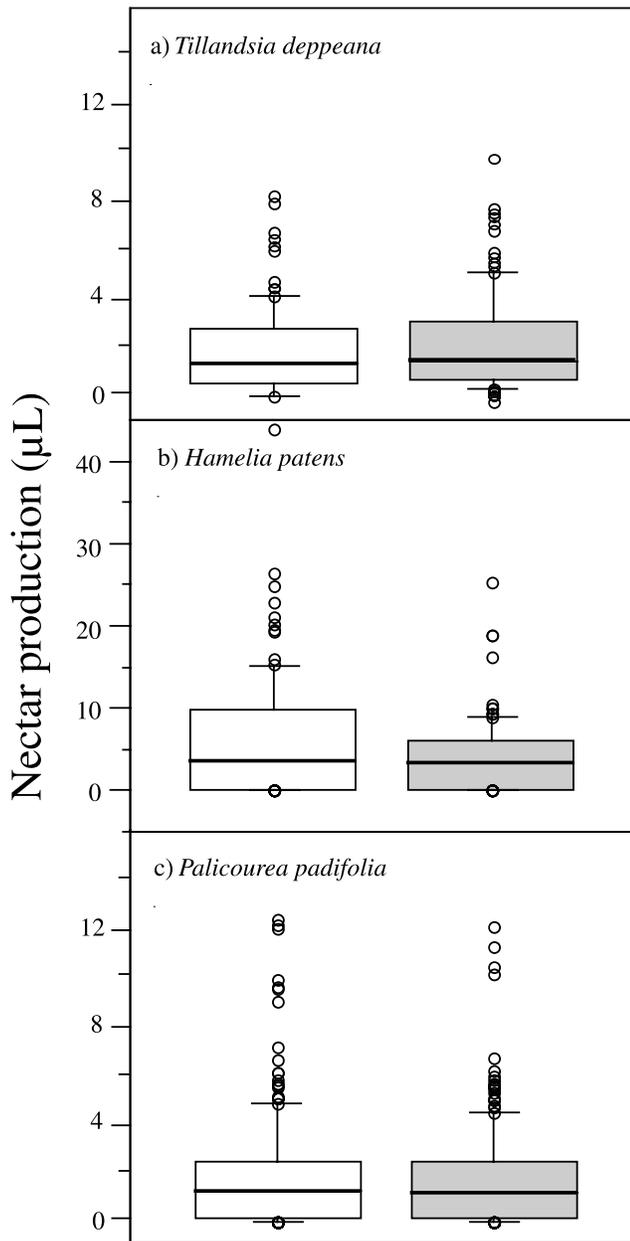
cases. In the future, it would be interesting to investigate whether plants are able to sense the presence of flower mites, and, consequently, respond quickly by producing additional nectar (see also Castellanos et al. 2002). If plants are able to distinguish between pollinators and robbers and (or) thieves, that would suggest that nectar secretion patterns might be adaptively plastic to both pollinators and nectar robbers and thieves (Irwin et al. 2001).

#### **Selection of floral traits by multiple-species interactions**

Nectar robbing is a common and complex phenomenon that may have ecological and evolutionary implications (Irwin et al. 2001). If a plant is robbed of nectar, a certain volume of nectar is still needed to keep the most effective pollinators as constant visitors (Maloof and Inouye 2000; Ornelas et al. 2002); these plants, or populations, producing enough nectar for both robbers and pollinators would be the most successful in terms of fitness. Pyke (1991) argued that optimal rates of nectar production should be higher in the presence of nectar robbers (see also Soberón and Martínez del Río 1985; Roubik et al. 1985; Morris 1996) and Roubik et al. (1985) showed less nectar production in flowers without robbers.

Over evolutionary time, plants in heavily robbed areas may have increased nectar production or robbers may preferentially use plants with higher nectar production, or both

**Fig. 4.** Effects of mite exclusion on nectar secretion ( $\mu\text{L}$ ) by short-lived flowers of (a) *Tillandsia deppeana*, (b) *Hamelia patens*, and (c) *Palicourea padifolia*. Because time of day  $\times$  treatment interactions were not significant, only the treatment effect (pooling across time of day) is presented. See Table 3 for statistical details and significance levels.  $n = 20$  flowers in each treatment. Open bars = without mites, shaded bars = with mites. Data presentation as in Fig. 3.



(see also Ornelas et al. 2002). If flower mites exert selective pressures on nectar volume, one would expect to observe higher nectar volumes among flowers hosting flower mites than flowers without mites. Here, we suggest that flower mites may have played an additional selective role in increasing nectar production among plants that have large, long-lived flowers and become heavily infested with mites.

Flower mites are reported for 20 plant families including Heliconiaceae, Rubiaceae, Lobeliaceae, Gesneriaceae, and

Ericaceae (Colwell 1985); however, other plant families rich in hummingbird-pollinated species such as Labiateae, Convolvulaceae, Malvaceae, Onagraceae, and Acanthaceae do not host flower mites and have long-lived flowers. Nectar robbers have been proposed as agents of selection on flower form (Waser 1979; Roubik et al. 1985; Soberón and Martínez del Río 1985; Lara and Ornelas 2001a), arrangement and (or) flower position (Colwell et al. 1974; Traveset et al. 1998), nectar volume (Roubik et al. 1985; Morris 1996), and floral protective mechanisms (Guerrant and Fiedler 1981; Inouye 1983). However, flower longevity is phylogenetically restricted at the family level (Stratton 1989); other factors may have played a role in the evolution of this floral trait including those selective forces to promote outcrossing and those imposed by the demands of multiple-species interactions. If so, there is an apparent “trade-off” between the reduction in inbreeding and the exposure time, not only to pollinators, but also to floral antagonists. This explanation does not necessarily exclude the alternative that flower mites have invaded host-plant systems with long-lived flowers more recently. As a working hypothesis, we propose that nectar production has increased over evolutionary time, not only by the selective pressures imposed by the pollinators, but also to compensate for the reduction they suffer after exploitation by nectar robbers and thieves such as flower mites.

### Acknowledgements

Comments by M.C. Arizmendi, J.L. Bronstein, R.K. Colwell, A.R. Davis, P.G. Kevan, J.G. García Franco, D.W. Inouye, J. López Portillo, M. Ordano, D.W. Roubik, and an anonymous reviewer greatly improved an earlier version of this paper. We also thank Citlalli Castillo for help during fieldwork and for photographs of some of the short-lived flowers. E. Quintero kindly photographed the flower mites. Thanks to G. Angeles for the facilities to conduct our research in his Arquitectura Hidráulica lab at the Instituto de Ecología, A.C. This work was supported by a scholarship from the Consejo Nacional de Ciencia y Tecnología, México (No. 112675) to C. Lara and the Departamento de Ecología y Comportamiento Animal, Instituto de Ecología, A.C., Xalapa, Veracruz, México. This work constitutes partial fulfillment of C. Lara’s doctorate in Ecología y Manejo de Recursos Naturales at the Instituto de Ecología, A.C.

### References

- Abacus Concepts Inc. 1989. Abacus Concepts, SuperANOVA. Abacus Concepts, Berkeley, Calif.
- Abacus Concepts Inc. 1996. Abacus Concepts, Statview Reference Abacus Concepts, Berkeley, Calif.
- Bronstein, J.L. 2001. The exploitation of mutualisms. *Ecol. Lett.* **4**: 277–287.
- Carpenter, F.L. 1979. Competition between hummingbirds and insects for nectar. *Am. Zool.* **19**: 1105–1114.
- Castellanos, M.C., Wilson, P., and Thomson, J.D. 2002. Dynamic nectar replenishment in flowers of *Penstemon* (Scrophulariaceae). *Am. J. Bot.* **89**: 111–118.
- Castillo-Campos, G. 1985. Integración de paisajes en la región de Jalcomulco, Veracruz. Bachelor’s Thesis. Universidad Veracruzana. Xalapa.

- Castillo-Campos, G. 1991. Vegetación y flora del municipio de Xalapa, Veracruz. Instituto de Ecología, A.C. Publication No. 30. Xalapa, Mexico.
- Colwell, R.K. 1973. Competition and coexistence in a simple tropical community. *Am. Nat.* **107**: 737–760.
- Colwell, R.K. 1979. The geographical ecology of hummingbird flower mites in relation to their host plants and carriers. In *Recent advances in acarology. Volume II. Edited by J.G. Rodríguez.* Academic Press, New York. pp. 461–468.
- Colwell, R. K. 1985. Stowaways on the hummingbird express. *Nat. Hist.* **94**: 56–63.
- Colwell, R.K. 1986a. Community biology and sexual selection: lessons from hummingbird flower mites. In *Ecological communities. Edited by T.J. Case and J. Diamond.* Harper and Row, New York. pp. 406–424.
- Colwell, R.K. 1986b. Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. In *Evolutionary process and theory. Edited by S. Karlin and E. Nevo.* Academic Press, New York. pp. 475–495.
- Colwell, R.K. 1995. Effects of nectar consumption by the hummingbird flower mite *Proctolaelaps kirmsei* on nectar availability in *Hamelia patens*. *Biotropica*, **27**: 206–217.
- Colwell, R.K. 2000. Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. *Am. Nat.* **156**: 495–510.
- Colwell, R.K., and Naeem, S. 1994. Life-history patterns of hummingbird flower mites in relation to host phenology and morphology. In *Mites: ecological and evolutionary analyses of life patterns. Edited by M.A. Houck.* Chapman and Hall, New York. pp. 23–44.
- Colwell, R.K., Betts, B.J., Bunnell, P., Carpenter, F.L., and Feinsinger, P. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flowerpiercer *Diglossa plumbea*, and its evolutionary implications. *Condor*, **76**: 447–452.
- Contreras, P.S., and Ornelas, J.F. 1999. Reproductive conflicts of *Palicourea padifolia* (Rubiaceae) a distylous shrub of a tropical cloud forest in Mexico. *Plant Syst. Evol.* **219**: 225–241.
- Devlin, B., and Stephenson, A.G. 1985. Sex differential floral longevity, nectar secretion, and pollinator foraging in a protandrous species. *Am. J. Bot.* **72**: 303–310.
- Dobkin, D.S. 1984. Flowering patterns of long-lived *Heliconia* inflorescences: implications for visiting and resident nectarivores. *Oecologia*, **64**: 245–254.
- Dobkin, D.S. 1985. Heterogeneity of tropical floral microclimates and the response of hummingbird flower mites. *Ecology*, **66**: 536–543.
- Dobkin, D.S. 1987. Synchronous flower abscission in plants pollinated by hermit hummingbirds and the evolution of one-day flowers. *Biotropica*, **19**: 90–93.
- Dobkin, D.S. 1990. Distribution patterns of hummingbird flower mites (Gamasidae: Ascidae) in relation to floral availability on *Heliconia* inflorescences. *Behav. Ecol.* **1**: 131–139.
- Elias, T.S. 1976. A monograph of the genus *Hamelia* (Rubiaceae). *Mem. N.Y. Bot. Gard.* **26**: 81–144.
- Faivre, A.E. 2000. Ontogenetic differences in heterostylous plants and implications for development from a herkogamous ancestor. *Evolution*, **54**: 847–858.
- Feinsinger, P., Wolf, J.A., and Swarm, L.A. 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology*, **63**: 494–506.
- García-Franco, J.G., and Rico Gray, V. 1991. Biología reproductiva de *Tillandsia deppeana* (Bromeliaceae). *Selbyana*, **9**: 76–87.
- García-Franco, J.G., Martínez-Burgoa, D., and Pérez, T.M. 2001. Hummingbird flower mites and *Tillandsia* spp. (Bromeliaceae) polyphagy in a cloud forest of Veracruz, México. *Biotropica*, **33**: 538–542.
- Guerrant, E.O., and Fiedler, P.L. 1981. Flower defenses against nectar-pilferage by ants. *Rep. Bot.* **7**: 25–33.
- Heyneman, A.J., Colwell, R.K., Naeem, S., Dobkin, D.S., and Hallet, B. 1991. Host plant discrimination: experiments with hummingbird flower mites. In *Plant–animal interactions: evolutionary ecology in tropical and temperate regions. Edited by P.W. Price, T.M. Lewinsohn, G.W. Fernandes, and W.W. Benson.* John Wiley and Sons, New York. pp. 455–485.
- Inouye, D.W. 1980. The terminology of floral larceny. *Ecology*, **61**: 1251–1253.
- Inouye, D.W. 1983. The ecology of nectar robbing. In *The biology of nectaries. Edited by B. Bentley and T. Elias.* Columbia University Press, New York. pp. 153–173.
- Irwin R.E., Brody, A.K., and Waser, N.M. 2001. The impact of floral larceny on individuals, populations, and communities. *Oecologia*, **129**: 161–168.
- Kearns, C.N., and Inouye, D.W. 1993. Techniques for pollination biologists. University Press of Colorado, Niwot, Colo.
- Lara, C. 2001. Colibríes como vectores de antagonistas: los riesgos de la polinización. Doctoral thesis (Ecología y Manejo de Recursos Naturales), Instituto de Ecología, A.C., Xalapa, Mexico.
- Lara, C., and Ornelas, J.F. 2001a. Preferential nectar robbing of flowers with long corollas: experimental studies of two hummingbird species visiting three plant species. *Oecologia*, **128**: 263–273.
- Lara, C., and Ornelas, J.F. 2001b. Nectar “theft” by hummingbird flower mites and its consequences for seed set in *Moussonia deppeana*. *Funct. Ecol.* **15**: 78–84.
- Lara, C., and Ornelas, J.F. 2002. Effects of nectar theft by flower mites on hummingbird behavior and the reproductive success of their host plant, *Moussonia deppeana* (Gesneriaceae). *Oikos*, **96**: 470–480.
- Maloof, J.E. and Inouye, D.W. 2000. Are nectar robbers cheaters or mutualists? *Ecology*, **81**: 2651–2661.
- McDade, L.A., and Kinsman, S. 1980. The impact of floral parasitism in two Neotropical hummingbird-pollinated plant species. *Evolution*, **34**: 954–958.
- McVaugh, R. 1942. Campanulaceae (Lobelioideae) in North America. *Flora*, **32**: 1–134.
- Morris, W.F. 1996. Mutualism denied? Nectar-robbing bumblebees do not reduce female or male success of bluebells. *Ecology*, **77**: 1451–1462.
- Naskrecki, P., and Colwell, R.K. 1998. Systematics and host plant affiliations of hummingbird flower mites of the genera *Tropicoseius* Baker and Yunker and *Rhinoseius* Baker and Yunker (Acari: Mesostigmata: Ascidae). Thomas Say Publ. Entomol. Monogr., Entomological Society of America, Lanham, Md.
- Novelo, A. 1978. La vegetación de la Estación El Morro de la Mancha. *Biótica*, **3**: 9–21.
- Ornelas, J.F., Ordano, M., Hernández, A., López, J.C., Mendoza, L., and Perroni, Y. 2002. Nectar oasis produced by *Agave marmorata* Roehl. (Agavaceae) lead to spatial and temporal segregation among nectarivores in the Tehuacán Valley, México. *J. Arid Environ.* **52**: 37–51.
- Paciorek, C.B., Moyer, B., Levin, R., and Halpern, S. 1995. Pollen consumption by the mite *Proctolaelaps kirmsei* and possible fitness effects on *Hamelia patens*. *Biotropica*, **27**: 258–262.
- Primack, R.B. 1985. Longevity of individual flowers. *Ann. Rev. Ecol. Syst.* **16**: 15–37.

- Proctor, H., and Owens, I. 2000. Mites and birds: diversity, parasitism and coevolution. *Trends Ecol. Evol.* **15**: 358–364.
- Pyke, G.H. 1991. How much does floral nectar cost? *Nature*, **350**: 58–59.
- Roubik, D.W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology*, **63**: 354–360.
- Roubik, D.W., Holbrook, N.H., and Parra, V. 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia*, **66**: 161–167.
- Sakai, S. 2001. Thrips pollination of androdioecious *Castilla elastica* (Moraceae) in a seasonal tropical forest. *Am. J. Bot.* **88**: 1527–1534.
- Smith, L.B., and Downs, R.J. 1977. Tillandsioideae (Bromeliaceae). *Flora Neotrop. Monogr.* **14**: 663–1494.
- Soberón, J., and Martínez del Rio, C. 1985. Cheating and taking advantage in mutualistic associations. *In* *The biology of mutualism*. Edited by D.H. Boucher. Croom Helm, London. pp. 192–216.
- Stiles, F.G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology*, **56**: 285–301.
- Stratton, D.A. 1989. Longevity of individual flowers in a Costa Rican cloud forest: ecological correlates and phylogenetic constraints. *Biotropica*, **21**: 308–318.
- Taylor, C.M. 1989. Revision of *Palicourea* (Rubiaceae) in Mexico and Central America. *Syst. Bot. Monogr.* **26**: 1–102.
- Traveset, A., Willson, M.F., and Sabag, C. 1998. Effect of nectar-robbing birds on fruit set of *Fuchsia magellanica* in Tierra del Fuego: a disrupted mutualism. *Funct. Ecol.* **12**: 459–464.
- Waser, N.M. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). *Oecologia*, **39**: 107–121.
- Williams-Linera, G., and Tolome, J. 1996. Litterfall, temperate and tropical dominant trees, and climate in a Mexican lower montane forest. *Biotropica*, **28**: 649–656.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, N.J.