The Effect of Hummingbird Flower Mites on Nectar Availability of Two Sympatric Heliconia Species in a Brazilian Atlantic Forest

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Background and Aims Hummingbird flower mites feed and reproduce in flowers of host plants pollinated by hummingbirds, and use the nostrils and bill of the hummingbird to move from plant to plant. These mites compete with the pollinator for the nectar produced by flowers. An investigation was made of the relationship between the pattern of nectar production and the effects of hummingbird flower mites in the flowers of two sympatric species of Heliconia (Heliconiaceae).

Methods Nectar production was sampled by carrying out two experiments: 2-hour intervals and accumulated nectar. Flowers with and without mites were used in both experiments.

Key Results Exclusion of mites increased nectar production, especially in accumulated daily production (a maximum of 49% more nectar). Both Heliconia species had the same pattern of nectar production: a high concentration in the morning, which was progressively reduced as the day passed. This pattern of nectar production coincides with the behaviour of the pollinator, which makes more frequent visits in the morning, as observed in a previous study.

Conclusions The results suggest that the impact of mites on nectar availability of Heliconia is more important with regard to total volume of nectar produced irrespective of flower longevity. A high variation among individuals in nectar produced in the populations was also observed. Hummingbird flower mites strongly affect availability of nectar for hummingbirds.

Key words: Brazilian Atlantic Forest, hummingbird flower mites, nectar production, Ascidae, nectarivory, Heliconia spathocircinata, Heliconia laneana var. flava.

INTRODUCTION

Nectar can have two important functions in the plant: it is an important component of the plant’s reproductive system because it attracts a pollinator as a reward for the energetic costs of its production or it is used to attract animals that defend the plant (Pacini et al., 2003). From the reproductive perspective, the efficiency of pollinator attraction ensures successful reproduction, which increases individual plant fitness. Many nectar robbers, such as bees (Irwin and Brody, 1999), ants (McDade and Kinsman, 1980) and birds (Navarro, 2001), affect the frequency of visits by pollinators, thus reducing pollen flow and consequently seed production (Irwin and Brody, 1998).

Flower mites are also considered to be nectar robbers (Colwell, 1973). Flower mites, mainly from the genera Rhinoseius Baker and Yunker, Tropicoiseus Baker and Yunker and Proctolaelaps Berlese (Colwell, 1985; Lara and Ornelas, 2001), live and reproduce in flowers of the host species, and feed on their nectar (Colwell, 1973) and pollen (Colwell, 1985; Paciorek et al., 1995). The only way for these mites to reach the host plant is by travelling on flower visitors, such as bees (Seeman and Walter, 1995), moths (Treat, 1975), butterflies (Boggs and Gilbert, 1987) and, more recently observed, bats (Tschapka and Cunningham, 2004). Hummingbird flower mites use the hummingbird’s bill and nostrils (phoresy; Proctor and Owens, 2000) to reach new plants, but they can move on their own among flowers of the same inflorescence (Colwell, 1973). Hummingbird flower mites are found in many plant families, but are more common in Heliconiaceae, Costaceae, Zingiberaceae, Amarillidaceae, Rubiaceae, Apocynaceae, Bromeliaceae, Gesneriaceae, Lobeliaceae and Ericaceae (Colwell, 1995; Naskrecki and Colwell, 1998). Hummingbirds are important pollinators of all these plants (Colwell, 1995).

In general, two mite–plant interaction systems are recognized: monophagy, in which a mite species feeds on a single plant species, which flowers all year round and thus produces a continuous food supply; or polyphagy, in which mites use different host plant species due to the short flowering period of each one (García-Franco et al., 2001). From the mite’s perspective some conditions are needed to ensure successful dispersal, and three are essential: the existence of an open flower, the correct temperature in the dispersal area (area used by mites to leave the flower) of the bract and the visit of a hummingbird (Dobkin, 1985). Moreover, mites recognize their host plants by floral nectar scent while the hummingbird is hovering on the flower for 1–5 s, and have to decide quickly whether to leave the bird or not (Colwell, 1985).

Hummingbird flower mites can deplete the nectar of their hosts. For instance, as much as 40 and 50% of the nectar produced by Hamelia patens (Rubiaceae) and Moussonia deppeana (Gesneriaceae), respectively, are consumed by...
mites (Colwell, 1995; Lara and Ornelas, 2001). However, Lara and Ornelas (2002a) showed that flower longevity is an important factor to be considered when measuring the impact of mites. For example, they showed that in plant species with 1-d flowers nectar availability does not differ between flowers with mites and without mites when compared with long-lived flowers. In the latter, they found a significant difference in nectar production between flowers with and without mites. The reduction in nectar availability may in turn affect pollinator behaviour or visitation rate (Lara and Ornelas, 2002b). This means that flower mites can potentially have a strong effect on reproductive success of plants. Lara and Ornelas (2002b) observed that pollinator visits to flowers of *Moussonia deppeana* lasted longer but became less frequent as a result of nectar reduction, and that this change in pollinator behaviour, surprisingly, also increased the seed production and reproductive success of the plant.

In the Atlantic Forest of Reserva Biológica União (Rio de Janeiro, Brazil) there are two sympatric species of *Heliconia* (Heliconiaceae): *H. laneana* var. *flava* and *H. spathocircinata*. These species have a sequential flowering model, in which both species have well-defined and asynchronous reproductive seasons, with only a short overlap (Cruz et al., 2006). The main pollinator of both *Heliconia* species is the hummingbird *Phaethornis idaliae* (Cruz et al., 2006) and hummingbird flower mites can be found in flowers of both *Heliconia* species (our pers. observ.).

The flowering and pollinating systems of both *Heliconia* species form good models to study evolutionary consequences of parasites on pollination. Therefore, we hypothesize that nectar production by both species of *Heliconia* is strongly affected by consumption by flower mites. The objectives were two-fold. First, nectar production by both *Heliconia* species was described to determine whether flowers produce nectar only just after the beginning of the anthesis or throughout the day. Second, the effect of mites on the production of nectar was evaluated by carrying out field experiments.

**MATERIALS AND METHODS**

**Study area**

Fieldwork was carried out in the Reserva Biológica União (hereafter Rebio União), Rio de Janeiro state, south-eastern Brazil (42°02’116”W, 22°25’035”S). Rebio União is covered by 3-126 ha of continuous Atlantic forest with endemic species and important water sources (SEMA, 2001). There are two well-defined seasons: one hot and rainy, from October to March, and a cooler and drier one from April to September. For a detailed description of the study area see Cruz et al. (2006).

**Species studied**

*Heliconia* is a tropical genus of the family Heliconiaceae, and its most conspicuous feature is the brightly coloured bracts of the inflorescence (Berry and Kress, 1991), which may vary from bright red to bright yellow. In general, these plants open only a few flowers per day, usually one, and flowers last 1 d (Stiles, 1975). Flowers of *Heliconia* are mainly pollinated by hummingbirds (Berry and Kress, 1991). However, the Old World species *H. salomonensis* is pollinated by the flying-fox *Melonycteris woodfordi* (Kress, 1985).

*Heliconia spathocircinata* Aristig. has a wide distribution all over South America and its inflorescence is red (Andersson, 1992). In Rebio União its flowering period occurs from November to February (Cruz et al., 2006). *H. laneana* Barr. var. *flava* (Barr.) occurs only in south-eastern Brazil (Andersson, 1985). In Rebio União its flowering season occurs from May to August, and its inflorescence is yellow (Cruz et al., 2006). The hummingbird *Phaethornis idaliae* is the pollinator of both these *Heliconia* species (Cruz et al., 2006). However, *H. laneana* is also pollinated by lepidopteran insects, although less frequently (less than 30%) (Cruz et al., 2006).

**Identification and counting of mites**

Eighteen *H. laneana* flowers and 13 *H. spathocircinata* flowers were collected for mite identification and counting. Each flower was preserved in individual glass vials with 70% ethanol. Flowers were dissected under a stereomicroscope in order to search for flower mites. All mites found in each flower were counted and identified. Voucher specimens were deposited in the museum of the Departamento de Zoologia Agrícola, Escola Superior de Agricultura ‘Luiz de Queiroz’/USP.

**Mites and nectar production**

Experiments were carried out in the flowering seasons of June and July, 2004 and May, 2005 for *H. laneana* and January and February, 2005 and January, 2006 for *H. spathocircinata*. All experiments (with and without mites – see below) were performed simultaneously and interspersed in space in both years. These species are rhizomatous and in order to ensure that different genets were sampled, individuals were tagged at least 5 m apart from each other. To avoid pseudoreplication only one flower of each genet (individual) was used for each experiment. In this way, the same genet could have only two flowers used for each experiment (hourly and accumulated nectar measures – see below).

The effect of mites on nectar secretion was tested by performing two treatments:

1. Exclusion of mites and hummingbirds – new inflorescences without open flowers or floral buds were protected with tulle bags, as suggested by Colwell (1995) to guarantee that hummingbird visits were not possible and, consequently, mites could not reach the inflorescence. This care was taken because, once in the flower, hummingbird flower mites can move freely within the inflorescence and reach new flowers. Before each measure the flowers were carefully checked to ensure that mites were not present.
Inflorescences remained bagged until the end of the experiment. Nectar volume and concentration were sampled at 2-h intervals, from 0630 to 1430 h (total = five samples per day per flower). Because flowers open around 0600 h, the first sample represents the initial nectar production. Sampling at 2-h intervals throughout the day is termed ‘hourly’ in the text. Hourly nectar production was sampled in 13 flowers of *H. laneana* and 12 flowers of *H. spathocircinata*. In other flowers, the volume and concentration of the accumulated nectar were also estimated only in the afternoon, at around 1500 h. This time of day was chosen because it is when pollinators cease to visit the flowers (Cruz et al., 2006). This sampling is referred to as ‘accumulated’ in the text. The accumulated nectar was sampled in eight flowers of *H. laneana* and 21 flowers of *H. spathocircinata*.

(2) Exclusion of hummingbirds – nectar was sampled in flowers from inflorescences with already opened flowers, which stayed bagged from the day before sampling started until the end of the experiment. In this treatment, hummingbirds could not visit the flowers, but mites were already present and could move freely within the inflorescence. Before each measure the flowers were checked to ensure that mites were present. In this treatment 25 flowers of *H. laneana* and 28 flowers of *H. spathocircinata* were used to sample the hourly nectar production and 18 flowers of *H. laneana* and 27 flowers of *H. spathocircinata* were used to sample the accumulated nectar.

Nectar volume and concentration were sampled using 25-μL Hamilton microsyringes and a portable refractometer (0–50 % brix) (WYT-4 and Fujian Quanzhou Optical Instrument Factory, respectively). Nectar concentration is referred to as ‘accumulated’ in the text. The accumulated nectar was sampled in eight flowers of *H. laneana* and 21 flowers of *H. spathocircinata*. The average number of mites per flower was 7.4 (s.d. = 3.27). Proctolaelaps species were observed: a novel species of the genus Proctolaelaps, which occurred in all flowers (*n* = 18), and Tropicoiseius heliconiae, which was observed in 11 flowers.

In *H. spathocircinata* 96 mites were found in 13 flowers. The average number of mites per flower was 7.4 (s.d. = 3.27). Three species of mites were observed: the same novel species of Proctolaelaps found in *H. laneana* occurred in 12 flowers; Tyrophagus sp. occurred in nine flowers; and one individual of Asca sp. occurred in one flower (the flower in which Proctolaelaps was not found).

**Mites and nectar production**

Flowers of *Heliconia laneana* always opened producing a high volume of nectar: 36 ± 14 μL (mean ± s.d.) in flowers with mites and 27 ± 21 μL in flowers without mites. Production decreased as the day passed (Fig. 1A, C) and this trend was observed in flowers with and without mites (Fig. 1). There was no significant difference (*F* = 0.0455, *P* = 0.8) among sampling times in hourly treatments. In the two experiments considerable individual variability was observed in the production of nectar (Fig. 1).

Variation in nectar concentration during the day in *H. laneana* flowers was similar to variation in nectar volume, with the highest concentration occurring at the beginning of the day and decreasing thereafter (Fig. 1B, D). There was no statistically significant difference among hourly treatments (*F* = 3.249, *P* = 0.08).

In *Heliconia laneana*, flowers with mites accumulated significantly less nectar (43 ± 17 μL) than those without mites (61 ± 22 μL; *t* = 2.16, d.f. = 24; *P* = 0.04) (Fig. 2A). However, accumulated nectar concentration did not differ (*P* > 0.05) between flowers with (24 ± 2 %) and without mites (23 ± 2 %) (Fig. 2B). Variation among individuals in nectar volume was greater than in nectar concentration (Fig. 2).

In flowers with mites of *H. laneana*, total nectar volume observed was higher in the hourly sample (72 ± 25 μL) than in the accumulated sample (43 ± 17 μL; *t* = 4.18, d.f. = 41, *P* < 0.001). Individuals of *H. spathocircinata* also showed high variation in the volume of nectar produced hourly and accumulated in flowers with and without mites (Figs 3 and 4). There was a significant difference in volume of nectar production hourly between flowers with and without mites (*F* = 14.190, *P* = 0.001), but no difference was observed in nectar concentration (*F* = 0.868, *P* = 0.362). However, the sum of the volumes of nectar produced hourly was significantly different between flowers with (41 ± 27 μL) and without mites (62 ± 33 μL; *t* = 2.08, d.f. = 38, *P* = 0.04). All comparisons made between hourly and accumulated nectar volume were significant: between hourly volume with mites (41 ± 27 μL) and accumulated volume with mites (18 ± 22 μL; *U* = 183, *Z* = 3.28, *P* = 0.001); between hourly volume without mites (62 ± 33 μL) and accumulated volume without mites (34 ± 20 μL; *t* = 2.91, d.f. = 31, *P* = 0.006); and between accumulated volume of flowers with (18 ± 22 μL) and without mites (34 ± 20 μL; *U* = 139, *Z* = −3.0, *P* = 0.002).

**RESULTS**

**Mites**

In total, 1896 mites (105.3 ± 106.1, mean ± s.d.; range 9–330) were collected in 18 flowers of *H. laneana*. Two mite species were observed: a novel species of the genus Proctolaelaps, which occurred in all flowers (*n* = 18), and Tropicoiseius heliconiae, which was observed in 11 flowers.

To test for data normality a Shapiro–Wilk’s test was used. In the hourly experiment we tested for differences between flowers with and without mites in all five samples, using a repeated-measures ANOVA. A t-test or Mann–Whitney (according to the normality test) test was used to compare hourly volume production (sum of volume in all samples) with accumulated nectar volume and to compare accumulated nectar production (volume and concentration) between flowers with and without mites (Zar, 1999). Statistical analyses were made using the software applications STATISTICA 6.0 and SYSTAT 10.0.
Heliconia spathocircinata presented the same pattern observed in H. laneana: a high concentration of sugar in nectar, which decreased before the second sample (Fig. 3B, D). There was also a high individual variation in nectar concentration in all experiments (Fig. 3), but this variation was lower in the accumulated nectar in flowers without mites (Fig. 4B). Significant differences were observed in the accumulated concentration between flowers with (14 ± 12 %) and without mites (28 ± 3 %; $U = 84.5$, $Z = -4.13$, $P < 0.001$).

DISCUSSION

At Rebio União mites affected the availability of nectar in Heliconia flowers. In H. spathocircinata mites greatly reduced the amount of nectar produced, not only for the accumulated nectar (flowers with mites had 49 % less accumulated nectar) but also hourly production (flowers with mites had 33 % less nectar than flowers without mites). For H. laneana flowers mites had a large impact in nectar availability, but this was more significant in the accumulated nectar (flowers with mites had 30 % less accumulated nectar than flowers without mites) than in the hourly nectar production (flowers without mites had 13 % more nectar than flowers with mites), despite the high number of mites found per flower.

Flower longevity is one aspect that may play an important role in the plant reproductive system, because it influences pollinator attraction, inbreeding level (Stratton, 1989) and also hummingbird flower mite – host plant interactions (Lara and Ornelas, 2002a). Lara and Ornelas (2002a) suggested that long-lived flowers are significantly more affected by consumption of nectar by mites than are short-lived (1-d) flowers because this influence is related to the nectar volume produced by flowers throughout its life time. So long-lived flowers produced greater amounts of nectar (>7 µL per flower) than short-lived ones and, consequently, mites consumed proportionately more nectar (Lara and Ornelas, 2002a). Although both Heliconia species studied have 1-d flowers, they produce a large amount of nectar (>20 µL per flower), especially at the beginning of the floral anthesis. It seems that for Heliconia at Rebio União the effect of mites is more important on total nectar volume irrespective of the longevity of the flower. If a 1-d flower produces a large amount of nectar, as in this study, mites can significantly reduce its availability.

Fig. 1. Nectar volume (µL) and concentration (% sugar) through the day (five samples) in flowers with (A, B, n = 25) and without (C, D, n = 13) mites in Heliconia laneana var. flavo in the Atlantic Forest of Reserva Biológica União (Rio de Janeiro, Brazil).
for hummingbirds. For Heliconia spathocircinata, mites consumed a similar proportion of the total nectar volume as observed in 1-d flowers of Hamelia patens (40%; Colwell, 1995) and in long-lived flowers of Moussonia deppeana (50%; Lara and Ornelas, 2001). Nevertheless, in H. laneana mites consumed less nectar than observed by these authors for these species. However, the hourly consumption in H. laneana was similar to the consumption observed for the 1-d flowers of Tillandsia deppeana (10 %) and for the long-lived flowers of Lobelia cardinalis (Lobeliaceae) (13 %) (Lara and Ornelas, 2002a). Nectar production by Heliconia flowers seems to fit within the hypothesis proposed by Lara and Ornelas (2002a) that high nectar volume is important not only to guarantee pollinator visitation, but also to compensate for the reduction caused by flower mites or other nectar robbers.

The main pollinator of the two Heliconia species studied here is the hummingbird Phaethornis idalie, which visits their flowers more frequently during the morning (Cruz et al., 2006), when nectar production is also higher as observed in the present study. Thus, it is probable that a higher visitation rate in the morning may increase the hummingbird’s chances of meeting its nutritional requirements. Lepidopteran species also made legitimate visits to H. laneana in the morning, but they changed their behaviour to illegitimate visits by the end of the morning and in the afternoon (Cruz et al., 2006), also probably due to a reduction in nectar supply. Given that mites may cause an even higher reduction in nectar supply later in the day, they could be responsible for a fitness decrease due to a reduction in pollination and thus in the number of viable seeds produced.

The reduction in nectar production by Moussonia deppeana in Mexico changed pollinator behaviour, which made fewer but longer and more frequent revisits (Lara and Ornelas, 2002b). However, if the pollinator makes more probes in the flower this may increase pollen exchange (Lara and Ornelas, 2002b). Due to this reduction in nectar offered by each flower, the pollinator is forced to visit more plants in search of food, and this thus may increase the chance of cross-pollination. In this way, the host plant could benefit by being able to spend more energy in nectar production (Dobkin, 1984). The effect of the mites on the variation of nectar produced by the flower and the individual variation in the population observed in both Heliconia species may affect the behaviour of Phaethornis, which makes a variable number of probes per flower at each visit (our pers. observ.).

The high individual variation in nectar volume and concentration production found in this study is common for many plant populations (Real and Ratcliffe, 1988, 1991; Pedersen and Kress, 1999; Leiss and Klinkhamer, 2005) and also in other Heliconia species (Feinsinger, 1983; McDade and Weeks, 2004). Variation among individuals in nectar production is energetically important for the plant because it is difficult for the pollinator to recognize which individual has the best reward (Leiss and Klinkhamer, 2005). This variation has been observed among individuals and also among different flowers of the same plant (Feinsinger, 1983). In this way, the plant invests differently in each of its flowers. Consequently, the hummingbird cannot know which flower has a high or low nectar supply, and visits a great number of flowers, potentially increasing pollen flow and seed production.

The pattern of nectar production by H. spathocircinata and H. laneana was similar to that of other Heliconia species (e.g. two Polynesian Heliconia – Pedersen and Kress, 1999; nine Costa Rican Heliconia – Stiles, 1975; and three Heliconia morphs in the West Indies – Temeles et al., 2005): a high volume of nectar when the flower opens and a subsequent decrease hour by hour. An exception is H. irissa in central Panama, in which production of nectar reportedly occurs at a constant rate until the afternoon (McDade and Weeks, 2004).

The sum of the hourly nectar production was higher than the accumulated nectar volume for both Heliconia species (H. laneana produced 28 % more nectar and H. spathocircinata produced 43 % more). Nectar consumption increases nectar volume production (Lara and Ornelas, 2002a; Ordano and Ornelas, 2004) but reduces nectar concentration. Differences in nectar volume production may be caused by consumption by hummingbirds or mites. Continuous nectar production is important to compensate for the loss of nectar consumption by the flower mites (Lara and Ornelas, 2002a). The negative effect on nectar concentration could be explained by a resource limitation (Ordano and Ornelas, 2004), as a high percentage of sugar in the nectar requires a high amount of energy. These differences in nectar production may also result...
from reabsorption by the flower (Búrquez and Corbet, 1991) or from evaporation (Búrquez and Corbet, 1991; Galetto and Bernadello, 1992). However, evaporation does not seem to provide an explanation here, given that nectar concentration was similar in the two experiments, both hourly (first sample) and accumulated nectar. Had evaporation been a factor in the flowers, nectar would probably have become more concentrated later in the day.

*Heliconia laneana* and *H. spathocircinata* have a sequential flowering pattern in Reserva Biológica União with only a short overlap (Cruz et al., 2006). Such a flowering system permits a polyphagous system as suggested for *Proctolaelaps* sp., which was the only mite species found in both *Heliconia* species. García-Franco et al. (2001) found a polyphagous system in six *Tillandsia* (Bromeliaceae) species in Mexico that showed sequential flowering. Nectar characteristics, such as taste and odour, are similar among plants of the same genus, facilitating this system. The two *Heliconia* species studied here have similar nectar production, with high volume and concentration, especially in the morning, and share the same main pollinator, allowing resources to be continuously available throughout the year for polyphagous mites. Colwell and Naeem (1994) have discussed other examples of sequential host specialists among hummingbird flower mites.

*Heliconia laneana* had more mites per flower than *H. spathocircinata*, probably because the latter species produces more open flowers per day (maximum of eight; Cruz et al., 2006), and therefore a lower number of mites per flower. This lower number of mites per flower could reduce competition among them, and this could be beneficial, because male encounters of different species are very ‘aggressive’ (Colwell, 1973). However, we cannot test this hypothesis because only one flower per plant, chosen at random, was collected thus the number of open flowers was not counted. The high variation observed in number of mites in *H. laneana* could be associated with the low number of open flowers per day (maximum of two; Cruz et al., 2006). The number of mites per flower found in *H. spathocircinata* was similar to that found in *Hamelia patens* (Colwell, 1995), *Moussonia deppeana* (Lara and Ornelas, 2001) and in some species of *Tillandsia* (García-Franco et al., 2001). All of these species have a high range of open flowers per day. It is not uncommon to find flowers with hundreds of mites, especially when the inflorescence is nearing the end of its flowering (our pers. observ.). In this case, it seems that

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**FIG. 3.** Nectar volume (μL) and concentration (% sugar) through the day (five samples) in flowers with (A, B, n = 25) and without (C, D, n = 13) mites in *Heliconia spathocircinata* in the Atlantic Forest of Reserva Biológica União (Rio de Janeiro, Brazil).
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LITERATURE CITED


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