EFFECT OF NECTAR SECRETION RATE ON POLLINATION SUCCESS OF *Passiflora coccinea* (PASSIFLORACEAE) IN THE CENTRAL AMAZON

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Received September 28, 2004 – Accepted January 14, 2005 – Distributed May 31, 2006

(With 3 figures)

ABSTRACT

The pollination of *Passiflora coccinea* by the hummingbird *Phaethornis superciliosus* was studied in Central Amazon, Brazil. We hypothesized that a greater nectar secretion rate (NSR) increases the pollination success of single flowers through *Ph. superciliosus* visiting behavior. For control flowers, NSR was an increasing function of flower base diameter (FBD). The total number of *Ph. superciliosus* probes per flower was an increasing function of FBD. Additionally, deposition of pollen on stigmas increased with the cumulative number of *Ph. superciliosus* probes. Our results show that larger *P. coccinea* flowers secrete nectar at higher rates, are probed more times during each hummingbird visit and are more successful at pollination. This seems to be the first non-manipulative study describing such an effect of NSR on the pollination of single flowers in nature.

Keywords: flower size, hummingbird, nectar secretion, *Phaethornis*, pollination, visiting behavior.

RESUMO

Efeito da taxa de secreção de néctar sobre o sucesso de polinização de *Passiflora coccinea* (Passifloraceae) na Amazônia Central

Estudamos a polinização de *Passiflora coccinea* por beija-flores *Phaethornis superciliosus* na Amazônia Central, Brasil. Nossa hipótese é que maiores taxas de secreção de néctar (TSN) aumentam o sucesso da polinização de flores individuais através do comportamento de visitas de *Ph. superciliosus*. Para flores controladas, a TSN foi uma função positiva do diâmetro da base da flor (DBF). O número total de visitas de *Ph. superciliosus* por flor foi uma função positiva do DBF. Adicionalmente, a deposição de pólen sobre os estigmas aumentou com o aumento do número acumulado de visitas de *Ph. superciliosus*. Nossos resultados indicam que flores maiores de *P. coccinea* secretam néctar em taxas mais altas, são visitadas mais vezes pelos beija-flores, e apresentam maior sucesso de polinização. Este parece ser o primeiro estudo não-manipulativo que descreve este efeito da TSN sobre o sucesso de polinização de flores individuais na natureza.

Palavras-chave: beija-flor, tamanho da flor, secreção de néctar, *Phaethornis*, polinização, comportamento de visitas.

INTRODUCTION

Flower availability and distribution have often been found to affect pollinator behavior, but how the nectar distribution among single flowers affects the visiting patterns of pollen vectors has received little attention (Mitchell & Waser, 1992; Rathcke, 1992). Flower nectar distribution can determine pollinator behavior with respect to visitation frequency to flowering plants, to the number of flowers probed per visit, and to the number of probes per flower (Fischer, 1992; Burd, 1995; Conner & Rush, 1996). Visits to single flowers can be an important component of pollinator foraging behavior that affects plant pollination. Based on experimental studies, the rate of nectar secretion by a given flower can affect the number and duration of pollinator probes, and ultimately its pollination success (Gill, 1988; Mitchell & Waser, 1992; Rathcke, 1992). One expects that flower traits have been selected in order to maximize pollen removal and deposition and to avoid self-pollination. However, this produces a dilemma for plants (Klinkhamer & Jong, 1993): how to be highly attractive to achieve effective pollination (female function) and at the same time induce visitors to travel to conspecific plants, so as to reduce geitonogamy and increase pollen exportation (male function). In addition, the rewards offered by a plant may involve a balance between the costs in producing them and the benefits gained from animal services (Heinrich, 1975).

Hummingbirds are nectar-dependent vertebrates that visit flowers to maintain a daily energy balance. Several hermit hummingbirds (Phaethorninae) are long-distance, high-reward trapliners (Feinsinger, 1983). They are often the exclusive pollinators of particular plant species (*e.g*., Stiles & Freeman, 1993; Araujo *et al*., 1994; 2004). In contrast to most non-hermit hummingbirds, the hermits commonly visit scattered flowering plants that only open a few flowers per day (Feinsinger, 1983; Araujo *et al*., 1994; 2004). In order to increase the rate of net energy intake, hermits tend to visit flowers at regular time intervals so that the amount of accumulated nectar is maximized relative to the energy spent in moving between plants (Stiles & Wolf, 1979; Gill, 1988).

The genera *Passiflora* (Passifloraceae) includes vine species pollinated by bees, hummingbirds, bats and wasps (*e.g*., Sazima & Sazima, 1978; Koschnitzke & Sazima, 1997; Varassin *et al*., 2001; Fischer *et al*., 2004). The hummingbird-pollinated *P. speciosa* and *P. vitifolia* present red and erect flowers exposed from above canopies, with approximately 20% nectar sugar concentration (Endress, 1994; Proctor *et al*., 1996; Longo, 2002). Most floral features of *P. coccinea* are similar to *P. speciosa* and *P. vitifolia*, but its pollination was apparently not described. In addition, to our knowledge, the effect of nectar secretion rate (NSR) on the pollination success of single flowers has never been investigated under natural field conditions, by comparing natural variations among individual flowers. Here we describe the pollination system of *P. coccinea* and ask if natural variation of NSR among non-manipulated flowers affects their pollination success by the Long-tailed Hermit *Phaethornis superciliosus* (Trochilidae) visiting them. We hypothesized that the variation in NSR affects the number of hummingbird probes to individual flowers, and that the number of pollinator probes per flower affects the quantity of pollen deposited on the stigma surface. We previously determined that the diameter of the floral cup could be an index for NSR of *P. coccinea* flowers and measurements of NSR from flowers being visited in the field were unnecessary.

MATERIAL AND METHODS

Study site and species

Fieldwork was carried out on forest edges, between km 60-62 of the road Manaus-Caracaraí (BR 174), Central Amazon, Brazil (2° 35' S and 60° 2' W). The road crosses 30-40 m-tall undisturbed "terra firme" forest, bordered by growth vegetation. The studied 2-km road section contained twenty large flowering plants of *P. coccinea*. The species flowers from July to February in the Central Amazon (personal observations). Plant voucher material was deposited at the Unicamp herbarium (EUC). The hummingbird *Phaethornis superciliosus* is the largest hermit species at the study site and the only hummingbird observed to visit *P. coccinea*; it forages for nectar on scattered understory plants and on those along forest edges. At the study site, twenty ant species visited the extra floral nectaries (EFN) on *P. coccinea* floral bracts. *Camponotus* spp. (Formicinae) and

Crematogaster spp. (Myrmicinae) were the most abundant and *Ectatomma* spp. (Ponerinae) and *Pseudomyrmex*spp. (Pseudomyrmecinae) the most aggressive. These ant species repelled visits of nymphalid and hesperiid butterflies, which acted as nectar thieves in flowers not patrolled by the ants; whereas hummingbirds were not disturbed by ants as they hovered during visits (Leal et al., 2006).

Pollination biology

To determine plant pollination and the local pollinator species, flowering *P. coccinea* individuals were observed daily from August 26 to September 3, 1993. We counted the number of open flowers per plant and determined the flower lifetime. The time of nectar and pollen availability, receptivity of stigmas (*cf.*, Zeisler, 1938), and animal visits were recorded over the lifetime of flowers. Nectar volume and nectar sugar concentration were measured unsystematically for flowers in several individuals at different hours and days with a syringe accurate to 1 μL and a pocket refractometer accurate to 1%. Measurements of floral cups and androgynophores were done with a caliper accurate to 0.1 mm. Activity and behavior of flower visitors were registered by direct observations and photographs. For focal plant individuals with different numbers of open flowers, the time and duration of visiting bouts and the number of hummingbird probes per flower were recorded. A visiting bout was defined as one hummingbird visiting any number of flowers before leaving the focal plant (Fischer, 1992); and a probe was defined as each insertion of the bird's bill into the flower nectar chamber. Since the number of open flowers on a plant might affect the frequency of visits, we tested if the mean time interval between *Ph. superciliosus* visits differed among plants with different numbers of open flowers.

Nectar secretion as a function of flower base diameter

To answer whether the nectar secretion rate (NSR) affects the number of hummingbird probes, we used the previously established relationship between NSR and the size of flower cups. The flower cup of *P. coccinea* has a circular base, so we used the easily measured external flower base diameter (FBD) as the independent variable. To test if NSR varies as a function of FBD, we selected five accessible flowers on different plant individuals that were open on the same day, so we standardized climatic conditions among flowers being measured. These five flowers were bagged before opening and the nectar volumes measured over three time intervals. Flowers emptied soon after opening (0530 h) were then revisited three times (0630, 0750, and 0920 h), for measurements of accumulated nectar volume. Each time, we visited the five flowers in the same sequence to maintain similar time intervals among them. The duration of the first time interval was 80-85 min (81 ± 2.2 min), the second 105-110 min (107 ± 2.7 min) and the third 130-145 min (135 ± 7.1 min). The NSR per flower was calculated as the total volume of nectar secreted divided by the total time of nectar accumulation. The relation between NSR and FBD was evaluated by linear regression.

Nectar secretion effect on pollination of single flowers

To determine if NSR affects the number of pollinator probes, on 2nd September eight focal flowers on eight different plant individuals were simultaneously observed by two people during their entire lifetime. These flowers were guarded by EFN-visiting ants, and visits from nectar thieves did not occur. Without disturbing the hummingbirds, the number of probes per flower was recorded for each flower's lifetime. Soon after *Ph. superciliosus* finished each visiting bout, the stigmas were inspected and the proportion of their surfaces covered with pollen was recorded. The large (diameter = 4.1 ± 0.2 mm, n = 11) whitish stigma surface of *P. coccinea* allowed us to identify the yellow pollen area promptly. The proportion of pollen cover on each stigma was scored as a percentage of its surface and used as an index of pollination success (*cf.*, Heithaus *et al.*, 1982). Since a flower has three stigmas, we considered as 100% of stigma surface the sum of their areas. At the end of the flower anthesis, the stigmas of each of the eight flowers were collected to inspect pollen grains in the laboratory. Regression analysis of the number of probes received per flower as a function of the FBD was performed. The Spearman rank-correlation analysis was used to test for correlation between the cumulative proportion of pollen cover on stigmas and the cumulative number of hummingbird probes per flower. All means cited in the text are followed by ± standard deviations.

RESULTS

Pollination biology

The odorless, scarlet flowers of *P. coccinea* opened before sunrise (0500-0530 h) and lasted for less than a morning. The petals and bracts began to close at 1000 h, and all flowers were closed by 1130-1200 h. Flowers were erect to slightly inclined, with radial symmetry (Fig. 1). The androgynophore length was 47.5 ± 3.8 mm (n = 12). Flowering individuals opened 0-4 flowers per day (1.9 ± 1.5, n = 41). The anthers already presented pollen in pre-anthesis buds. The amount of pollen available in the anthers was higher at 0530 h and decreased with hummingbird visitation, being almost absent in most of the regularly visited flowers after 0900-0930 h. Inspected stigmas (n = 21) were receptive after 0600 h and remained so at least until 1200 h. Flowers are protandrous, as the anthers were ready to contact the pollinator's head 30-90 min before the stigmas were (for drawings of similar floral phases, see Fig. 1e, f in Buzato & Franco, 1992). Flowers began to secrete nectar at 0530-0600 h and stopped by 1030-1100 h. Among flowers sampled unsystematically at different hours and days, the nectar volume was positively correlated with nectar sugar concentration (r = 0.80, $p < 0.01$, n = 22). Among these flowers, the mean nectar volume and the standard deviation were greatest between 0830-0940 h, whereas the mean nectar sugar concentration decreased continuously throughout the morning (Fig. 2).

Phaethornis superciliosus was the only hummingbird recorded visiting *P. coccinea* flowers, although other hummingbird species occurred at the study site. Its visiting activity started between 0530 and 0600 h and finished when the flowers stopped nectar secretion. Individuals of *Ph. superciliosus* drank almost all the nectar from the flowers before leaving a plant; we found no nectar in the flowers just after visiting bouts. During a visiting bout, a hummingbird commonly visited all flowers of a plant and probed each flower more than once, by inserting the bill in different parts of the nectar chamber. The number of hummingbird probes per flower per visiting bout was 3.1 ± 1.5 (n = 36), and the cumulative number of probes per flower at the end of its lifetime was 16.1 ± 5.3 (n = 8). Daily, one or more *Ph. superciliosus* (we were unable to determine how many birds visited the plants) made 9-11 visiting bouts per flowering plant, with intervals averaging 18.3 ± 8.3 min (n = 13) between

Fig. 1 — *Phaethornis superciliosus* visiting a bright red *Passiflora coccinea* Aubl. flower in the Central Amazon, Brazil. Note that the bill and the androgynophore lengths combine to determine the effective contact between the bird's head and the sexual flower parts.

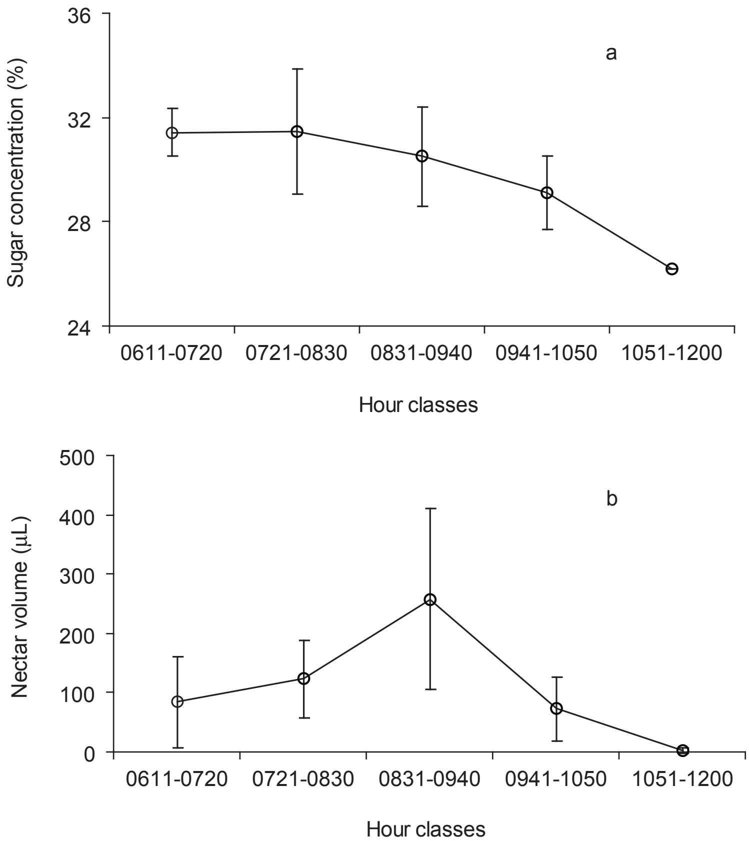

Fig. 2 — Mean ± standard deviation of a) nectar sugar concentration (%); and b) nectar volume (µL) in five hour classes for *Passiflora coccinea* Aubl. flowers (n = 22), in Central Amazon, Brazil.

them. One visiting bout lasted 5-20 sec. Encounters between hummingbirds were not registered.

The sexual flower parts were touched by the hummingbird's crown in almost all probes (Fig. 1). However, in the earliest visits the flowers were still in the male phase, and *Ph. superciliosus* did not contact the stigmas. The time interval between visits was not different ($F_{2,19} = 1.84$, $p = 0.19$) among plants with one, three or four simultaneously open flowers. Nonetheless, plants with one open flower were visited with intervals (24.2 ± 9.3 min, n = 5) longer than those with three or four open flowers (respectively, 15.0 ± 7.9 min, n = 9; and 16.8 ± 9.5 min, n = 8).

Nectar secretion effect on pollination by hummingbirds

For the five bagged flowers monitored during one morning, the nectar secretion rate ($\mu L.min^{-1}$) varied due to the flower base diameter (mm) (NSR = - 4.24 + 0.35 FBD; $p < 0.03$; $r^2 = 0.84$). The mean NSR was 0.9 ± 0.13 $\mu L.min^{-1}$ and the mean FBD was 14.6 ± 0.34 mm (n = 5). Among these five flowers, both the nectar secretion rate and the nectar sugar concentration decreased throughout the morning (Table 1). The number of *Ph. superciliosus* probes per flower of *P. coccinea* was greater in flowers with larger base diameters (Y = - 52.4 + 4.4 X; $r^2 = 0.81$; $p < 0.01$; n = 8) (Fig. 3a). In addition, the proportion of the stigma surface covered with pollen was positively correlated with the cumulative number of hummingbird probes (Spearman Coefficient = 0.94; $p < 0.01$; n = 27) (Fig. 3b). Cumulative pollen on stigmas increased slowly with the first probes. These probes occurred when most flowers were still in the male phase and hummingbirds rarely contacted stigmas at this time. Following this relatively brief male phase, the proportion of stigmas covered with pollen quickly increased with additional *Ph. superciliosus* probes, until reaching a plateau after a flower received approximately 15 probes. Later probes may not increase the pollen area because they tend to cover previous ones and because available pollen decreases as the morning advances. In the laboratory we found only *P. coccinea* pollen grains deposited on the stigmas of the eight flowers monitored for the number of *Ph. superciliosus* probes.

DISCUSSION

Passiflora coccinea flowers appear to be specialized for pollination by long-billed hummingbirds, such as the Long-tailed Hermit at the study site. The color, morphology, time of

TABLE 1

Nectar secretion rate and nectar sugar concentration for three consecutive time intervals for five bagged flowers of *Passiflora coccinea* Aubl. (Passifloraceae) controlled throughout their lifetime, in Central Amazon, Brazil.

Hour intervals	Rate of nectar secretion ($\mu L.min^{-1}$)		Sugar concentration (%)	
	Mean (SD)	N	Mean (SD)	N
0530-0700	1.4 (0.8)	5	31.4 (0.9)	5
0700-0830	1.3 (0.7)	5	28.2 (3.7)	5
0830-1000	0.2 (0.3)	5	27.1 (0.9)	3[a]

[a]Two flowers did not contain enough nectar to measure sugar concentration

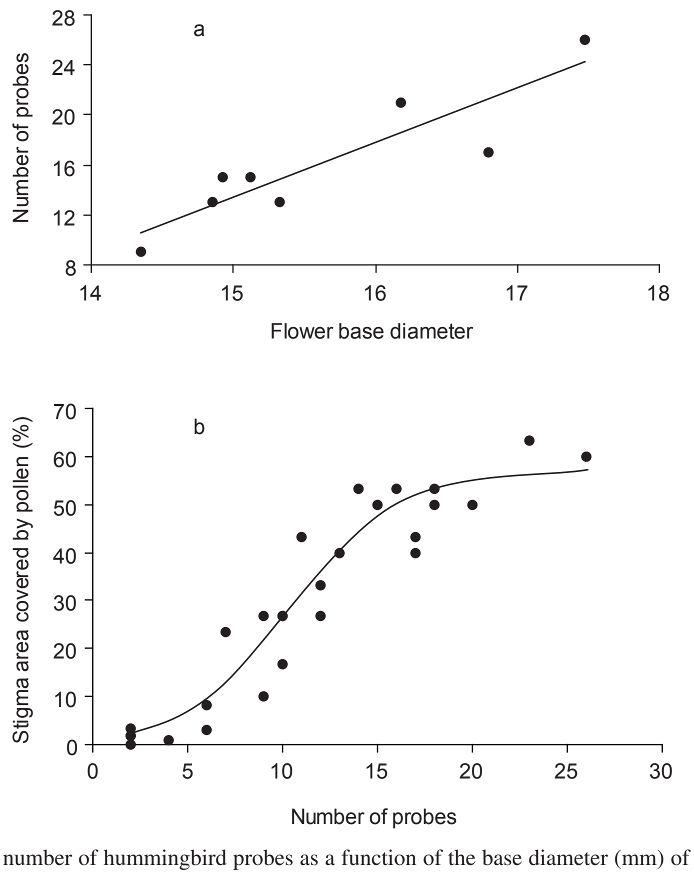

Fig. 3 — a) The total number of hummingbird probes as a function of the base diameter (mm) of *Passiflora coccinea* Aubl. flowers ($Y = -52.4 + 4.38 X$; $r^2 = 0.81$, $p < 0.01$, $n = 8$); and b) Cumulative proportion of the stigmatic surface (%) covered with pollen as a function of the cumulative number of probes by hummingbirds (Spearman's Coefficient = 0.94; $p < 0.01$). The sigmoid curve was the best-fitted equation ($Y = 56/\{1 + e^{-([X-10.5]/2.7)}\}$).

anthesis, nectar volume and sugar concentration of *P. coccinea* flowers are compatible with traits described for most hummingbird-pollinated species, but contrasts with passionflowers pollinated by different vectors (Endress, 1994; Koschnitzke & Sazima, 1997; Buzato *et al*., 2000; Fischer *et al*., 2004). *Passiflora coccinea* plants open few flowers per day and secrete sugar-rich nectar over a short period, as already found for specialized flowers regarding pollinators (*e.g*., Feinsinger, 1983; Ashman & Schoen, 1994; Araujo *et al*., 1994; 2004). The flowers of *P. coccinea* place pollen exactly on the hummingbird's crown, as do several other species exclusively pollinated by hermit hummingbirds (*e.g*., Araujo *et al*., 2004; Varassin *et al*., 2001). The increased length of the androgynophore indicates that *P. coccinea* flowers are adapted for pollination by long-billed rather than by short-billed hummingbirds (*sensu* Feinsinger; 1983). It seems likely that hummingbirds with bills shorter than that of *Ph. superciliosus* would be less effective for pollination since their heads would not touch anthers and stigmas at each visit. In the Peruvian Amazon, *P. coccinea* flowers are nectar-robbed by little hermit hummingbirds (J. M. Olesen, personal communication).

A positive relation between nectar volume and nectar sugar concentration like that found in *P. coccinea* flowers has been previously described for the hummingbird-pollinated *P. speciosa* Gardn. in the Southern Pantanal, and for some bat-pollinated flowers in Central Amazon (Fischer, 2000; Longo & Fischer, 2006). These results indicate that nectar sugar concentration increases while the secreted nectar accumulates, so visitors may find a higher sugar concentration if they return to flowers after total nectar replenishment. *Passiflora coccinea* flowers with larger base diameters secrete nectar faster. The variation in nectar secretion rate due to the flower base diameter might allow us to study the nectar intake by *Ph. superciliosus*. However, the nectar secretion rate may continuously decrease as the accumulated nectar volume increases (Galetto *et al*., 1994; Varassin *et al*., 2001), indicating that large flowers, if visited more often, might secrete even more nectar. In the five bagged flowers we measured the nectar in intervals longer than those between visiting bouts by *Ph. superciliosus*, thus the estimated function for NSR = f (FBD) may not accurately estimate the nectar intake by this hummingbird.

Considering that *Ph. superciliosus* probed more times those *P. coccinea* flowers with a larger base diameter - and assuming the flower base diameter is an index of nectar secretion rate - it may be concluded that hummingbirds probe more times from flowers that secrete nectar at higher rates. The visiting behavior of *Ph. superciliosus*, therefore, seems sensitive to the variation of the nectar secretion rate by single *P. coccinea* flowers at the study site. These results for *P. coccinea* under natural conditions are consistent with experimental data for *Ipomopsis* (Mitchell & Waser, 1992).

The number of flowers that open each day can also affect the visit frequency of pollinators to individual plants (*e.g*., Trombulak, 1990; Fischer, 1992; Conner & Rush, 1996). However, for *P. coccinea* we did not find an effect of the number of open flowers per plant on the time interval between *Ph. superciliosus* visits. The absence of such an effect supports the fact that the nectar secretion rate alone determines the variation in the number of *Ph. superciliosus* probes in *P. coccinea* flowers at the study site.

The proportion of the stigmatic surface covered with pollen increased asymptotically with the number of hummingbird probes, reinforcing the fact that pollination success of *P. coccinea* flowers is strongly affected by the *Ph. superciliosus* visiting behavior at the study site. Because the mean number of hummingbird probes per flower is higher than 15 (16.1 ± 5.3; n = 8), and considering that the stigmatic area covered with pollen reaches a plateau after approximately 15 probes, all the *P. coccinea* flowers studied by us appeared to reach high pollination success through the *Ph. superciliosus* visits. We highlight that the proportion of stigmatic area covered with pollen is only a rough estimator for pollination success (see other procedures in Dafni, 1992) and, additionally, we do not know the amount of pollen required to maximize a seed set. In *Passiflora speciosa* the number of hummingbird probes explained approximately 30% of the total variation in the number of seeds per fruit (Longo & Fischer, 2006). The present study allows one to speculate that, ultimately, the large flower size increases the reproductive success of *P. coccinea* and, therefore, the flower size could be a subject of selection through the *Ph. superciliosus* visiting behavior at the study site (see Burd, 1995; Campbell *et al*., 1996).

Acknowledgments — A. C. Araujo, J. M. Olesen, P. S. Oliveira, I. Sazima and M. Sazima provided helpful comments on the manuscript; W. W. Benson, J. Hay and G. B. Williamson made suggestions during the field work. The study was done during the field course "Ecologia da Floresta Amazônica" offered by UNICAMP and OTS, sponsored by PDBFF (INPA-Smithsonian Institution), and supported by Conservation International, USAID Brazil, Grupo Caemi and Varig Airlines. Authors were supported by CNPq grants.

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