Floral syndrome, resources and pollinator guilds: a case study of *Heliconia psittacorum* L. f. (*Heliconiaceae*)

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ABSTRACT – Flower resources can affect the guilds, frequency, and behaviour of visitors. This study compared the pollinator guilds and nectar energy of *Heliconia psittacorum* L. f. (*Heliconiaceae*) during the peak and at the end of the flowering period in a fragment of the Atlantic Forest, northeastern Brazil. Nectar production and the availability of calories were highest in the early morning, coinciding with the highest activities of flower visitors. Calorie availability affects pollinator guilds. During the peak of the flowering, we recorded the hummingbirds *Amazila leucogaster* Gmelin (territorialist) and *Phaethornis ruber* Linnaeus (trapliner), the butterfly *Talides* sp. (*Hesperiidae*), and the bee *Exaerete smaragdina* Guérin-Méneville. During the final flowering period, *Talides* sp. and the hummingbirds *P. ruber* and *P. pretei* Lesson & DeLattre were recorded. *Heliconia psittacorum* is an important resource in the area, and the flower-pollinator syndrome could not predict some of the observed pollinators.

Key words: *Hesperiidae*, hummingbird behaviour, nectar energy

RESUMO – **Síndrome floral, recursos e guilda de polinizadores: um estudo de caso em *Heliconia psittacorum* L. f. (*Heliconiaceae*)**. Recursos florais podem afetar a guilda, a frequência e o comportamento dos visitantes. Este estudo comparou a guilda de polinizadores e a energia do néctar de *Heliconia psittacorum* L. f. (*Heliconiaceae*), no pico e no final do período da floração em um fragmento de Floresta Atlântica, Nordeste do Brasil. A produção de néctar e a disponibilidade de calorias foram maiores no início da manhã, coincidindo com a maioria das atividades dos visitantes florais. A disponibilidade de calorias afetou a guilda de polinizadores. No pico da floração, foram registrados os beija-flores *Amazila leucogaster* Gmelin (territorialista) e *Phaethornis ruber* Linnaeus (trapliner), a borboleta *Talides* sp. (Hesperiidae) e a abelha *Exaerete smaragdina* Guérin-Méneville. No final do período de floração, *Talides* sp. e os beija-flores *P. ruber* e *P. pretei* Lesson & DeLattre foram registrados. *Heliconia psittacorum* é um recurso importante na área e a síndrome de polinização não previu alguns dos polinizadores observados.

Palavras-chave: comportamento do beija-flor, energia do néctar, *Hesperiidae*

INTRODUCTION

The pollination of many types of angiosperms is dependent on biotic agents, such as bees, birds, bats, butterflies and flies (Endress 1998). Many plants invest energy-producing resources in order to attract pollinators. The availability of these resources influences the pollinator guilds, as well as their behaviours and frequencies (Faegri & van der Pijl 1979, Endress 1998). The flower characteristics, such as corolla colour, size and shape, resource produced, and the anthesis period are used to define "pollination syndromes" (Faegri & van der Pijl 1979).

Pollination syndromes can predict primary pollinators, however, recent works have demonstrated that predicting the primary pollinator based on these syndromes can be difficult for some plant species (Johnson & Steiner 2000, Ollerton *et al.* 2009). In addition, using these syndromes to predict if it is generalists or specialists pollinate species is not always accurate (Johnson & Steiner 2000, Suzuki *et al.* 2007, Dalsgaard *et al.* 2009).

Heliconiaceae comprise a single genus, *Heliconia*, which is primarily neotropical. *Heliconia* has inflorescences with brightly coloured bracts, one-day flowers with diurnal anthesis, flowers with relatively long corollas, no odour, and produce large amount of dilute nectar (Stiles 1975). These features clearly suggest that the flower pollination syndrome is ornithophilous. Hummingbirds are the main pollinators of the American species of *Heliconia* (Stiles 1975, 1981, Feinsinger 1983, Temeles & Kress 2003, Temeles *et al.* 2005, Cruz *et al.* 2006), while honeyeaters (*Meliphagidae*) are the pollinators in the South Pacific (Pedersen & Kress 1999) and bats act as pollinators of a few *Heliconia* species in the Solomon Island (Kress 1985).

A high intensity of flower production and, consequently, higher nectar production, can influence pollinator attraction and behaviour (Harder *et al.* 2004). The goal of this study was to compare the pollinator guilds of *Heliconia psittacorum* L. f. during two periods of its flowering cycle: 1) in the flowering peak, when it has most inflorescences and flowers produced, and 2) at the end of the flowering cycle, when few inflorescences had open flowers. *Heliconia psittacorum* has ornithophilous flowers. This work was based on the hypothesis that its flowers have hummingbird species that act as the main pollinator throughout their reproductive period. The work presented here discusses flower, nectar and calorie production in these two phenology moments and the temporal differences in the nectarivorous community.

MATERIAL AND METHODS

Fieldwork was conducted in a fragment of the Atlantic Forest in the "Jardim Botânico Benjamim Maranhão" (JBBM), a botanical garden in João Pessoa, Paraíba, in northeastern Brazil. The area is a 417 ha fragment of secondary forest in an urban region. The climate is hot (annual mean temperature of 26°C) and humid (annual mean rainfall 1800 mm) (CEPED 2011), with a rainy season between March and August.

Heliconia psittacorum is a large herb, approximately 0.75 m tall, with red to orange inflorescences and orange to yellow flowers. *Heliconia psittacorum* flowers from December to August, and the peak flowering time is in March (Cruz 2009).

Floral features and Pollinator Observations

Measurements of the corolla, stamens, and stigma were taken from eight flowers in a laboratory using a plastic calliper (accuracy 0.01 mm). The number of flower/ inflorescences was counted in the peak (17 inflorescences) and in the final flowering period (16 inflorescences). These were compared using the Student's t-test with the Statistica 8.0 software.

Floral visitors were observed during the peak flowering (March 2010 and 2014) and the final flowering (July 2009 and 2014) periods. Observations started at 4:30 a.m. and ended at 2:30 p.m. when there was no more nectar production and senescence had started. The same group of *H. psittacorum*, which occupied an area of approximately 55×20m along the trail, was observed during four days in each flowering period. This is the main area of occurrence of the species in the botanical garden. From the observation point, about 100 open flowers per day could be observed during the peak flowering period, and 7–12 open flowers per day could be observed during the final flowering period.

The "focal individual" method (Altmann 1974) was used and visitor behaviour and frequency were recorded. One "visitation activity" noted was the behaviour of a visitor to probe one or more flowers sequentially. In this case, the number of flowers visited was counted.

Nectar and calories production

Nectar volume and concentration were recorded throughout the day in five measurements, beginning at 6:00 a.m. and taken every two hours until 2:30 p.m. Nectar was collected from 15 flowers that were part of nine inflorescences. They were covered with thin netting bags on the day before the measurements were taken in order to avoid visits from nectar consumers. Hummingbird flower mites were observed in the studied flowers, consuming some of the nectar produced by the flowers (Cruz *et al.* 2007). Therefore, nectar measurements taken in this study reflect the nectar that was available to visitors on each one of the five observations and not the total nectar produced by each flower. Nectar volume and concentration were taken using a 25-µL Hamilton microsyringe and a portable refractometer (Quimis 90% Brix), respectively.

The calories offered in each flowering period were estimated considering the nectar production (volume and concentration) and the number of flowers produced. First, the concentration was transformed from 'g of sugar/g of solute' to 'mg of sugar/µL of nectar' following Galetto & Bernadello (2005). It was considered that the energy of 1mg of sugar is equivalent 4 cal (Galetto & Bernadello 2005). Then, the mean energy produced by one flower was multiplied by the total of flowers observed in each reproductive period. The total amount of calories produced in both periods of flowering was compared using the Student's t-test and was analysed using the Statistica 8.0 software.

RESULTS AND DISCUSSION

Floral features and pollinator guild and interactions

The inflorescences produced 20.31±7.86 (N = 17) flowers/inflorescence during the peak of flowering period and 20.43±0.86 (N = 16) during the final flowering period. There was no significant difference in flower production/inflorescence between the two periods (P>0.05). Flowers opened at approximately 4:30 a.m., a few minutes before sunrise. The stigma length was 39.5±3.7 mm, the stamen length was 43±3.2 mm, and the corolla length was 45±4 mm (N = 8).

There was a difference in the visitor guild, frequency, and behaviour between the two flowering periods. During the peak of flowering, 122 legitimate visits from hummingbirds, bees and butterflies were recorded (Fig. 1a), while during the final flowering period, there were 72 legitimate visits by hummingbirds and butterflies (Fig. 1b).

The main visitor observed (55%, N = 122) during the peak of flowering was the hummingbird *Amazilia leucogaster* Gmelin (Fig. 2a). This hummingbird was more active at the beginning of the day (Fig. 1a) and spent the morning defending its territory, which consisted of about one quarter of the observed group of plants. Two individual specimens of *A. leucogaster* were also observed defending opposite sides of the plant group. This species is usually perched in a high tree in front of the area and exhibited defending displays consisting of flying down quickly and vocally threatening the "invader". Individuals of *A. leucogaster* displayed this behaviour against other individuals of the same species, as well as against the hummingbird *Phaethornis ruber* Linnaeus, the bee *Exaerete smaragdina* Guérin-Méneville (Fig. 2b), and other animals, such as crickets. *Amazilia leucogaster* was always a legitimate visitor, which exploited different areas of the plant group. However, they never visited more than 15 flowers in the same visit. During the intervals, this hummingbird spent from 10 to 30 min on a perch.

The hummingbird *Phaethornis ruber* acted as legitimate pollinator, representing 26% (N = 122) of the visits observed in the peak of flowering. In general, this hummingbird visited the flowers a few times during each hour in the morning, trying to avoid the aggressive behaviour of *Amazilia leucogaster* (Fig. 1a).

During the peak of flowering, the butterfly *Talides* sp. (Hesperiidae) (Fig. 2c) was observed just before sunrise visiting the flowers for about 30 minutes, corresponding to 10% (N = 122) of the total visits observed (Fig. 1a). This species legitimately visited the flower, and usually spent approximately 1–2 minutes on each flower (a maximum of 10 minutes was observed). The butterfly perched on the flower and touched the reproductive structures with its legs and proboscis. Sometimes, this species also touched the reproductive structures of the flower with its head. Two individuals were also observed visiting the same flower simultaneously. In this situation, each butterfly perched on one side of the corolla, and touched the stamens with the proboscis. *Talides* sp. was often seen flying within the studied group of plants, visiting many inflorescences.

Another legitimate visitor observed during the peak of flowering was the bee *Exaerete smaragdina* (Euglossine) (Fig. 2b). These visits were more common after 7:30 a.m. and accounted for 9% of the total visits (N = 122) (Fig. 1a). *Exaerete smaragdina* perched on the corolla and touched the reproductive structures while it inserted its glossa into the flower to collect nectar. During each visit, this species spent approximately two minutes visiting each flower, and it visited many flowers in the area.

During the final flowering period, *Talides* sp. was the most common legitimate visitor observed (90%, N = 72). Individuals of this species started to visit the flowers before sunrise, and continued to visit them throughout the morning (Fig. 1b). Only a few visits from hummingbirds were observed during this time (Fig. 1b). *Phaethornis ruber* and *P. pretei* Lesson &

DeLattre accounted for 8% and 2% (N = 72) of the total visits, respectively, and displayed legitimate visits.

Illegitimate visits were observed during both of the study periods. During the peak of flowering, the hummingbird *Phaethornis ruber* and the bee *Trigona fulviventris* Guérin-Méneville (Fig. 2d) acted as nectar robbers. Both illegitimate visitors were observed throughout the morning. *Phaethornis ruber* displayed different behaviours throughout the flowering period. During the peak of flowering, *P. ruber* acted mainly as legitimate pollinator; however it also act as nectar robber, visiting flowers quickly and inserting its beak into the lateral side of the corolla to collect nectar without touching the reproductive structures. *Trigona fulviventris* had the same behaviour during both flowering periods, collecting pollen or boring a hole in the base of the corolla to collect nectar. It was more common to see *T. fulviventris* collecting pollen early in the morning.

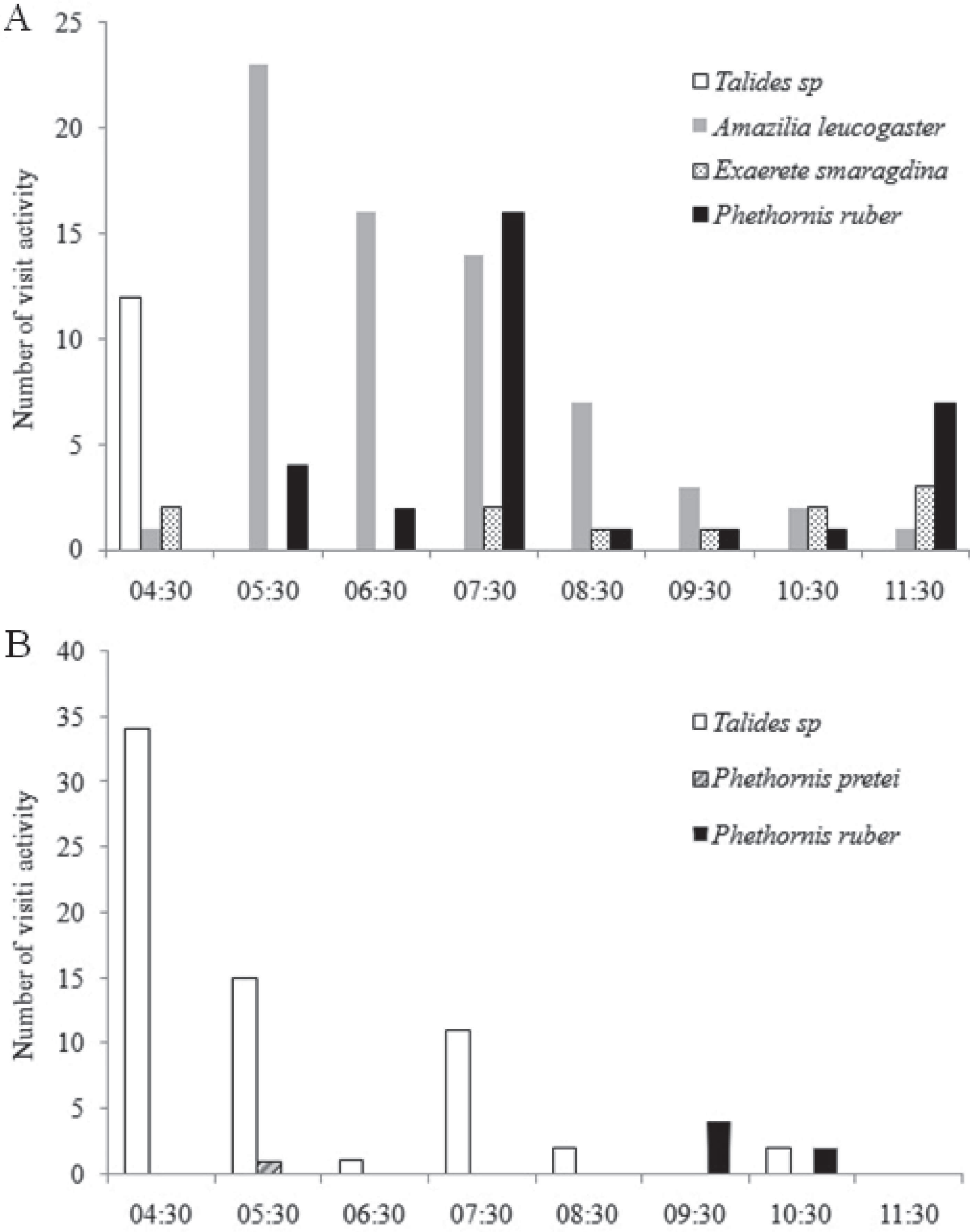

Fig. 1. Number of visit activity to the *Heliconia psittacorum* flowers during the A) peak (N = 100 open flowers/day) and the B) final flowering periods (N = 12 open flowers/day).

Figs. 2A-D. Visitors to the *Heliconia psittacorum*. A. *Amazilia leucogaster*; B. *Exaerete smaragdina*; C. *Talide* sp. (Hesperiidae); D. *Trigona fulviventris* (nectar and pollen robber). Bars = 1 cm.

Nectar and calories production: influence in pollinator behaviour

The total nectar volume available/day was 66.3±22.2 µL (considering the sum of the five measures). The highest volume and concentration of nectar was produced early in the morning, with these parameters decreasing throughout the day until 12:30 p.m., when production stopped (Fig. 3a,b). Despite this well-defined pattern of nectar production, there was individual variation in the amount of nectar produced (varying from 24 µL to 90 µL) (Fig. 3).

Considering flowers produced/day, in the early morning (6:30 a.m.), nectar offers 5,849.63±2,489 cal during the peak flowering period (N = 100 flowers) and 701.95±298.68 cal at the end of the flowering periods (N = 12 flowers) (Fig. 4). Energy production was statistically different in the first and the second measurements taken between the two flowering periods ($t = -7.95$; $p<0.0001$ to the first measure and $t=-3.93$; $p<0.0005$ to the second measure). In the last three measurements between the two flowering periods, there was no statistical difference in the calorie availability ($P>0.05$). During both periods of flowering, the amount of calories offered decreased throughout the day (Fig. 4), following the same pattern observed in the nectar production.

The pattern of nectar production from the *Heliconia psittacorum* was similar to the patterns observed in other *Heliconia* species (Pedersen & Kress 1999, Temeles *et al.* 2005, Cruz *et al.* 2007). The highest nectar production (volume and concentration) in the morning seems to influence the behaviour of *Amazila leucogaster*. This species did not visit all of the open flowers available, but altered the area it visited within the defended group. During interval periods (when the bird was perched or not visiting a certain area), the flowers had enough time to produce and accumulate more nectar. This behaviour guarantees that the hummingbird will have nectar during each visit throughout the morning. In addition, it also justifies the defensive behaviour, keeping pollinators in the area (Canela & Sazima 2003).

There was a high individual variation in the volume and concentration of nectar produced,

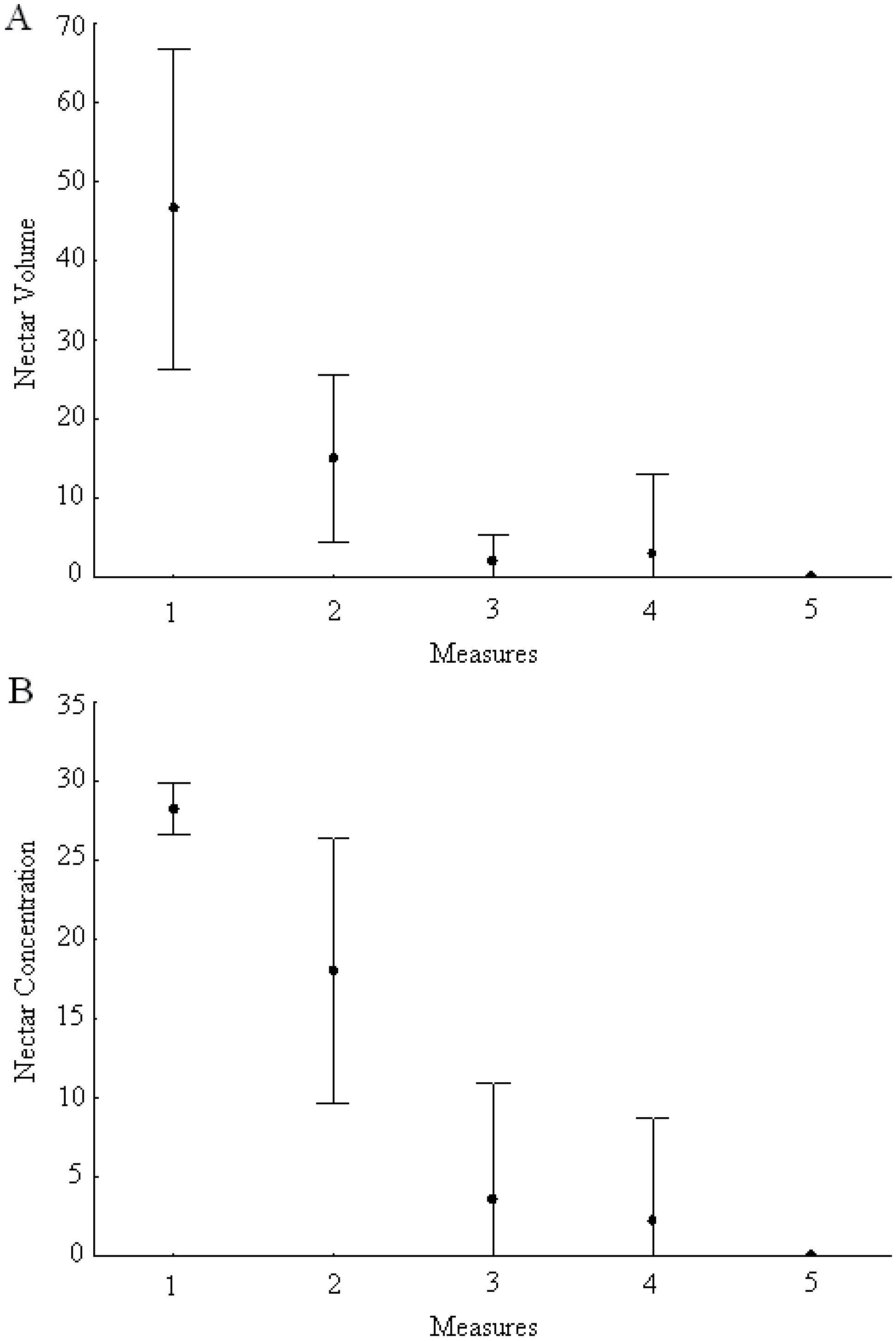

Fig. 3. Mean (±s.d.) A) volume (µL) and B) concentration (%) of nectar available throughout the day from *Heliconia psittacorum*.

primarily when comparing the first and second measurements (Fig. 3a). Because of this variation, a hummingbird is not sure which individual flower will produce more nectar (Real & Rathcke 1991) and remains interested in each flower it is visiting (McDade & Weeks 2004). This strategy allows a plant to invest less energy in producing a resource while keeping a pollinator interested in its flowers. For *A. leucogaster*, the individual variability in nectar production did not affect its energy level because the hummingbird defended a large group of plants, which allowed it to visit many of the "bonanza" flowers.

There is a significant variation in the flowers and calories offered by *Heliconia psittacorum* throughout its flowering phenophase, affecting the pollinator guild composition and pattern of visits. In the present study, *H. psittacorum* was legitimately visited by three functional groups of pollinators (hummingbird, butterfly, and Euglossini bees), which classifies it as a generalised pollination system ('polyphily pollination system', *sensu* Ramirez 2004). The *Heliconia* flower is considered a specialised flower and its pollination syndrome did not allow us to predict the diversity of observed visitors. *Heliconia* species are known to have ornithophilous flowers (Stiles 1975, 1981); however, some features of bird-pollinated flowers can be shared with butterfly-pollinated flowers, such as a long corolla, the time of anthesis, and the concentration of the nectar (Faegri & van der Pijl 1979, Ramirez 2004). These similarities can justify the behaviour and frequency of birds and butterflies observed in *H. psittacorum*.

Despite the fact that trapliner hummingbirds have been described as the most common pollinators of the *Heliconia* species (Stiles 1975, Feinsinger 1983, Cruz *et al.* 2006, Taylor & White 2007), territorial hummingbirds have already been recorded (Temeles & Kress 2003). Hummingbirds can act as territorial pollinators when the guarantees of enough energy justify the defence of plants (Temeles & Kress

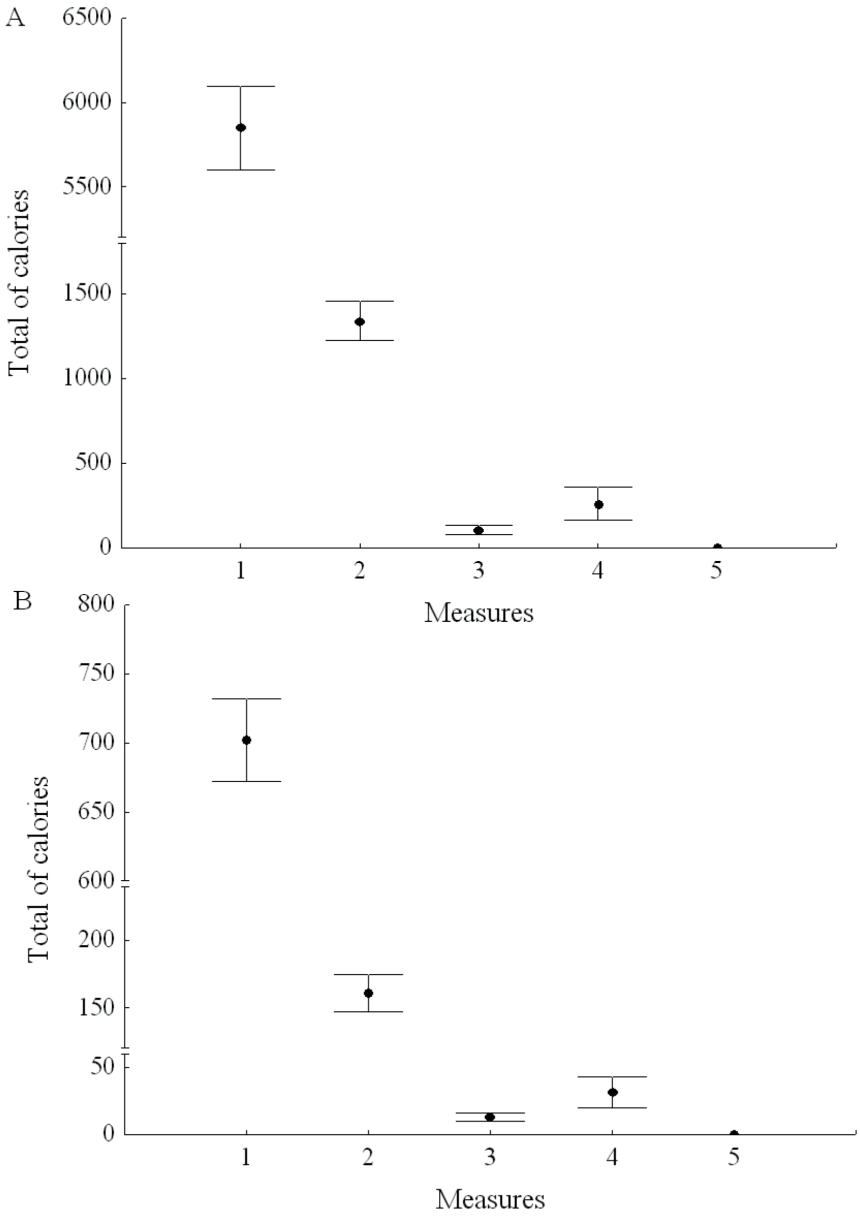

Fig. 4. Calories produced (mean±s.d.) by the *Heliconia psittacorum* flowers during the A) peak (N = 100 open flowers/day) and B) final flowering periods (N = 12 open flowers/day).

2003, Temeles *et al.* 2005). An important pollinator (when considering the number of legitimate visits) of *H. psittacorum* was the territorialist hummingbird *Amazilia leucogaster*. *Heliconia* flowers are recognised as a "bonanza" resource because they produce high amounts of nectar (Feinsinger 1983, Cruz *et al.* 2007) and can provide enough energy to justify its defence by certain animals (Temeles *et al*. 2005). Considering that a hummingbird needs more than 27 kJ/ day (Powers & McKee 1994) (about 6.45 kcal/ day) and *H. psittacorum* produces 5.85±2.49 kcal just in the first measures of the day during the peak of the flowering, *A. leucogaster* can get enough energy throughout the day visiting and defending its flowers. However, at the end of the flowering, the calories produced by *H. psittacorum* did not support the needs of *A. leucogaster*, and another pollination guild is observed. Beyond the legitimate visit of *A. leucogaster*, another important factor that can guarantee *H. psittacorum* pollination is its beak length, which varies from 22 to 23 mm (Ruschi, 1986), allowing it to access the nectar and transport the pollen on its forehead.

Hesperiidae butterflies and Euglossini bees can also pollinate these flowers, primarily due to their behaviour. The lengths of the mouthparts of these legitimate visitors are shorter than are the *H. psittacorum* reproductive structures. *Exaerete smaragdina* is a long-tongued bee (ca. 20 mm long, Lopes & Machado 1999). However, there is no study regarding the size of *Talides* proboscis, although a study with two others species of the same family shows that it varies from 10.62 to 13.13 mm (Dolibaina 2011). Despite the shorter mouthparts, their behaviour allows the pollination because they can touch the reproductive structures of the flower. Although they are different species (within different systematic groups), they have similar evolutionary pressure in the flower pollination mechanisms (Ramirez 2004, Freitas & Sazima 2006).

The foraging behaviour of flower visitors can positively or negatively influence the plant's fitness. *Talides* sp. and *E. smaragdina* were predominantly trapliners that visited different plants throughout the group around the study area (Feinsinger & Colwell 1978, Wikeski *et al*. 2010). In spite of their low frequency during the peak of flowering, these pollinators could contribute to the reproductive success of *Heliconia*. The butterflies and bees visited *H. psittacorum* individuals in small clumps along the trail that *A. leucogaster* was not interested in or defending, increasing the chance of cross-pollination. Moreover, *Talides* sp. played an important role as the main pollinator during the final flowering period. The peculiar activity schedule of Hesperiidae before sunrise is noteworthy as most butterflies become active after birth, around eight or nine o'clock, depending of climatic sazonality (Brown 1992).

Nectar robbers are commonly observed visiting species of Heliconiaceae (Stiles 1975, Cruz *et al.* 2006, 2007, Taylor & White 2007). *Trigona fulviventris* generally acts as a pollen robber. The difference in the length of the stamens and the stigma makes it difficult for *T. fulviventris* to touch the stigmatic surface, and reproductive experiments showed that it is not able to promote pollen flow (unpublished data). Moreover, the bees spend a long time (8 min 19 sec on average) visiting each flower and visiting all of the open flowers in an inflorescence.

Understanding floral syndromes is useful when first considering the pollinators of a plant. However, understanding visitor guilds and their efficiency requires observation and knowledge about the local animals. Only 2% of the original Atlantic Forest is well preserved in northeastern Brazil (Silva & Tabarelli 2000). This forest is reduced to small fragments, which can significantly affect plant-animal interactions. Based on this perspective, the JBBM is an important fragment in the state of Paraíba, and research about plant-animal interactions can provide information about the structure and diversity of this forest. Despite the pollinators being observed for four days during each reproductive period (in the peak and at the end), it is clear that *H. psittacorum* plays an important role as a resource for many animals over a long period each year (flowering time lasts over five months).

The hypothesis proposed in this work was not accepted because in addition to the previewed hummingbirds, other legitimate visitors are important to the plant reproduction. For example, it is unusual that a species of Euglossine bee acts as a legitimate *Heliconia* visitor (recorded only in two studies, Janzen 1971, Taylor & White 2007) and there is no record of *Exaerete* as pollinator of this group. *Talides* sp. can also act as an important pollinator (the main pollinator during the final flowering period) and the time of its activity was a new register for the group. Although many studies have shown hummingbirds to be the exclusive pollinators of South American *Heliconia* species, our results agree with Waser *et al.* (1996), who say that plant species rarely depend on a single pollinator, despite the fact that flower and pollinator morphology and physiology often suggest this type of relationship.

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REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227-267.

Brown, K.S. 1992. Borboletas da Serra do Japi: diversidade, habitats, recursos alimentares e variação temporal. *In: História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil* (L.P.C. Morellato, ed.). Campinas, p.142-186.

Canela, M.B.F. & Sazima, M. 2003. *Aechmea pectinata*: a hummingbird-dependent bromeliad with inconspicuous flowers from the rainforest in south-eastern Brazil. Annals of Botany 92:731-737.

Centro Universitário de Estudos e Pesquisas sobre Desastres - CEPED. 2011. Atlas brasileiro de desastres naturais 1991 a 2010: volume Paraíba. Centro Universitário de Estudos e Pesquisas sobre Desastres, Florianópolis. 57 p.

Cruz, D.D. 2009. Fenologia e biologia reprodutiva de *Heliconia psittacorum* na Reserva Biológica Guaribas. Relatório de Pesquisa – ICMBio (dados não publicados).

Cruz, D.D., Mello, M.A.R. & Van Sluys, M.V. 2006. Phenology and floral visitors of two sympatric *Heliconia* species in the Brazilian Atlantic forest. Flora 201:519-527.

Cruz, D.D., Abreu, V.H.R. & Van Sluys, M.V. 2007. The effect of hummingbird flower mites on nectar availability of two sympatric *Heliconia* species in a Brazilian Atlantic forest. Annals of Botany 100:581-588.

Dalsgaard, B., González, A.M., Olesen, J.M., Ollerton, J., Timmetmann, A., Andersen, L.H. & Tossas, A.G. 2009. Plant–hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. Oecologia 159:757-766.

Dolibana, D.R. 2011. *Cumbre* Evans, 1955 (Hesperiidae: Hesperiinae: Moncini): taxonomia, filogenia e morfologia comparada Dissertação 189 f, Universidade Federal do Paraná, Paraná.

Endress, P.K. 1998. Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge. 511 p.

Faegri, K. & van der Pijl, L. 1979. The Principles of Pollination Ecology, 3rd ed. Pergamon Press, Oxford. 244 p.

Feinsinger, P. & Colwell, R.K. 1978. Community organization among neotropical nectar-feeding birds. American Zoology 18:779-795.

Feinsinger, P. 1983. Variable nectar secretion in a *Heliconia* species pollinated by hermit hummingbirds. Biotropica 15:48-52.

Freitas, L. & Sazima, M. 2006. Pollination biology in a tropical high-altitude grassland in Brazil: Interactions at the community level. Annals of the Missouri Botanical Garden 93:465-516.

Galetto, L. & Bernadello, G. 2005. Nectar. *In*: *Practical Pollination Biology* (A. Dafni, P.G. Kevan, B. C. Husband, eds). Enviroquest, Ontario, p. 261-312.

Harder, L.D., Jordan, C.Y., Gross, E. & Routley, M.B. 2004. Beyond floricentrism: the pollination function of inflorescences. Plant Species Biology 19:137-148.

Janzen, H.D. 1971. Euglossine bees as long-distance pollinators of Tropical plants. Science 171:203-205.

Johnson, S.D. & Steiner, K.E. 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology and Evolution 15:140-143.

Kress, W.J. 1985. Bat pollination of an Old World *Heliconia*. Biotropica 17:302-308.

Lopes, A.V. & Machado, I.C. 1999. Pollination and reproductive biology of *Rauvolfia grandiflora* Apocynaceae: Secondary pollen presentation herkogamy and self-incomaptibility. Plant Biology 1:547-553.

McDade, L. & Weeks, J.A. 2004. Nectar in hummingbird-pollinated Neotropical plants I: Patterns of production and variability in 12 species. Biotropica 36:196-215.

Ollerton, J., Alarcón, R., Wase, N.M., Price, M.V., Watts, S., Cranmer, L., Hingston, A., Peter, C.I. & Rotenberry, J. 2009. A global test of the pollination syndrome hypothesis. Annals of Botany 103:1471-1480.

Pedersen, L.B. & Kress, W. J. 1999. Honeyeater *Meliphagidae* pollination and the floral biology of Polynesian *Heliconia* (Heliconiaceae). Plant Systematics and Evolution 216:1-21.

Powers, D.R. & McKee, T. 1994. The effect of food availability on time and energy expenditures of territorial and non-territorial hummingbirds. The Condor 96:1064-1075.

Ramirez, N. 2004. Pollination specialization and time of pollination on a tropical Venezuelan plain: variation in time and space. Botanical Journal of the Linnean Society 145:1-16.

Real, L.A. & Rathcke, B.J. 1991. Individual variation in nectar production and its effect on fitness in *Kalmia latifolia*. Ecology 72:149-155.

Ruschi, A. 1986. Aves do Brasil. Expressão e Cultura, Rio de Janeiro. 335 p.

Silva, J.M.C. & Tabarelli, M. 2000. Tree species impoverishment and the future flora of the Atlantic Forest of northeast Brazil. Nature 404:72-74.

Stiles, F.G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56:285-301.

Stiles, F.G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. Annals of Missouri Botanical Garden 68:323-351.

Suzuki, K., Dohzono, I. & Hiei, K. 2007. Evolution of pollinator generalization in bumblebee-pollinated plants. Plant Species Biology 22:141-159.

Taylor, J. & White, S.A. 2007. Observations of hummingbird feeding behavior at flowers of *Heliconia beckneri* and *H. tortuosa* in southern Costa Rica. Ornitologia Neotropical 18:133-138.

Temeles, E.J. & Kress, W.J. 2003. Adaptation in a plant-hummingbird association. Science 300:630-633.

Temeles, E.J., Goldman, R.S. & Kudla, A.U. 2005. Foraging and territory economics of sexually dimorphic purple-throated caribs Eulampis jugularis on three Heliconia morphs. The Auk 122:187-204.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. 1996. Generalization in pollination systems, and why it matters. Ecology 77:1043-1060.

Wikeski, M., Moxley, J., Eaton-Mordas, A., López-Uribe, M.M., Holland, R., Moskowitz, D., Roubik, D. & Kays, R. 2010. Large-range movements of neotropical orchid bees observed via radio telemetry. PLoS ONE 5:e10738.