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POLLINATION OF *NEMATANTHUS BRASILIENSIS*: AN EPIPHYTIC GESNERIACEAE ENDEMIC TO THE SOUTHEASTERN ATLANTIC FORESTS OF BRAZIL

IVONNE SANMARTIN-GAJARDO*

Fundação Oswaldo Cruz, Programa de Implantação do Campus Fiocruz da Mata Atlântica, Av. Sampaio Correia 1A, Taquara, CEP 22713-374, Rio de Janeiro, Brasil. Email: icgajardo@gmail.com

JOSÉ RENATO SANTANA VIANNA

Centro Sócio Ambiental, Instituto de Pesquisa Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão 915, Jardim Botânico, CEP 22460-030, Rio de Janeiro, Brasil.

ABSTRACT. The floral biology and visitors of *Nematanthus brasiliensis* were studied in a submontane rainforest in Mangaratiba, Rio de Janeiro, Brazil. This species presents a flowering peak between October and February. Its flowers usually last eight days and show marked protandry. The floral features of *N. brasiliensis* suggest an ornithophilous pollination syndrome: tubular shape, pendent position, brightly colored, absence of perceptible odors. Nectar volume (21.3 μ l) and sugar concentration (31.8%) are also indicative of bird pollination. Field observations have verified this hypothesis: the flowers of *N. brasiliensis* are visited by two hummingbird species, *Ramphodon naevius* and *Phaetornis ruber*. Our data show that *P. naevius* is the main pollinator of *N. brasiliensis* and that it promotes cross-pollination. In addition, configuration of the reproductive structure in *N. brasiliensis* may avoid inter-specific pollen competition in style.

Key words: *Nematanthus*, floral biology, hummingbird pollination, *Ramphodon naevius*, pollinator behavior

INTRODUCTION

Gesneriaceae is a moderate-size plant family comprising more than 3500 species in 140–150 genera, distributed mainly in the tropics (Weber 2004). In Brazil, 25 genera and about 230 species of gesneriads are found, occurring mostly in rain forests in the Amazonia region and along the Atlantic coast (Souza & Lorenzi 2005, A. Chautems pers. comm.). Wiehler (1983) estimated that about 60% of the Neotropical Gesneriaceae is hummingbird-pollinated, and it is an important source of nectar for hummingbirds in southeastern Brazil (Snow & Teixeira 1982, Buzato et al. 2000).

Inhabiting the coastal rain forest in Brazil, 31 species have been recognized for the genus *Nematanthus*, all characterized by their epiphytic and sometimes lithophytic habit (Chautems et al. 2005). Due to their brightly colored flowers, species of *Nematanthus* are commonly used as ornamental plants and several species have been introduced into cultivation in the US and Europe (Arnold 1978). Flowers with ornithophilous pollination syndrome (cf. Faegri & van der Pijl 1980) are a common feature for this genus, although three recently described species with large funnel-shaped white flowers exhibit a melittophilous pollination syndrome (Chautems et al. 2005).

Nematanthus brasiliensis (Vell.) Chautems is an epiphytic shrub restricted to a small stretch of

Atlantic coastal rain forest around the border of the São Paulo and Rio de Janeiro states, between 50 and 1200 meters (Chautems & Kiyama 2003). Its pendent flowers present brightly colored corollas that are tubular to cylindrical, suggesting that this species is hummingbird-pollinated. So far, effective visitors have been confirmed by fieldwork for the following six other species of *Nematanthus*: *N. fritschii* (Franco & Buzato 1992), *N. fissus*, *N. fluminensis*, *N. fornix*, and *N. sericeus* (Buzato et al. 2000). In this paper we add to this body of knowledge in presenting descriptions of the floral biology of *N. brasiliensis*, as well as observations on the behavior of its visitors, especially of *Ramphodon naevius*, thought to be its effective pollinator.

MATERIAL AND METHODS

Fieldwork was conducted from August 2004 to February 2005 and included observations in four populations along the North side of the river Rio Grande, in the Reserva Ecológica Rio das Pedras, a private ecological reserve (RPPN) that belongs to Club Mediterranée, in the Mangaratiba district (22°59'S 44°05'W, 30 m elevation), Rio de Janeiro, Brazil. Annual average temperature is 22°C and annual rainfall reaches 1200 to 2500 mm, with a wet season from December to February (Mynssen & Windisch 2004).

The flowers were observed in-situ to determine floral longevity and phases of anthesis. Effective

* Corresponding author.

corolla length (Wolf et al. 1976) and diameter of corolla opening were taken from fresh flowers sampled from different plants. Plant vouchers were deposited at the Herbarium of Rio de Janeiro Botanical Garden (RB, Jardim Botânico do Rio de Janeiro; RB6703637). Nectar production was measured in flowers bagged at the pre-anthesis phase. Two variables were measured: volume of nectar, using a graduated microliter syringe (Hamilton, NV, USA), and sugar concentration (percentage sucrose, w/w), with a pocket refractometer (Atago HSR 500, Japan).

Floral visitors were recorded monthly, by selecting groups of *Nematanthus brasiliensis* plants with at least five open flowers. Visual observations of the hummingbird visitors were made using binoculars and photographs were taken to analyze visiting behavior. Bird identification was confirmed through the descriptions and illustrations of Grantsau (1989). A total of 60 hours during daylight hours (06:00 hs to 18:00 hs) over eleven days were spent monitoring flower visitation.

RESULTS AND DISCUSSION

Floral Biology

The flowers of *Nematanthus brasiliensis* are solitary and inserted in the axils of the leaves. The corolla is tubular, gradually widening and laterally compressed at the apical extremity, with mouth widely open (FIGURE 1). The corolla tube is resupinate, yellow with wine-red strips and spots and the reflexed lobes are yellow with wine-red spots. The calyx is wine-red on the internal and wine-red to green on the external face, and, as is typical for the genus, the lobes spread open (FIGURE 1A). Flower pedicels measured 15 to 21 cm long (mean = 17.5 cm, SD = 1.8, $N = 18$), a length which keeps the flower pendent and vertically oriented with its opening towards the ground. The observed floral characteristics, such as color, position on the plant, time of anthesis, as well as nectar concentration and volume, are similar to those recorded in other ornithophilous species in tropical environments (e.g., Arizmendi & Ornelas 1990, Sazima et al. 1996, Buzato et al. 2000). The mean of internal corolla length, from base to opening ("effective length" cf. Wolf et al. 1976) is 58 mm (SD = 4, $N = 18$) and the mean of the major diameter of the apical corolla opening is 35 mm (SD = 3, $N = 12$). Buzato et al. (2000) have noted that most hummingbird-pollinated species in the Atlantic Forest have long corollas (>25 mm). These authors have also suggested that the trend of divergence in pollen placement on hummingbirds is associated mainly with width of flowers, since the ones with a large corolla

aperture correspond to varying locations of pollen deposition on the bodies of hummingbirds. In *Nematanthus brasiliensis*, anthers and stigma are 0.9–2.0 cm longer than corolla length, showing a pronounced exertion of the reproductive structures (FIGURES 1C, 1D). This character is thought to affect pollen placement on the body of the pollinator of *N. brasiliensis* (see discussion below).

The flowers last about eight days. During the first four days, the exerted anthers expose the pollen away from the corolla opening, whereas the stigma is kept inside the tube (male phase; FIGURES 1B, 1C). In the female phase, the style elongates, exposing the stigma well beyond the corolla tube. At this stage, the anthers retract toward the corolla mouth due to the wilting of the filaments (FIGURE 1D). Most species of neotropical Gesneriaceae have separate male and female phases of anthesis, with protandry predominating overwhelmingly (Wiehler 1983). Temporal separation of mature anther and receptive stigma is commonly known in gesneriad species of south-eastern Brazil (*Besleria longimucronata* - SanMartin-Gajardo & Freitas 1999, *Sinningia* spp. *Vanhouttea* spp. and *Paliavana* spp. - SanMartin-Gajardo & Sazima 2004, 2005a, 2005b).

The nectar is secreted by a single gland and is retained within the nectar chamber at the dorsal corolla base. Nectar volume and concentration were measured from bagged flowers after 24 hours, 21.3 μ l (DP = 9.6; $N = 10$) and 31.8% (DP = 5.26; $N = 10$), respectively. This concentration is higher than recorded for other ornithophilous Gesneriaceae occurring in the Atlantic Forest (e.g., *Nematanthus fluminensis* 20.6%, *N. fornicis* 21.9%, *N. fissus* 27.5%, Buzato et al. 2000; *Vanhouttea* species 26%, SanMartin-Gajardo & Sazima 2005). High nectar sugar concentrations in *N. brasiliensis* suggest that this species, along with species in the Bromeliaceae (Buzato et al. 2000), are the main nectar suppliers for the hummingbirds in the region.

Hummingbird Visitors

The Reddish Hermit *Phaetornis ruber* (Spix) and the Saw-billed Hermit, *Ramphodon naevius* (Dumont) were the observed hummingbirds visiting flowers of *Nematanthus brasiliensis*. *P. ruber* obtains nectar by piercing the nectar chamber at corolla base (FIGURE 2A). This hummingbird does not touch the reproductive organs, thus we considered it a nectar thief of *N. brasiliensis*. *P. ruber* was shown in other studies to be opportunistic (Feinsinger & Colwell 1978, Sazima et al. 1996) and often parasites the territories of other hummingbirds (Cardoso & Araujo 2004).

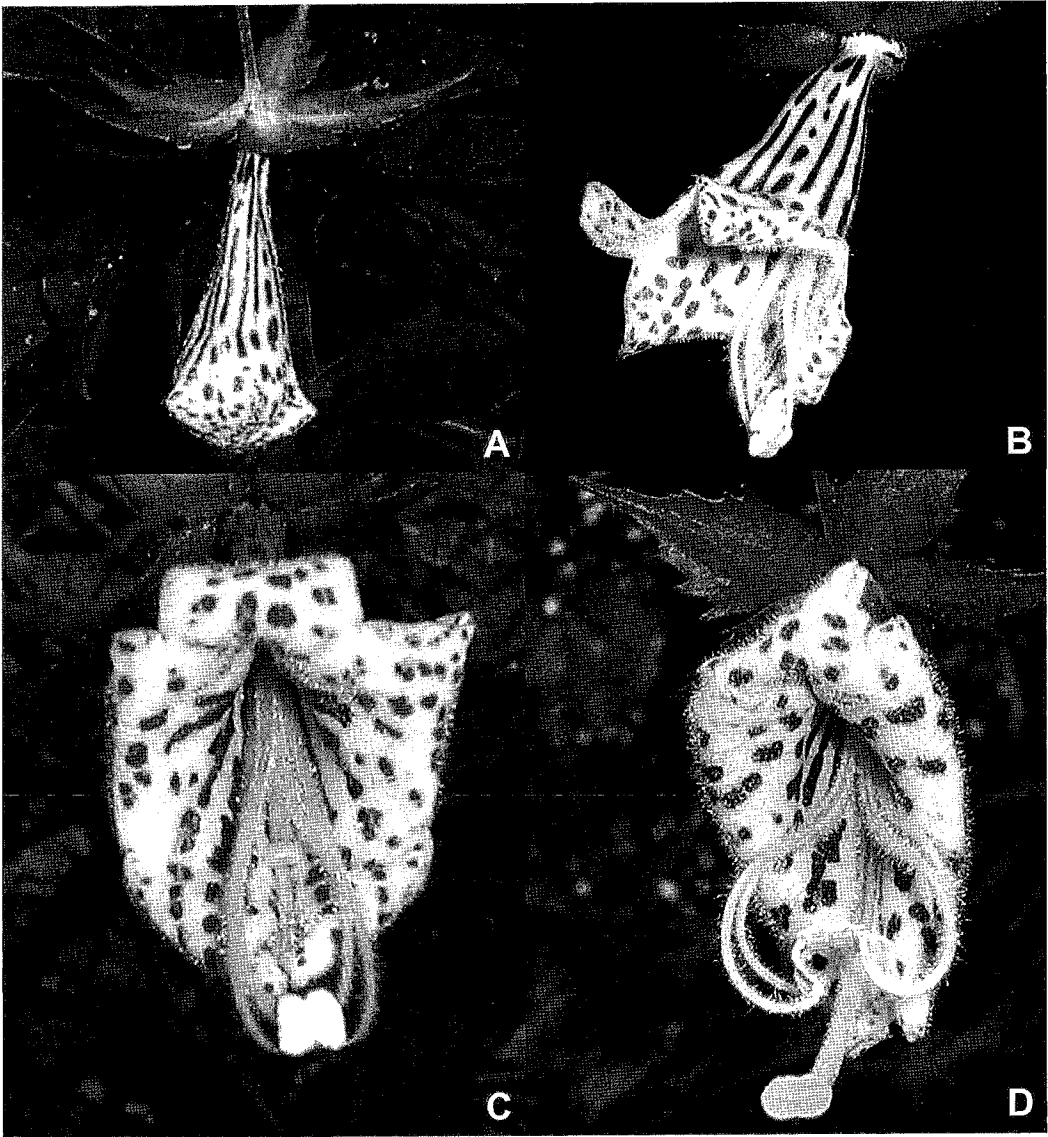


FIGURE 1. Phases of anthesis of *Nematanthus brasiliensis* flower. A. Bud one day before anthesis. B. Anthesis begins with slow petal separation. C. First day of anthesis (male phase) showing the characteristic anther disposition. D. Female phase with long style that expose the stigma.

On the basis of the behavior of *Ramphodon naevius* and the frequency of its visits to the flowers, we determined this hummingbird to be the effective pollinator of *Nematanthus brasiliensis*. *R. naevius* is a year-round resident along the coastal region of the Atlantic Forest (Willis & Oniki 1981, Araujo et al. 1994). It is a specialist on long-tube flowers in southeastern Brazil, often observed visiting species of Bromeliaceae and Heliconiaceae (Araujo et al. 1994, Sazima et al. 1995) as well as Gesneriaceae (Franco & Buzato 1992, Buzato et al. 2000). The

visit frequency of the *R. naevius* to *N. brasiliensis* is quite variable, with intervals between visits lasting 50 to 120 min., similar to times recorded for *N. fluminensis* (90–120 min., Sazima et al. 1995). *R. naevius* is most likely the primary hummingbird pollinator for the Atlantic lowland forests of Brazil (Sazima et al. 1995, Buzato et al. 2000) and has been labeled a “high-reward trapline” (cf. Feinsinger & Clowell 1978, Sazima et al. 1995), whereby the species dominates the use of hummingbird-pollinated flowers in the region.

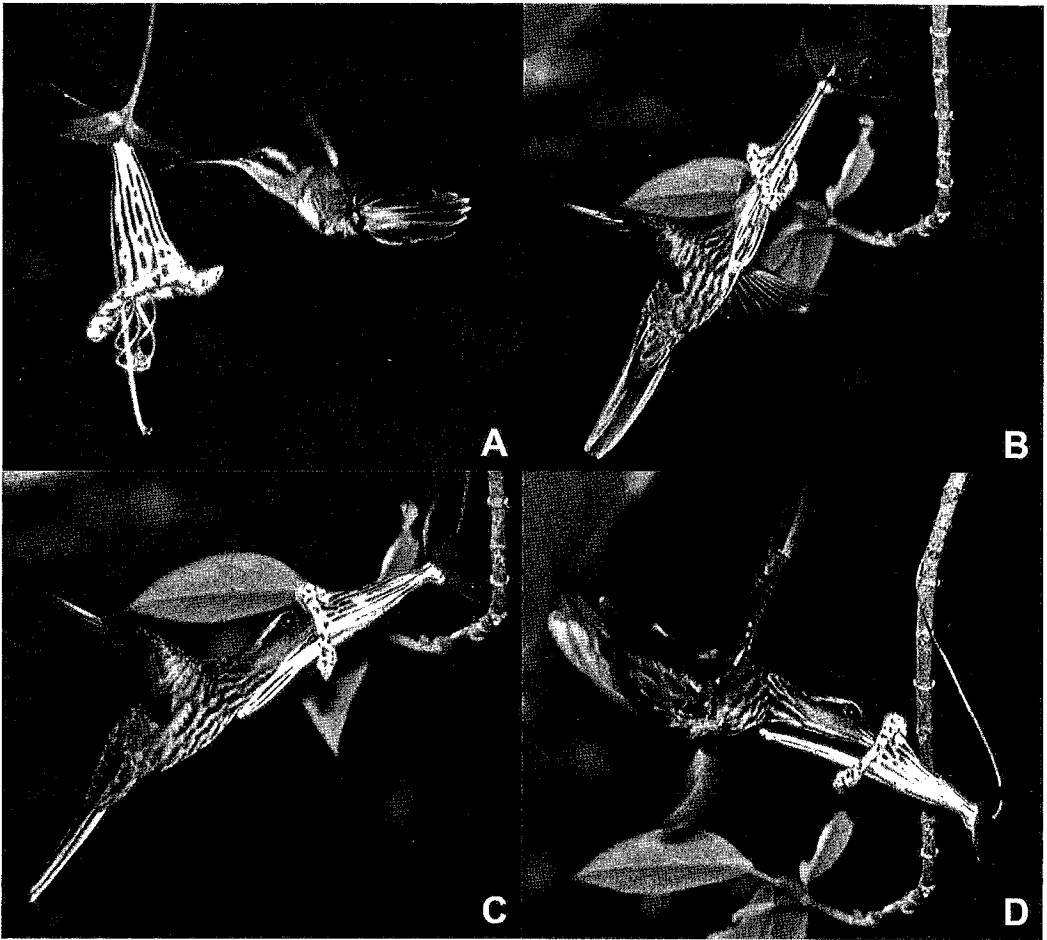


FIGURE 2. Visitor hummingbirds in a flower of *Nematanthus brasiliensis*. **A.** *Phaethornis ruber* approaching the flowers of *Nematanthus brasiliensis* in an illegitimate way (nectar thieving). Visit of *Ramphodon naevius* in a single flower. **B.** Early visit with flower pendent (note pollen placement on the breast). **C.** Hummingbird raising flower and moving it sideways. **D.** Corolla turned totally upwards (note the long pedicel of flower).

Visitation behavior of *Ramphodon naevius* has been observed to vary extensively, depending on flower size, shape, and presentation (Sazima et al. 1995). During visits to the *N. brasiliensis*, a particularly involved behavior was observed: *R. naevius* inserts its beak into the vertically held corolla tube and lifts it to a horizontal position (FIGURES 2C, 2D). It then rotates the flower up to 360 degrees, sometimes reaching a vertical position (i.e., the opening of the corolla tube turned upwards). This behavior in *R. naevius* appears to be uniquely associated with visits to *N. brasiliensis*. The more common behavior, where the hummingbird hovers in front of the flower and inserts its beak into the corolla opening without pronounced movements has been observed during visits to flowers of other species. Apparently, the additional expenditure of energy during visits to *N.*

brasiliensis is offset by the higher sugar reward presented in comparison to other species visited by *R. naevius* (31.8% versus 27% on average, respectively, Sazima et al. 1995). This hypothesis might be tested in experimental studies in which visitation behavior is observed in flowers with artificially varied concentrations of nectar.

During each visit to a *Nematanthus brasiliensis* flower, *Ramphodon naevius* contacted the flower's reproductive organs with its breast (FIGURE 2B), as confirmed by a dusting of pollen at this location on the body. According to Sazima et al. (1995), in 18 other species visited by *R. naevius* the pollen load was received on bill tip, lower or upper bill, forehead or crown, and chin or throat. Pollen placement on various hummingbird species' body parts was summarized for a series of Atlantic Forest plants by Buzato et al. (2000), but

deposition of pollen on the breast has not been previously recorded. The rather unique position of the reproductive structures of *N. brasiliensis* may be a strategy of the plant to prevent inter-specific pollen competition and in-situ hybridization. Natural hybrids are occasionally observed in the wild (e.g., *Nematanthus crassifolius* × *N. fluminensis* in the Reserva Ecológica Rio das Pedras; T. Lopes pers. comm.), including those previously described as species (*N. kuhlmannii* and *N. mattosianus*, Chautems et al. 2005). However, no putative in-situ hybrids involving *N. brasiliensis* have been identified, supporting the hypothesis that its unique presentation of reproductive organs may limit or even preclude inter-specific pollination.

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