

## Bird Pollination of Explosive Flowers While Foraging for Nectar and Caterpillars<sup>1</sup>

Kayna Agostini<sup>2</sup>, Marlies Sazima

Departamento de Botânica, Instituto de Biologia, Caixa Postal 6109, Universidade Estadual de Campinas, 13083-970 Campinas, São Paulo, Brasil

and

Ivan Sazima

Departamento de Zoologia e Museu de História Natural, Caixa Postal 6109, Universidade Estadual de Campinas, 13083-970 Campinas, São Paulo, Brasil

### ABSTRACT

*Mucuna* (Fabaceae) has explosive flowers that open only if a pressure is applied on their wings and keel. The cacique *Cacicus haemorrhous* inserts its bill into a flower and spreading its mandibles apart it opens the flower to take nectar. This icterine bird also preys upon caterpillars of the butterfly *Astrartes talus* that pupates within the flowers. Foraging with use of bill movements to take nectar or insects within a flower is an adequate mechanism to open and pollinate explosive flowers. We suggest that a plausible behavioral scenario for the pollination relationship between icterines and *Mucuna*-like flowers might start with the birds' searching for insects within flowers.

### RESUMEN

El género *Mucuna* (Fabaceae) tiene flores explosivas que abren cuando se aplica una presión sobre sus alas o quillas. El boyero cacique, *Cacicus haemorrhous*, introduce su pico dentro de la flor y expande sus mandíbulas abriendo la flor para beber el néctar. Esta ave Icterinae también depreda larvas de la mariposa *Astrartes talus*, la cual empupa dentro de las flores. El forrajeo con uso de movimientos del pico, para consumir el néctar o de insectos dentro de una flor, es un mecanismo adecuado para abrir y polinizar las flores explosivas. Sugerimos que este es un escenario comportamental razonable para la relación de la polinización entre especies de Icterinae y flores del tipo *Mucuna*, que podría iniciar con la búsqueda de las aves por insectos dentro de las flores.

*Key words:* *Astrartes talus*; Atlantic Forest; *Cacicus haemorrhous*; explosive flowers; *Mucuna japura*; perching bird pollination; southeastern Brazil.

FLOWERS OF THE GENUS *MUCUNA* (Fabaceae, Phaseoleae) display an explosive mechanism of pollen-delivery. They open only if a given pressure is applied on their wings and keel, which results in the release of the reproductive organs and projection of pollen onto pollinators (van Leeuwen 1938, van der Pijl 1941, Baker 1970). Flagelliflory is well developed in *Mucuna* (van der Pijl 1941, Faegri & van der Pijl 1980), the flowers hang on long, dangling peduncles suited to visits by large flying animals as this arrangement results in flying room among branches and foliage (Baker 1970). In the Neotropics, several *Mucuna* species are pollinated by bats (van der Pijl 1941, Dobat & Peikert-Holle 1985) including *Mucuna urens* (Sazima & Sazima 1978), although Arroyo (1981) suggests that this latter species is hummingbird-pollinated. As far as we are aware, however, the only reliable record of bird pollination for this genus is that of *Mucuna rostrata* in Central America (Cotton 2001).

The generalization that New World bird-flowers are exploited by hovering birds, whereas Old World bird-flowers are generally visited by perching birds has become common in the literature

(Westerkamp 1990). However, recent studies in the Neotropics show that passerine birds have an important role as pollinators of several species of Bromeliaceae (Sazima & Sazima 1999) and Marcgraviaceae (Sazima *et al.* 1993) in addition to the better known Fabaceae (mostly within the genus *Erythrina*, see Cruden & Toledo 1977, Toledo & Hernández 1979, Morton 1979, Steiner 1979, Etcheverry & Truco Alemán 2005). Pollination by icterine birds (orioles, caciques, and oropendulas) is well documented for *Erythrina fusca* (Morton 1979, Cotton 2001). Icterines are insect eaters that also feed on fruits and nectar, as documented for the caciques *Cacicus haemorrhous*, *C. chrysopterus* and *C. cela*, and the oropendula *Psarocolius decumanus* (Sick 1985, Robinson 1986, Pizo 1996, Ragusa-Netto 2002). While foraging for insects, several species of icterine birds insert their bill into a fruit, a bunch of wrapped leaves, or a flower, and access otherwise hidden food by spreading apart their mandibles and widening the initial gap ("bill-spacing," see Morton 1979, Sick 1985).

We found that a recently described species, *Mucuna japura*, the Yellow Duckbill from southeastern Brazil (Tozzi *et al.* 2005) is another bird-pollinated example within the genus *Mucuna*. Here besides general observations on the flower-visiting behavior of three perching bird species, we focused on the most common effective

<sup>1</sup>Received 8 September 2005; revision accepted 21 December 2005.

<sup>2</sup>Corresponding author; e-mail: kayna@mailcity.com

pollinator, the Red-Rumped cacique (*C. haemorrhous*) and addressed three main questions: (1) Is the morphology of *M. japira* flowers suited for perching bird visits? (2) Is the Red-Rumped cacique's foraging technique suited for pollination of explosive flowers? and (3) Are there other food resources for birds in the flowers?

The study area is a subhumid, evergreen, broad-leaf forest in coastal lowlands (Eiten 1970, Sazima *et al.* 1999, 2003) at Picinguaba (about 23°20'S, 44°52'W) in Ubatuba, São Paulo, southeastern Brazil. Average annual rainfall at the study site is 2526 mm and average annual temperature is 22.7°C (Sazima *et al.* 1999, 2003). Fieldwork was conducted from May to June 2002–2004, beginning at dawn (0500 h) and ending at late afternoon (1700 h), totaling 169 person-hours. Bird visits to flowers were observed directly or with the aid of binoculars, and were photographed for analyses of visiting behavior (Grant & Grant 1968, Vogel 1968, Lehner 1979). A sample of 74 flowers was examined for the occurrence of butterfly caterpillars or pupae. Morphology and floral biology observations were made *in situ* and in the laboratory. Nectar concentration (% sucrose, w/w) and volume ( $\mu$ l) were measured from ten bagged flowers (from ten different plants) per day during the 7 d anthesis with a pocket refractometer (Atago, N-1E, Japan) and microlitre syringes, respectively (Sazima *et al.* 1999, 2003).

*Mucuna japira* is a woody climber with pseudo-racemose inflorescences on dangling peduncles 4.4–25.3 cm long (Tozzi *et al.* 2005). Flagelliflory (flowers placed on the end of long peduncles) is nowhere better developed than in the leguminous vine genus *Mucuna* (Baker 1970). Bird-pollinated species within the genus seem to have peduncles shorter than 40 cm, such as those found in the bird-pollinated *M. kraetkei* at Papua-New Guinea (van Leeuwen 1938). On the other hand, the peduncles of bat-pollinated *Mucuna* species may reach up to 10 m (van der Pijl 1941, Baker 1970, Faegri & van der Pijl 1980, Hopkins & Hopkins 1992). Each *M. japira* inflorescence bears 12–21 showy, yellow, and odorless flowers, which are in anthesis simultaneously and remain fresh and active for 7 d (Tozzi *et al.* 2005). Features such as vivid color and lack of odor fit well into the ornithophilous syndrome (Faegri & van der Pijl 1980). Simultaneous anthesis and a large number of flowers per inflorescence are well suited to the needs of perching birds, which thus are able to reach several flowers from a single perch without much movements (Pyke 1981); additionally, the birds can land on the inflorescences (Westerkamp 1990).

The nectar is available upon flower opening and is produced throughout the 7 d anthesis. Nectar volume averages 192.2–337.7  $\mu$ l, the highest volume being available on the fifth day of anthesis, and nectar concentration averages 9.7–10.8 percent ( $N = 70$  flowers). A large amount of dilute nectar is a feature related to bird pollination, especially when perching birds are involved (Sazima *et al.* 1993, Baker *et al.* 1998, Cotton 2001). Floral visitors to *M. japira* reach the nectar legitimately only after pushing the base of the keel, thus triggering the explosive opening of the flower (Fig. 1A). Nectar production stops right after the explosive opening of the flower, a feature probably related to the fact that pollination occurs only once in a single event, a characteristic of all *Mucuna* species studied so far (*e.g.*, Sazima & Sazima 1978, Endress 1994, von Helversen & von Helversen 2003).

Therefore, we conclude that the Yellow Duckbill flowers display several features favoring pollination by perching birds, and the visitors have to press the base of the keel to reach the otherwise unavailable nectar. Although Vogel (1968) mentions no bird-pollinated *Mucuna* species with explosive flowers, this type of flower opening is recorded for the ornithophilous *M. kraetkei* (Van Leeuwen 1938) in Papua-New Guinea.

We recorded the Red-Rumped cacique (*C. haemorrhous*) foraging and taking nectar from 84.4 percent of the 32 Yellow Duckbill flowers it was recorded visiting. In 15.6 percent ( $N = 5$ ) of the observed flowers, the bird extracted pupating caterpillars of the butterfly *Astrartes talus* (Hesperiidae) from the visited flowers (Table 1). Besides foraging on *M. japira* flowers this cacique foraged on other food resources such as fruits of *Trichilia* sp. (Meliaceae), nectar of *Combretum fruticosum* (Combretaceae), and was recorded carefully inspecting bunches of senescent leaves probably searching for insects (see Sick 1985 for the latter behavior).

While foraging on Yellow Duckbill flowers, the Red-Rumped cacique perched on the inflorescence axis, peduncle, or on adjacent branches, bowed its head toward the flower, inserted the bill into the flower, and through bill movements it pressed the base of the wings and keel at the same time, thus triggering the explosive opening of the flower and releasing the enclosed reproductive organs (Fig. 1A). While taking nectar or larvae, the bird received pollen on its head and touched the stigma due to the explosive mechanism of pollen delivery (Fig. 1B). After the first visit to a given Yellow Duckbill flower, the cacique was unable to contact the reproductive organs due to their now released position (see Fig. 1A), and in the subsequent visits to the same flower it took the remaining nectar.

Searching either for nectar or larvae on *M. japira* flowers renders the Red-Rumped cacique an effective pollinator, since in both situations the bird contacts the reproductive organs. Thus, the cacique's foraging behavior is an adequate technique to open and pollinate explosive flowers such as those of *M. japira*. Bill movements are used by perching birds to open and pollinate *E. fusca* flowers in Panama and *E. dominguezii* (Fabaceae) in Brazil (Morton 1979, Ragusa-Netto 2002) which, however, have no explosive opening characteristic of *Mucuna*. Flower-opening techniques possibly evolved separately in different bird lineages, allowing them to exploit a particular source of flower nectar successfully and at the same time promoting pollination (Stiles 1981, Sick 1985).

The large-crested oropendula (*P. decumanus*) also visited the Yellow Duckbill flowers legitimately, triggered explosive opening, and fed on nectar. However, its visits were uncommon (Table 1) and due to its weight some flowers occasionally dropped from the inflorescences it perched on. Thus, the oropendula may be regarded as an occasional visitor and pollinator. The Bananaquit (*Coereba flaveola*) pierced the base of the wings and keel of the flowers, and robbed the nectar in 96.3 percent of its visits (Table 1), which characterizes it mostly as a nectar thief (Snow & Snow 1971).

Larvae of the butterfly *A. talus* (Hesperiidae) were found in about 35 percent ( $N = 26$ ) of the 74 *M. japira* flowers examined for caterpillars. The larvae browsed on the leaves and pupated between the keel and the wings (Fig. 1C) but they did not damage the

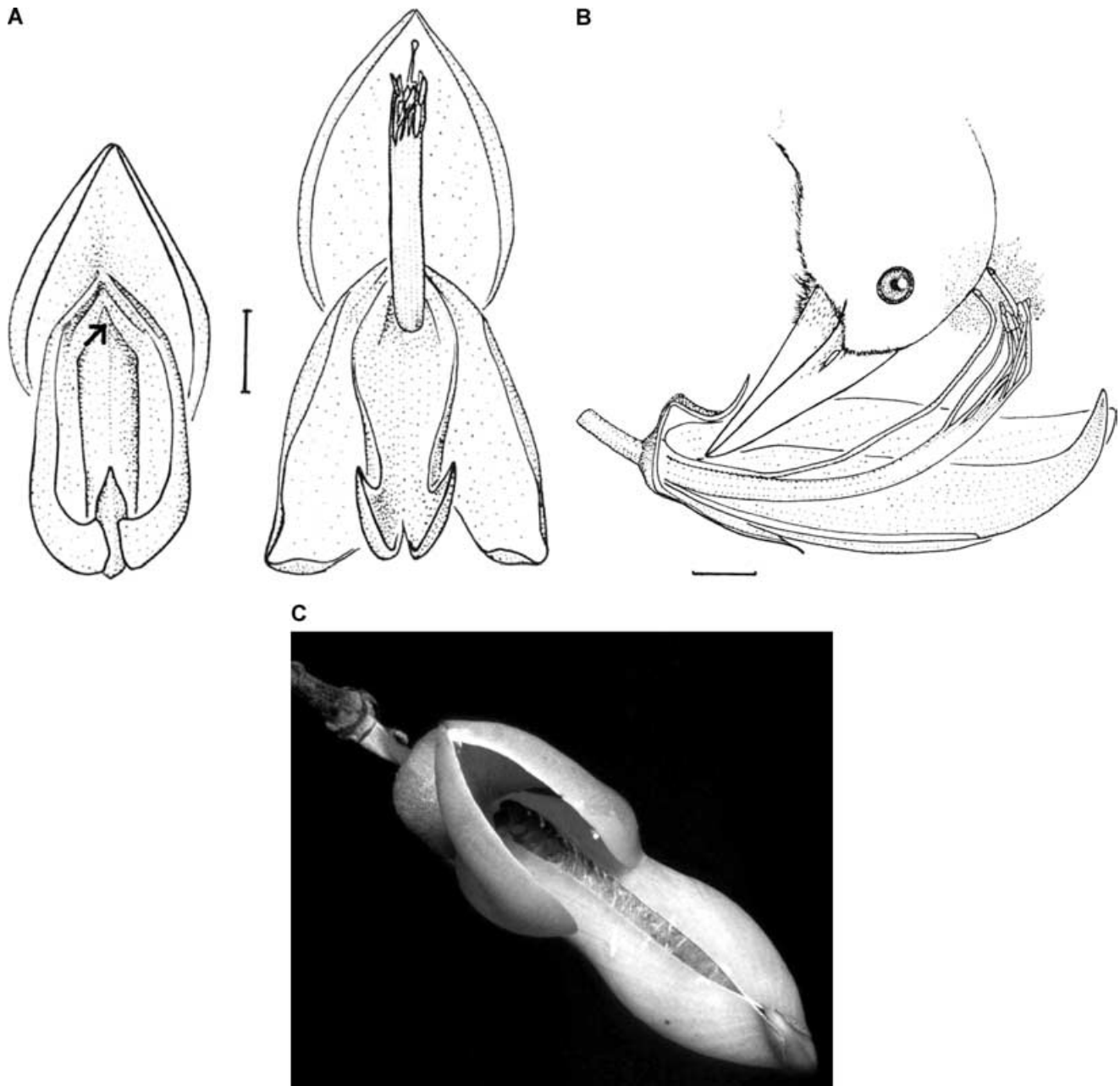


FIGURE 1. (A) Frontal view of a Yellow Duckbill flower intact (left), and after a Red-Rumped cacique's (*C. haemorrhous*) visit (right) with opened keel and the reproductive organs exposed and close to the flag petal. Arrow points to the place the bird must press its bill to release the flower's explosive opening. Scale = 25 mm. (B) A Red-Rumped cacique searching for nectar at the staminal column base of a Yellow Duckbill flower (flag petal removed for a better view of the spatial relationship between the visitor's head and the flower's reproductive organs). Note a cloud of pollen and the stigma touching the bird's crown during the explosive opening. Scale = 15 mm. (C) A hesperiid butterfly larva (*Astraptus talus*) pupating within a still closed Yellow Duckbill flower.

reproductive organs, and therefore the flowers remained available for pollination. The caterpillars of *A. talus* were found on *M. japura* leaves during the blossoming period only, and the flowers probably acted as a shelter for the completion of their larval life cycle. These caterpillars specifically eat leaves of *Mucuna* species (Janzen & Hallwachs 1999) and build leaf shelters to pupate (Greeney & Jones 2003).

We suggest that caterpillars have the potential to drive the Red-Rumped cacique to inspect *M. japura* flowers because, while we found that 35 percent of all *M. japura* flowers are occupied by caterpillars, birds extracted larvae from about 50 percent of the flowers they visited suggesting that they may be searching preferentially for caterpillars. If the birds were foraging primarily or entirely for larvae, they would be expected to neglect flowers with nectar

TABLE 1. Total number of bird visits to *Mucuna japira* flowers: exploited resources, and consequence to the flowers.

Visitors	Visits			Total of visits (N = 194)
	Nectar only, with explosive opening	Larvae only, with explosive opening	Nectar only, through piercing and no opening	
<i>Cacicus haemorrhous</i>	27 (84.4%)	5 (15.6%)	0	32 (16.5%)
<i>Coereba flaveola</i>	6 (3.7%)	0	154 (96.3%)	160 (82.5%)
<i>Psarocolius decumanus</i>	2 (100.0%)	0	0	2 (1.0%)

only and favor those which show potential for sheltering larvae (e.g., those with insect silhouettes or some damage). This prediction is amenable to field tests. Thus, we suggest that a plausible behavioral scenario for the pollination relationship between icterines and *Mucuna*-like flowers might start with the birds' searching for insects within flowers.

## ACKNOWLEDGMENTS

We thank L. Freitas and M. A. Pizo for reading early versions of the manuscript; K. S. Brown and A. V. L. Freitas for identification of the butterfly larvae; A. Midori for rendering the drawings; the Instituto Florestal for the logistical support and the opportunity to work at the Parque Estadual da Serra do Mar, Picinguaba; the CAPES, CNPq, and FMB for financial support. We thank Sandra Oblando for translating the abstract to Spanish.

## LITERATURE CITED

- ARROYO, M. T. K. 1981. Breeding systems and pollination biology in Leguminosae. In R. M. Polhill and P. H. Raven (Eds.), *Advances in legume systematics*, part II, pp. 723–769. Kew, Royal Botanic Gardens, Kew.
- BAKER, H. G. 1970. Bat pollination in Central America. *Rev. Biol. Trop.* 17: 187–197.
- , I. BAKER, AND S. A. HODGES. 1998. Sugar composition of nectars and fruits consumed by birds and bats in tropics and subtropics. *Biotropica* 30: 559–586.
- COTTON, P. A. 2001. The behavior and interactions of birds visiting *Erythrina fusca* flowers in the Colombian Amazon. *Biotropica* 33: 662–669.
- CRUDEN, R. W., AND V. M. TOLEDO. 1977. Oriole pollination of *Erythrina breviflora* (Leguminosae): Evidence for polytypic view of ornithophily. *Plant Syst. Evol.* 126: 393–403.
- DOBAT, K., AND T. PEIKERT-HOLLE. 1985. Blüten und Fledermäuse. Bestäubung durch Flederermäuse und Flughunde (Chiropterophilie). Waldemar Kramer, Frankfurt.
- EITEN, G. 1970. A vegetação do Estado de São Paulo. *Bol. Inst. Bot.* 7: 1–147.
- ENDRESS, P. K. 1994. *Diversity and evolutionary biology of tropical flowers*. Cambridge University Press, Cambridge.
- ETCHEVERRY, A. V., AND C. E. TRUCO ALEMÁN. 2005. Reproductive biology of *Erythrina falcata* (Fabaceae: Papilionoideae). *Biotropica* 37: 54–63.
- FAEGRI, K., AND L. VAN DER PIJL. 1980. *The principles of pollination ecology*. Pergamon Press, New York.
- GRANT, K., AND V. GRANT. 1968. *Hummingbirds and their flowers*. Columbia University Press, New York.
- GREENEY, H. F., AND M. T. JONES. 2003. Shelter building in the Hesperidae: A classification scheme for larval shelters. *J. Res. Lepid.* 37: 27–36.
- HOPKINS, H. C. F., AND M. J. G. HOPKINS. 1992. Rediscovery of *Mucuna macropoda* (Leguminosae: Papilionoideae), and its pollination by bats in Papua New Guinea. *Kew Bull.* 48: 297–305.
- JANZEN, D. H., AND W. HALLWACHS. 1999. Philosophy, navigation and use of a dynamic database ("ACG Caterpillars SRNP") for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica [on line]. URL: <http://janzen.sas.upenn.edu>.
- LEHNER, P. N. 1979. *Handbook of ethological methods*. STPM Press, Garland.
- MORTON, E. S. 1979. Effective pollination of *Erythrina fusca* by the orchard oriole (*Icterus spurius*)—co-evolved behavioral manipulation. *Ann. Mo. Bot. Gard.* 66: 482–489.
- PIZO, M. A. 1996. Feeding ecology of two *Cacicus* species (Emberizidae, Icterinae). *Ararajuba* 4: 87–92.
- PYKE, G. H. 1981. Why hummingbirds hover and honeyeaters perch. *Anim. Behav.* 29: 861–876.
- RAGUSA-NETTO, J. 2002. Exploitation of *Erythrina dominguezii* Hassl. (Fabaceae) nectar by perching birds in a dry forest in western Brazil. *Braz. J. Biol.* 62: 877–883.
- ROBINSON, S. K. 1986. Three-speed foraging during the breeding cycle of yellow-rumped Caciques (Icterinae: *Cacicus cela*). *Ecology* 67: 394–405.
- SAZIMA, I., AND M. SAZIMA. 1978. Polinização por morcegos em *Mucuna urens* (Leguminosae). Resumos da XXX Reunião da Sociedade Brasileira para o Progresso da Ciência. pp. 419.
- , S. BUZATO, AND M. SAZIMA. 1993. The bizarre inflorescence of *Norantea brasiliensis* (Marcgraviaceae)—visits of hovering and perching birds. *Bot. Acta* 106: 507–513.
- SAZIMA, M., AND I. SAZIMA. 1999. The perching bird *Coereba flaveola* as a co-pollinator of bromeliad flowers in southeastern Brazil. *Can. J. Zool.* 77: 47–51.
- , S. BUZATO, AND I. SAZIMA. 1999. Bat-pollinated flowers assemblages and bat visitors at two Atlantic forest sites in Brazil. *Ann. Bot.* 83: 705–712.
- , ———, AND ———. 2003. *Dysochroma viridiflorum* (Solanaceae): A reproductively bat-dependent epiphyte from the Atlantic Rainforest in Brazil. *Ann. Bot.* 92: 725–730.
- SICK, H. 1985. *Ornitologia brasileira, uma introdução*. Editora da Universidade de Brasília, Brasília.
- SNOW, B. K., AND D. W. SNOW. 1971. Feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88: 291–322.
- STEINER, K. E. 1979. Passerine pollination of *Erythrina megistophylla* (Fabaceae). *Ann. Mo. Bot. Gard.* 66: 490–502.
- STILES, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. *Ann. Mo. Bot. Gard.* 68: 323–351.

- TOLEDO, V. M., AND H. M. HERNÁNDEZ. 1979. *Erythrina oliviae*: A new case of oriole pollination in Mexico. *Ann. Mo. Bot. Gard.* 66: 503–511.
- TOZZI, A. M. G. A., K. AGOSTINI, AND M. SAZIMA. 2005. A new species of *Mucuna* Adans. (Leguminosae, Papilionoideae, Phaseoleae) from southeastern Brazil, with a key to Brazilian species. *Taxon* 54(2): 451–455.
- VAN DER PIJL, L. 1941. Flagelliflory and cauliflory as adaptations to bats in *Mucuna* and other plants. *Ann. Jard. Bot. Buitenzorg* 51: 83–93.
- VAN LEEUWEN, W. M. D. 1938. Observations about the biology of tropical flowers. *Ann. Jard. Bot. Buitenzorg* 48: 27–68.
- VOGEL, S. 1968. Chiropterophilie in der neotropischen Flora. *Neue Mitteil. I. Flora* 157: 562–602.
- VON HELVERSEN, D., AND O. VON HELVERSEN. 2003. Object recognition by echolocation: A nectar-feeding bat exploiting the flowers of a rain forest vine. *J. Comp. Physiol. A* 189: 327–336.
- WESTERKAMP, C. 1990. Bird-flowers: Hovering versus perching exploitation. *Bot. Acta* 103: 366–371.