

OBSERVATIONS OF HUMMINGBIRD FEEDING BEHAVIOR AT FLOWERS OF *HELICONIA BECKNERI* AND *H. TORTUOSA* IN SOUTHERN COSTA RICA

Joseph Taylor¹ & Stewart A. White

Division of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow, CB23 6DH, UK.

Observaciones de la conducta de alimentación de colibríes con flores de *Heliconia beckneri* y *H. tortuosa* en El Sur de Costa Rica.

Key words: Pollination, sympatric, cloud forest, Cloudbridge Nature Reserve, Green Hermit, *Phaethornis guy*, Violet Sabrewing, *Campylopterus hemileucurus*, Green-crowned Brilliant, *Heliodoxa jacula*.

INTRODUCTION

Interactions between closely related sympatric flowering plants may involve competition for pollinators, interspecific pollen loss and hybridization (e.g., Feinsinger 1987). These processes drive the divergence of genetically based floral phenotypes that influence pollinator assemblages and behavior. However, floral convergence may be favored if the increased nectar supplies and flower densities, for example, increase the regularity and rate of flower visitation for all species concerned (Schemske 1981). Sympatric hummingbird-pollinated plants probably face strong selection pressures against simultaneous pollinator sharing, since the mobility of birds combined with their high energy needs may result in them visiting several widely scattered nectar

sources in a single foraging bout (Stiles 1978). The flower preferences shown by hummingbirds (Trochilidae) are influenced by a complex array of factors including their bill dimensions, body size, habitat preference and relative dominance, as influenced by age and sex, and how these interact with the morphological, caloric and visual properties of flowers (e.g., Stiles 1976).

Hummingbirds are the primary pollinators of most *Heliconia* species (Heliconiaceae) (Linhart 1973), which are medium to large clone-forming herbs that usually produce brightly colored floral bracts (Stiles 1975). Some species of hummingbirds are known to visit several *Heliconia* species, probably resulting in substantial interspecific pollen transfer (Kress 1983). Many *Heliconia* species are sympatric; however the number of naturally occurring hybrids is small in proportion to the number of sympatric associations. Interactions between *Heliconia* species will probably favor a divergence in spatial and temporal

¹Current address: Cambridgeshire and Peterborough Biological Records Centre, The Manor House, Broad Street, Cambourne, Cambridge, CB3 6DH, UK. E-mail: joe.taylor@cpbrc.org.uk

flowering patterns (Stiles 1979). Mechanical isolation may occur through deposition of pollen from different species in different places on a given species of hummingbird, through variation in corolla morphology and positioning of the anthers (Stiles 1975, 1979; Kress 1983). The ultimate mechanisms preventing hybridization in *Heliconia* species may be pre-fertilization barriers such as the inhibition of foreign pollen tubes, and these are probably favored by pollinator sharing (Kress 1983).

On the Pacific slope of the Cordillera Talamanca, in southern Costa Rica, *Heliconia beckneri* R. R. Smith, a species endemic to this mountain range and probably of hybrid origin (Daniels & Stiles 1979), and *H. tortuosa* Griggs occur together in mid-elevation habitats. The flowering peaks of these two species overlap in June and July (Daniels & Stiles 1979), and they are predicted to share the same primary and secondary pollinators (Stiles 1979), but hybridization apparently does not occur. Stiles (1979) identifies the Green Hermit (*Phaethornis guy*) as the primary pollinator of both species, and the Violet Sabrewing (*Campylopterus hemileucurus*) as the secondary pollinator of *H. tortuosa* and the possible secondary pollinator of *H. beckneri*. In addition, the Rufous-tailed Hummingbird (*Amazilia tzacatl*) is given as an occasional pollinator of *H. tortuosa*. If the services of pollinators are indeed shared it might be expected that selection has favored mechanisms that reduce the chances of hybridization and pollen loss between these species. The aim of this research was to investigate the extent of pollinator sharing and the presence of such mechanisms.

METHODS

Field work was carried out by the principal researcher (JT) between 22 May and 17 July 2005 at Cloudbridge Nature Reserve, San Gerardo de Rivas, Pérez Zeledón, Costa Rica

(approx. 09°50'N, 83°55'W). The reserve covers over 200 ha adjacent to the Chirripó National Park on the southern Pacific slope of the Talamanca mountain range. *H. beckneri* and *H. tortuosa* were often found growing within metres of one another, in both primary forest and secondary growth, and were both flowering abundantly during the study period, thus there was no indication of staggered flowering peaks as an isolation mechanism (Stiles 1979).

Focal observations were carried out from 06:00 h to 12:00 h (CST), through all conditions, at seven plants or clumps of plants (presumed clones) of both species, each with at least one fresh inflorescence, resulting in 42 h of observations for each species. Most focal plants were in oak-dominated lower montane primary forest, but two clumps of *H. tortuosa* plants were watched in secondary growth at similar elevations. The elevation range of focal plants, as measured with a global positioning system, was 1561–1678 m for *H. beckneri*, and 1560–1607 m for *H. tortuosa*.

During observations, the observer sat or stood approximately 4 m away from the focal plants, and 8×30 binoculars were used. Pollinating flower visits were counted, including repeat visits to the same flower, and were classed as those that probably involved contact with the reproductive parts of flowers. Insect flower visitors were at least identified to Order, but to a lower taxonomic level where possible. All hummingbird flower visitors were identified to species, and where possible the sex of birds was noted at all focal plants and clumps of *H. tortuosa* and at five of the focal plants and clumps of *H. beckneri*. Hummingbirds were sexed by differences in plumage (Stiles & Skutch 1989). The primary and secondary pollinators of each *Heliconia* species at Cloudbridge during the study period were identified in terms of the percentage of all pollinating visits that they accounted for. Observations of feeding meth-

TABLE 1. The proportion (%) of all pollinating flower visits (n) by each taxa observed at seven plants or clumps of plants each of *Heliconia beckneri* and *H. tortuosa* at Cloudbridge Nature Reserve, Costa Rica, in June and July 2005.

Taxa of flower visitors	Proportion (%) of all pollinating visits (n)	
	<i>H. beckneri</i> (n = 318)	<i>H. tortuosa</i> (n = 271)
Apodiformes (Trochilidae)		
Green Hermit	19	17
Violet Sabrewing	0	68
Green-crowned Brilliant	69	0
Hymenoptera		
Euglossine species	8	7
Probable <i>Trigona</i> species	4	8

ods were made for most flower visits, sometimes with binoculars, including the angle at which hummingbirds inserted their bills into the corolla and the resulting points of contact on the hummingbird by the anthers and stigma; that is, the likely pollen deposition sites.

RESULTS

Focal observations revealed that pollinating flower visits were carried out at both species of *Heliconia* by hummingbirds and bees (Apoidea) (Table 1). The Green Hermit was only the secondary pollinator of both *Heliconia* species; its services, though, appeared to be partitioned, with males accounting for 92% of all flower visits by this species at *H. beckneri* (n = 24), and females or juveniles accounting for 96% of all flower visits by this species at *H. tortuosa* (n = 46). The Violet Sabrewing was the primary pollinator of *H. tortuosa*, but was only seen to visit one clump of *H. beckneri* in secondary growth during trial observations. The Green-crowned Brilliant (*Heliodoxa jacula*) was the primary pollinator of *H. beckneri*, but was never seen to approach inflorescences of *H. tortuosa*. Euglossine bees and probable

Trigona bees were occasional pollinators of both *Heliconia* species (Table 1).

Observations of feeding behavior suggest that flower shape influenced the feeding methods of hummingbirds. The flowers of *H. beckneri* are virtually straight from the corolla entrance to just before the nectar chamber, where there is a slight curvature (Fig. 1) and all the species observed (Table 1), including the Green Hermit and Violet Sabrewing, which have long decurved bills, were seen to probe from in front of the flowers (Figs 2A and 2B). In contrast, the moderately and evenly curved flowers of *H. tortuosa* (Fig. 1) appeared to force birds with long decurved bills to insert them from above and behind the flowers (Figs 2C and 2D), and almost certainly excluded the straight bill of the Green-crowned Brilliant. The Green-crowned Brilliant always perched on bracts when feeding from *H. beckneri* flowers and the anthers and stigma appeared to touch its chin, cheeks and throat (Fig. 2A). In contrast, the Green Hermit was always seen to hover whilst feeding from flowers. The anthers and stigma of *H. beckneri* appeared to touch its lower mandible and probably its chin (Fig. 2B), while those of *H. tortuosa* appeared to touch its upper mandi-



FIG. 1. Three fresh flowers of *Heliconia tortuosa* (left) and *H. beckneri* (right) picked at Cloudbridge Nature Reserve, Costa Rica, in July 2005. Photo by Joseph Taylor.

ble and probably its forehead (Fig. 2C). The Violet Sabrewing usually fed whilst hovering, and rarely perched to feed. At *H. tortuosa* flowers the anthers and stigma appeared to touch the forehead or crown (Fig. 2D). Trial observations at a large clump of *H. beckneri* plants in secondary growth suggested that the anthers and stigma of this species touched the bird's chin. It should be noted that there is no quantitative data to support these observations of differing feeding methods, and no additional fieldwork was carried out to confirm the pollen deposition sites.

DISCUSSION

The identities of the primary and secondary pollinators of *H. beckneri* and *H. tortuosa* at Cloudbridge did not conform to those that

were expected, however explaining the roles of species is difficult without a study of their relative abundances in the locality. Whilst the presence of the Green-crowned Brilliant and Violet Sabrewing as the primary pollinators of these *Heliconia* species was probably strongly influenced by season and elevation, respectively (see Stiles 1979, Stiles & Skutch 1989), the relative preferences of all three hummingbird species were probably influenced by exploitation competition, flower morphology, bract and floral coloration, and nectar production (e.g., Stiles 1976). The limited sampling of accumulated nectar in protected flowers by picking and dissection revealed that there was a significantly higher energy content ($J \text{ flower}^{-1}$) in those of *H. beckneri* at both sampling times of 06:00 h (Mann-Whitney *U*-test, $U = 138.0$, $P = 0.014$, $n = 10$

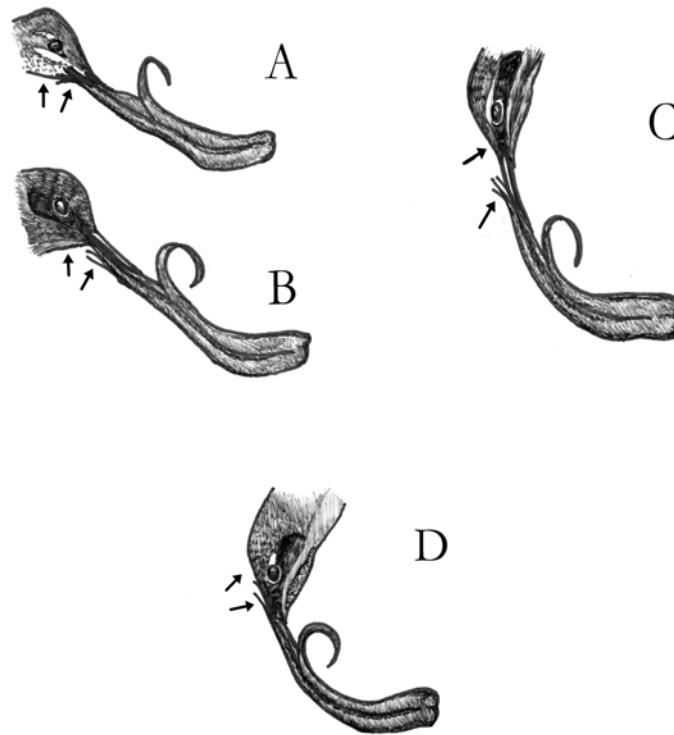


FIG. 2. Feeding methods of three hummingbird species at *Heliconia* flowers as observed at Cloudbridge Nature Reserve, Costa Rica, between 22 May and 17 July 2005: A) *Heliodoxa jacula* at *H. beckneri*; B) *Phaethornis guy* at *H. beckneri*; C) *P. guy* at *H. tortuosa*; and D) *Campylopterus hemileucurus* at *H. tortuosa*. Arrows indicate probable pollen deposition sites. Drawings by Joseph Taylor.

flowers per species) and 12:00 h ($U = 136.0$, $P = 0.021$, $n = 10$ flowers per species). The partitioning of the pollination services of the Green Hermit by sex and possibly age could be due to the interaction of a dominance hierarchy and the difference in the energy content of flowers, as female hummingbirds are generally subordinate (Stiles 1976). Although Euglossine bees were only occasional pollinators of both species, they are thought to promote outcrossing among tropical plants with low population densities (Janzen, 1971). Flower mites (Acari: Mesostigmata: Ascidae) were observed on the flowers of both species and may contribute to self-pollination

(Dobkin 1984).

The data suggest that the pollination services of the Green Hermit and Violet Sabrewing are shared by populations of *H. beckneri* and *H. tortuosa* at Cloudbridge to only a limited extent. If interspecific pollen transfer did take place, hybridization might occur, since *H. tortuosa* is known to hybridize with *H. latipatha* (Stiles 1979), one of the suspected parent species of *H. beckneri* (Daniels & Stiles 1979). However, the observed differences in flower curvature, feeding methods and the likely pollen deposition sites, probably reduce the risk of pollen loss and cross-fertilization. Thus, there is unlikely to be selection against

both the sharing of pollinators and simultaneous flowering in these two species. Both of the *Heliconia* species studied at Cloudbridge were abundant in primary forest, and Stiles (1975) noted that under the forest canopy low light intensity may make it difficult for a species to photosynthesize the metabolic reserves necessary for flowering. Therefore simultaneous flowering may create sufficient nectar resources to maintain pollinator traplines (Schemske 1981) where only one species would be unable to. Stiles (1975, 1979) also noted that, at La Selva, Costa Rica, *H. irrasa* and *H. umbrophila* flowered simultaneously in most years. These species are plants of the forest understory, and simultaneous flowering perhaps allows hermits to extend their foraging routes through the forest more frequently than usual. The different flower curvatures of *H. irrasa* and *H. umbrophila* result in pollen being placed at dorsal and ventral sites on their shared pollinator, the Long-tailed Hermit (*P. superciliosus*) (Stiles 1979). The flower morphologies and resulting pollen deposition sites noted by Stiles (1975, 1979) mirror the observations in the present study surprisingly closely, suggesting that this could be a reoccurring pattern in sympatric *Heliconia* species. Stiles (1975) suggested that the less abundant *H. umbrophila* had converged in flowering season with *H. irrasa*; a change favored because it would make its clumps more accessible to traplining hermits. Further research on whether other sympatric *Heliconia* species, such as *H. beckneri* and *H. tortuosa*, have influenced one another's populations may uncover interesting relationships.

ACKNOWLEDGMENTS

Many thanks to I. and G. Giddy for making this project possible and for their hospitality and advice. I. Giddy and two anonymous referees made some useful comments on earlier

drafts of this paper. We are grateful for the help and advice kindly provided by E. Kang at Cloudbridge, P. McLaughlin, J. Freel and G. Hancock at the University of Glasgow, and L. D. Gómez at Las Cruces Biological Station, Costa Rica.

REFERENCES

- Daniels, G. S., & F. G. Stiles. 1979. The *Heliconia* taxa of Costa Rica: Keys & descriptions. *Brenesia* 15 (Suppl): 1–150
- Dobkin, D. S. 1984. Flowering patterns of long-lived *Heliconia* inflorescences: implications for visiting and resident nectarivores. *Oecologia* 64: 245–254
- Feinsinger, P. 1987. Effects of plant species on each other's pollination: Is community structure influenced? *Trends Ecol. Evol.* 2: 123–126
- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171: 203–205
- Kress, W. J. 1983. Crossability barriers in Neotropical *Heliconia*. *Ann. Bot.* 52: 131–147
- Linhart, Y. B. 1973. Ecological and behavioural determinants of pollen dispersal in hummingbird-pollinated *Heliconia*. *Am. Nat.* 107: 511–523
- Schemske, D. W. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology* 62: 946–954
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56: 285–301
- Stiles, F. G. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. *Condor* 78: 10–26
- Stiles, F. G. 1978. Ecological and evolutionary implications of bird pollination. *Am. Zool.* 18: 715–727
- Stiles, F. G. 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. *Brenesia* 15 (Suppl): 151–180
- Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York.
- Accepted 28 August 2006.*