Do Sympatric Heliconias Attract the Same Species of Hummingbird?
Observations on the Pollination Ecology of *Heliconia beckneri* and *H. tortuosa* at Cloudbridge Nature Reserve

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The Hummingbird-*Heliconia* Project

The hummingbird family (Trochilidae), endemic to the Neotropics, is remarkable not only for its beauty but also because of its ability to hover over a flower while feeding, its wing movements a blur. These lively birds require frequent, nutritious feeding to sustain their expenditure of energy, and some plants have evolved to attract and feed them in exchange for pollination services. Prominent among such plants are most species in the genus *Heliconia* (Heliconiaceae), which are medium to large clone-forming herbs with banana-like leaves (Stiles, 1975). The hummingbird-*Heliconia* interdependence is a good example of co-evolution, and this study is concerned with one aspect of this relationship. Since several species of hummingbird and *Heliconia* exist at Cloudbridge, a middle-elevation nature reserve in Costa Rica, we wondered whether particular species of *Heliconia* had evolved an attraction for particular hummingbird species, which might reduce the chances of hybridisation and pollen loss; or whether the plants compete for a variety of hummingbirds.

At Cloudbridge, on the Pacific slope of southern Costa Rica's Talamanca mountain range, *Heliconia beckneri*, an endangered species (website 1) restricted to this area and thought to be of hybrid origin (Daniels and Stiles, 1979; website 2), and *H. tortuosa* occur together. Stiles (1979) names 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*. These two *Heliconia* species are superficially similar in the form and structure of their flowers and inflorescences and overlap in their flowering peaks but hybridisation apparently does not occur. The aim of this study was to discover whether there are any differences in the pollinator assemblages of these two species where they are sympatric (occur in the same habitats), or whether, as predicted by Stiles (1979), they share the same primary and secondary pollinators.

Our field research suggests that the primary pollinators of these *Heliconia* species are different hummingbirds, that they share only their secondary and occasional pollinators, and that there is a difference in pollen deposition sites, which probably reduces the risk of interspecific pollen loss and hybridisation.

Figure 1. An inflorescence of *Heliconia beckneri* var. Yellow Gyre photographed in July 2005 (left) and an inflorescence of *Heliconia tortuosa* var. Red Twist photographed in May 2005 (right) at Cloudbridge Nature Reserve.

Background

Relations between simultaneously flowering sympatric plants that are closely related may involve competition for pollinators, interspecific pollen loss and hybridisation (e.g. Feinsinger, 1987). The divergence of genetically based floral phenotypes that influence pollinator assemblages and behaviour is driven by selection against these processes. However, floral convergence may be favoured if it leads to a higher rate of flower visitation for all species concerned (Schemske, 1981). Sympatric hummingbird-pollinated plants may face selection pressures against simultaneous pollinator sharing. The mobility of birds combined with high energy needs may result in them visiting several widely scattered nectar sources in a single foraging bout (Stiles, 1978).

Many *Heliconia* species are sympatric; however, the number of naturally occurring hybrids is small in proportion to the number of sympatric associations (Kress, 1983). The interactions of *Heliconia* species will probably select for a divergence in flowering, in time and space, between the species concerned (Stiles, 1979). Mechanical isolation may occur through deposition of pollen from different species in different places on a given type of hummingbird through variation in corolla morphology and positioning of the anthers (Stiles, 1975, 1979; Kress, 1983).

Methods

Fieldwork was carried out from 22 May to 17 July 2005. *H. beckneri* R.R. Smith var. Yellow Gyre and *H. tortuosa* Griggs var. Red Twist occur together at Cloudbridge, in both primary forest and secondary growth, often within metres of one another. *H. lankesteri* Standley var. *lankesteri* was also abundant in the reserve but nearly all plants had reached the end of their flowering period. Two clumps of *H. beckneri* var. Hall Red were also found in the reserve but were not included in this study. Of note, one plant was found with an inflorescence that appeared to be intermediate between that of *H. beckneri* var. Yellow Gyre and *H. lankesteri* var. *lankesteri*. The centre of *Heliconia* abundance was in the riparian forest and scrub close to the Rio Chirripó, with lower densities elsewhere, particularly along small streams.

An indication of the assemblage of taxa visiting the flowers of *H. beckneri* and *H. tortuosa* was gathered through focal observations at *Heliconia* plants. In order to help understand the similarities and differences between the two pollination systems, some flower characteristics were studied in both species, since these may influence pollinator energetics and behaviour.

Accumulated nectar was sampled from flowers that were protected from animals in order to gain an indication of the energy available in the flowers of each species. In addition, the total and effective corolla lengths were measured for both species.

Observations were carried out from 06:00 to 12:00 at seven plants or clumps of plants (presumed clones) with at least one fresh inflorescence, of both *H. beckneri* and *H. tortuosa*, resulting in 42 hours of observations for each species. Focal plants were not randomly selected, but chosen based on their accessibility. 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. It was necessary to manipulate the vegetation of some plants with the aid of plant twist tie one or two days before observations so that each inflorescence could be seen from a chosen vantage point. The number of open flowers, and those at anthesis, was noted. Flowers of both species usually remained open and fresh for at least two days, although on their second day they started to discolour and most of the pollen had been removed.

During the observations the observer sat or stood approximately 4m away from each focal plant. All hummingbirds were identified to species and the sex of most hummingbird visitors was identified at plant and clump numbers 3-7 of *H. beckneri* and all seven focal plants and clumps of *H. tortuosa*. A tally counter was usually used to log each probable pollinating and illegitimate visit to fresh flowers, including repeat visits to the same flower. Pollinating visits involved the probing of the flower through the opening of the corolla, thus probably involving contact with the reproductive parts of the flower, while illegitimate visits were defined as the apparent consumption of nectar by means other than through the opening of the corolla (Lyon and Chadek, 1971; McDade and Kinsman, 1980).

Each probable pollinating and illegitimate visit by an insect was logged. Where visits did not appear to involve nectar consumption and were unlikely to result in pollination, these were classed as ambiguous flower visits. Insect flower visitors were at least identified to Order, but to a lower taxonomic level where possible. The identification of some hummingbirds and all insects was aided by the use of 8×30 binoculars. Observations were continued through all weather conditions.

Flower visitation rates (visits flower^{-1} hour^{-1}) were calculated for each plant or clump of plants, for each taxon that showed probable pollinating flower visits, by dividing the total number of flower visits by the number of fresh flowers at each plant or clump and by the number of observation hours. A population mean flower visitation rate was calculated for each *Heliconia* species from visitation rates by each visiting taxon at each plant or clump (following methods in Kay and Schemske, 2003). The proportional similarity of the pollinator assemblages of the two species was calculated from an equation taken from Kay and Schemske (2003):

$$1 - \frac{1}{2} \sum_{i=1}^{n} |Pai - Pbi|$$

Where *Pai* and *Pbi* are the proportion of the total pollinating visitation rate made up by taxon *i* for plant species *a* and *b* respectively. The index ranges from 0 to 1.

A global positioning system was used to estimate the elevation of focal plants. The elevation range of the focal plants of *H. beckneri* was 1561–1678m, and for plants of *H. tortuosa* this was 1560–1607m.

The volume and concentration of accumulated nectar was measured in new flowers of both species. Inflorescences that contained immature flowers were bagged with cotton muslin on the day prior to nectar sampling, usually in the afternoon, in order to prevent access by animals to new flowers. Bags were attached and closed by using plant twist tie. Flowers that had opened on the day of nectar sampling were picked at 06:00 and 12:00 for both species. After the inflorescence bags had been removed, and just before the flowers were picked, measurements were made of the temperature and humidity by holding a thermo-hygrometer within 0.3m of the flowers. Dissection usually took place outdoors in fine weather and under a shelter or indoors during rain. In every case the temperature and humidity were measured at the beginning of each dissection. Nectar was extracted and the volume measured to the nearest 1µl using a Hamilton™ micro-syringe (photo). The micro-syringe was flushed with distilled water before and after each dissection. The °Brix percentage mass of sucrose equivalents was measured to the nearest 0.5% by use of a Bellingham & Stanley™ hand-held refractometer. Refractometer readings were converted to sugar content (mg µl^{-1} or mg flower^{-1}) and then to the total energy available (J flower^{-1}) following methods given by Bolten *et al*. (1979) and Dafni (1992). Statistical analysis of nectar characteristics was carried out in Minitab. Pairs of sample groups were consistently compared using the Mann-Whitney *U*-test, as it was found that in many of the comparisons the data showed a departure from normality, and normal distributions could not be achieved through data conversion.

Total and effective corolla lengths were measured for a total of 35 flowers from each species. The effective corolla length is the approximate minimum distance between the entrance of the corolla tube and the nectar chamber (Stiles, 1975). The flowers of both species are curved, therefore the corolla lengths were measured in millimetres by use of a ruler and some plant twist tie, which can be manipulated to match the curvature of each flower.

Results and Interpretation
We found that these two species of *Heliconia* were frequented mostly by different species of hummingbird. The Green-Crowned Brilliant (*Heliodoxa jacula*) tended to pollinate *H. beckneri* while the Violet Sabrewing was the principal pollinator of *H. tortuosa*. The Green Hermit visited both species. The results of the fieldwork are summarized in Table 1.

Table 1. Population means for probable pollinating flower visitation rates at seven plants or clumps each of *H. beckneri* and *H. tortuosa* and the percentage of all probable pollinating visits by each taxa at each *Heliconia* species, as observed at Cloudbridge Nature Reserve in June and July 2005.

| Visitors to the flower	*H. beckneri*		*H. tortuosa*	
	Visits fl^{-1} hr^{-1}	% Fl visits	Visits fl^{-1} hr^{-1}	% Fl visits
Apodiformes (Trochilidae)				
Campylopterus hemileucurus (Violet Sabrewing)	-		0.65	68
Heliodoxa jacula (Green-crowned Brilliant)	1.22	69	-	
Phaethornis guy (Green Hermit)	0.46	19	0.10	17
Hymenoptera				
Tribe: Euglossini	0.18	8	0.06	7
Probable *Trigona* species	0.14	4	0.05	8

Table 1 shows that both species of *Heliconia* received pollinating visits by hummingbirds as well as by bees (Apoidea). These *Heliconia* species showed a low overlap of their pollinator assemblages, as measured by the proportional similarity index, only 0.19, of flower visitation rates (Kay and Schemske, 2003). Primary and secondary pollinators were identified in terms of their mean flower visitation rate and the percentage of all pollinating visits that they accounted for. Flower mites (Acari: Mesostigmata: Ascidae) were observed on the flowers of both species and may contribute to self-pollination (Dobkin, 1984).

The **Green-crowned Brilliant** was on average the most frequent visitor to flowers of *H. beckneri*. This species is known to frequent riverside *Heliconia* early in rainy season (Stiles and Skutch, 1989) when the data collection for this study was carried out, and it may be the case that the Green Hermit is the most consistent pollinator throughout the year across the species' range. This highlights the importance of spatial and temporal influences when assessing pollinator assemblages. The comparatively low average visitation rate by Green Hermits may be due to the dominance of the Green-crowned Brilliant, which has a greater body mass (Stiles, 1976; see Stiles and Skutch, 1989 for body masses). The absence of the Green-crowned Brilliant in the pollinator assemblage of *H. tortuosa* is undoubtedly due to the incompatibility of this hummingbird's straight bill and the moderate, even curvature of *H. tortuosa* flowers (see Figure 2 below).

On average the most frequent visitor to flowers of *H. tortuosa* was the **Violet Sabrewing**. This may be a result of the partial replacement of the Green Hermit, which, at the elevations of the focal plants, is approaching its upper limit of 2000m (Stiles and Skutch, 1989). The Violet Sabrewing is a non-hermit that has converged with the hermits and become a long-billed, long-distance trapliner, mostly at high elevations
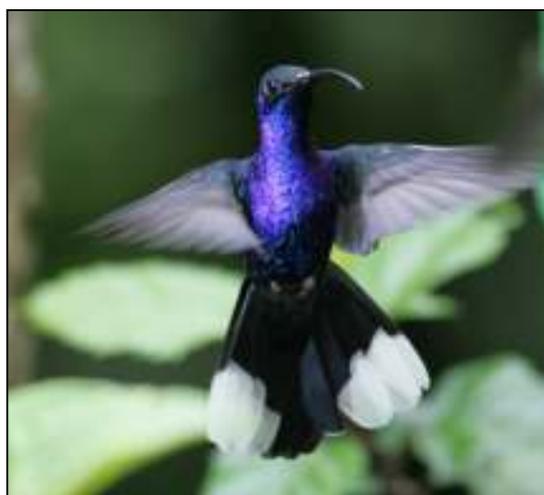
where hermits are absent (Stiles, 1979).

The Violet Sabrewing was only seen to visit inflorescences of *H. beckneri* at one large clump in secondary growth during trial observations. *H. beckneri* flowers had on average significantly higher energy content (Table 2 below) but it may be the case that differences in the width of the corollas (Snow and Snow, 1972; Temeles *et al*., 2002) make feeding at *H. beckneri* flowers less energetically efficient for this species. The Violet Sabrewing may have an innate attraction to the red bracts or yellow flowers of *H. tortuosa*. Perhaps the presence of the Green-crowned Brilliant as the principal visitor to flowers of *H. beckneri* alters the preferences of the Violet Sabrewing.

The **Green Hermit** visited flowers of both species, although the mean visitation rate was higher at flowers of *H. beckneri* perhaps because of the significantly higher mean energy content of *H. beckneri* flowers (Table 2). The Rufous-tailed Hummingbird was uncommon on the reserve and was not seen to visit either *Heliconia* species. This hummingbird species occurs locally up to an elevation of 1850m (Stiles and Skutch, 1989), which may explain the scarcity of this species at Cloudbridge.

The pollination services of the Green Hermit were partitioned between the *Heliconia* species. Males accounted for 92% of all flower visits at clumps 3-7 of *H. beckneri*, while 96% of all flower visits at *H. tortuosa* were by females or juveniles. This may be due to the interaction of a dominance hierarchy and a difference in the energy content of flowers, as female hummingbirds are generally subordinate (Stiles, 1976).

Why do the hummingbirds favour different species of *Heliconia*? To gain an insight into this issue, we examined some aspects of the two plant species and how they matched differences between the hummingbirds. First, the *Heliconia* species had significantly different nectar contents. Measurements of accumulated nectar at 06:00 and 12:00 revealed that at both of these times there was a significantly higher mean volume of nectar in the flowers of *H. beckneri* compared with those of *H. tortuosa* (Table 2). The mean percentage sugar concentration and sugar content of nectar were significantly higher in *H. beckneri* at 06:00 compared with *H. tortuosa*, but the higher mean sugar content and concentration in *H. tortuosa* flowers at 12:00 did not represent a significant difference. As a result mostly of the difference in nectar volume, the mean total energy content (J) of flowers was significantly higher in *H. beckneri* at both 06:00 and 12:00. It is assumed that differences in the mean temperature and relative humidity measured at picking and dissection only had a minor influence on the volume of accumulated nectar, but may account for differences in the concentration of nectar.

Table 2. Mean nectar volume (µl), percentage sugar concentration (refractometer reading), sugar content of nectar (mg µl^{-1}) and energy content (J flower^{-1}) in flowers of *Heliconia beckneri* and *H. tortuosa* at Cloudbridge Nature Reserve in June and July 2005. The results and significance of Mann-Whitney *U*-tests are displayed for each species comparison. SD = standard deviation. *N* = 10 flowers at each sampling time for both species.

Variable	Time	H. beckneri		H. tortuosa		Mann-Whitney U	P
		Mean	± 1 SD	Mean	± 1 SD		
Volume (µl)	06:00	61	56	20	14	139.5	0.010**
	12:00	141	91	41	32	72.0	0.014**
Percent sugar*	06:00	21.3	5.2	18.5	4.8	137.0	0.017**
	12:00	21.2	1.6	22.4	4.7	85.0	0.135
Sugar content	06:00	0.2330	0.0588	0.2001	0.0543	137.0	0.017**
(mg µl^{-1})	12:00	0.2302	0.0186	0.2453	0.0547	85.0	0.135
Energy content	06:00	248.82	237.58	74.22	53.98	138.0	0.014**
(J flower^{-1})	12:00	556.80	358.78	183.26	155.87	136.0	0.021**

* °Brix. % mass sucrose equivalents.
** Significant if $P < 0.05$

Another aspect we studied was the morphology (shape) of the birds' bills and their match with the morphology of the *Heliconia* flowers. Surprisingly, the mean total and effective corolla lengths of the two *Heliconia* species were identical (58mm and 36mm respectively), with very similar ranges. What differed was the curvature of the flowers. Those of *H. beckneri* have a slight curvature just before the nectar chamber, while flowers of *H. tortuosa* have a moderate, even curvature throughout the length of the corolla (Figure 2).

Figure 2. Three fresh flowers of *Heliconia tortuosa* (left) and *H. beckneri* (right) with millimetre scale.

The difference in flower curvature forced birds to feed from different angles and thus pollen was probably deposited on different parts of their bodies. At *H. beckneri* flowers Green Hermits and Violet Sabrewings inserted their bills from in front of the flowers, probably resulting in the anthers and stigma touching their lower mandible and chin. However, at *H. tortuosa* flowers these species inserted their bills from above and behind the flowers, sometimes at an angle, so that the anthers and stigma probably touched the upper mandible, forehead and crown. Interspecific pollen transfer might result in the hybridisation of *H. tortuosa* and *H. beckneri*, since *H. tortuosa* is known to hybridise with *H. latispatha* (Stiles, 1979), one of the probable parent species of *H. beckneri* (Daniels and Stiles, 1979; website 2). However, the differences in the probable pollen deposition sites are likely to reduce the risk of pollen loss and cross-fertilisation.

In conclusion, any competition for pollinators between these *Heliconia* species at Cloudbridge is lower than predicted by the shared pollinator identities given by Stiles (1979). The flowering of *H. beckneri* and *H. tortuosa* are both predicted to be at peak early in the rainy season (Daniels and Stiles, 1979), thus there is no evidence of a change in their flowering

seasons at Cloudbridge. It is likely that simultaneous flowering is favoured in these species. This can help to maintain pollinator traplines (Schemske, 1981) and extend them through dense forest, a habitat that hermit hummingbirds do not favour, and where low light intensity may inhibit flower production (Stiles, 1975). The assumption that *H. beckneri* is the 'younger' species may lead to the suggestion that its survival and population growth has been facilitated by similar sympatric species such as *H. tortuosa*; however, this is simply conjecture.

Most *Heliconia* species produce 1-day flowers in which the corolla and style normally abscise by the next morning (Kress, 1983). In this study the flowers of *H. beckneri* and *H. tortuosa* usually remained fresh for two days. Stiles (1975) suggested that the half-day life spans of flowers of some lowland *Heliconia* species may result from selection pressures imposed by flower-destroying animals. However, the *Heliconia* populations at mid-elevations at Cloudbridge may not be under the same selection pressures. During the present study visits by flower-destroying animals observed by Stiles (1975, 1979) were uncommon; ambiguous flower visits by weevils (Curculionidae) were infrequent and illegitimate visits by probable *Trigona* bees and Little Hermits (*P. longuemareus)* were observed at only one clump of *H. tortuosa*. Alternatively, if the duration of anthesis is correlated with the number of visits required to optimise male and female function (McDade and Weeks, 2004) then anthesis may be longer where hummingbirds are scarce relative to flowers.

Further research on mid-elevation *Heliconia* populations seems likely to uncover interesting relationships between pairs or groups of similar species. Detailed investigations into the affect of altitude on the pollinator assemblages of *Heliconia* species might yield interesting results. Ultimately, the differing selection pressures faced by lowland and mid-elevation *Heliconia* populations provide researchers with an ideal system in which to study variation in a co-evolved pollination system. An interesting research project at Cloudbridge might involve observations of the use of 2-day old flowers by hummingbirds combined with an investigation into stigma receptivity and nectar production.

The Author

Joseph Taylor is a researcher and masters student at the University of Glasgow, Scotland. While his research has been in ornithology and behavioural ecology, he has become increasingly interested in the social issues that surround biodiversity conservation. He has an honours degree in Ecology from the University of East Anglia.

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