

## *Heliconia*-hummingbird interactions in the Lesser Antilles: A geographic mosaic?

BO DALSGAARD<sup>1,2,4,\*</sup>, ALLAN TIMMERMANN<sup>1</sup>, ANA M. MARTÍN GONZÁLEZ<sup>2,5</sup>,  
JENS M. OLESEN<sup>1</sup>, JEFF OLLERTON<sup>3</sup>, AND LAILA H. ANDERSEN<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Aarhus, Ny Munkegade, Building 1540, DK-8000 Aarhus, Denmark.

<sup>2</sup>Unit of Ecology and Center for Ecological Research and Forestry Applications (CREAF),  
Autonomous University of Barcelona, ES 08193 Bellaterra, Barcelona, Spain.

<sup>3</sup>Landscape and Biodiversity Research Group, School of Science and Technology, University of Northampton,  
Newton Building, Avenue Campus, Northampton, NN2 6JD, UK.

<sup>4</sup>Current addresses: Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street,  
Cambridge CB2 3EJ, UK, and Center for Macroecology, Evolution and Climate, Department of Biology,  
University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark.

<sup>5</sup>Pacific Ecoinformatics and Computational Ecology Lab, 1604 McGee Avenue, 94703 Berkeley, CA, USA,  
and Center for Macroecology, Evolution, and Climate, Department of Biology, University of Copenhagen,  
Universitetsparken 15, 2100 Copenhagen Ø, Denmark.

\*Corresponding author. Email: b.dalsgaard@zoo.cam.ac.uk

**ABSTRACT.**—One of the most striking examples of plant-pollinator co-adaptation is between the heliconias *Heliconia bihai* and *H. caribaea*, and the Lesser Antillean hummingbird - the purple-throated carib *Eulampis jugularis*. To date, the purple-throated carib is the only reported pollinator of these heliconias on the islands of St. Lucia and Dominica. Here, we show that the pollination of *H. bihai* and *H. caribaea* in the Lesser Antilles is more complex than previously hypothesized, locally involving several hummingbird species, specifically the green-throated carib *Eulampis holosericeus*, rufous-breasted hermit *Glaucis hirsuta*, blue-headed hummingbird *Cyanophaia bicolor*, and the antillean crested hummingbird *Orthorhynchus cristatus*. Hopefully, our observations will stimulate research into whether *H. bihai* and *H. caribaea* show local co-adaptation toward hummingbird pollinators other than the purple-throated carib. This would further verify the co-adaptation hypothesis between heliconias and Lesser Antillean hummingbirds, although, depending on locality, more hummingbird species have to be added as mutualistic partners.

**KEYWORDS.**—hummingbird pollination, spatial variation, *Heliconia*, Lesser Antilles

The flowers of *Heliconia bihai* and *H. caribaea* in the Lesser Antillean islands of St. Lucia and Dominica have recently been hypothesized to be tightly co-adapted for pollination by the purple-throated carib *Eulampis jugularis* (Temeles et al. 2000, Temeles & Kress 2003). The purple-throated carib is a large, dimorphic hummingbird, the male having a larger body mass but shorter and straighter bill than the female (e.g. Temeles et al. 2000). Although the purple-throated carib eats insects (Chavez-Ramirez & Dowd 1992) and drinks nectar from flowers of several plant species, its main food resource is probably nectar obtained from flowers of *H. bihai* and *H. caribaea* (Wolf & Hainsworth

1971, Temeles et al. 2000, Temeles & Kress 2003, Dalsgaard et al. 2008). The preferred flower choice of each sex corresponds to the size and nectar reward of the floral morphs of both heliconias, i.e. males feed on shorter, straighter and more rewarding flowers than females (Temeles et al. 2000, Temeles & Kress 2003). On St. Lucia, in areas with both *H. bihai* and *H. caribaea*, the males feed predominantly on *H. caribaea* and the females on *H. bihai*. In areas where *H. caribaea* is lacking, *H. bihai* has evolved a second colour morph with a corolla morphology and nectar reward matching the bill morphology and energy demand of the male purple-throated carib (Temeles et al.

2000). The reverse occurs on Dominica, i.e. in areas where *H. bihai* is lacking, *H. caribaea* has evolved a second colour morph matching the bill morphology and energy demand of the female purple-throated carib (Temeles & Kress 2003).

To date, no other hummingbird species has been reported to visit *H. bihai* and *H. caribaea* in St. Lucia and Dominica, and the purple-throated carib has therefore been regarded as their sole pollinator (Temeles et al. 2000, Temeles & Kress 2003). Here, we report for the first time that all four hummingbird species of Dominica visit *H. caribaea*. Moreover, we report that all three hummingbirds of the Lesser Antillean island of Grenada visit *H. bihai*. Our observations reported here form part of an investigation of local plant-pollinator communities on Dominica (15° 25 N, 61° 20 W) and Grenada (12° 07 N 61° 40 W) conducted during several months of research on each island: Dominica (10 April to 17 July 2005)

and Grenada (10 March to 25 June 2006). The observations in Grenada and the Dominican highland were within our plots (size of 200 x 5 and 400 x 5 m, respectively) for our main studies (e.g. Dalsgaard et al. 2008), whereas the remaining observations in Dominica were observed in two similar-sized localities outside our main research areas (Table 1). All observations were made during 30-min observation periods at a distance of ca. 10 m from each individual heliconia plant. All observed visits were legitimate, i.e. the hummingbirds touched anthers and stigma while drinking nectar. Hence, all the hummingbirds which visited are potential pollinators of *H. bihai* and *H. caribaea*.

In Dominica, we observed that all the hummingbirds on the island visit *H. caribaea* (Figure 1; Table 1). This is in contrast to observations made by Temeles & Kress (2003) that reported the purple-throated carib as the sole visitor of *H. caribaea* on

TABLE 1. Hummingbird visitation rates (visits/hour) for each *Heliconia* species in each locality. The hummingbirds are arranged by increasing body size (g) and culmen length (mm). A dash (-) indicates that the hummingbird species is not present in the given locality.

Plant species	Locality	Hummingbird species <sup>1</sup>					Sampling effort <sup>2</sup>
		ACHU 2.7 g / 10.7 mm	BHHU 4.6 g / 16.4 mm	GTCA 5.6 g / 22.7 mm	RBHE 6.8 g / 32.3 mm	PTCA 8.7 g / 23.6 mm	
<i>H. caribaea</i>	Secondary growth (503-548 m a.s.l.), Dominica.	0.3	-	1.5	-	3.7	n <sub>h</sub> = 6; n <sub>p</sub> ≥ 7; n <sub>f</sub> = 141
	Rainforest (579-622 m a.s.l.), Dominica.	-	2.0	-	-	4.0	n <sub>h</sub> = 0.5; n <sub>p</sub> = 1; n <sub>f</sub> = 1
<i>H. bihai</i>	Rainforest (579-622 m a.s.l.), Dominica.	-	0	-	-	1.3	n <sub>h</sub> = 5.5; n <sub>p</sub> ≥ 7; n <sub>f</sub> = 37
	Cloud Forest (779-847 m a.s.l.), Dominica.	0	0	0	-	0.4	n <sub>h</sub> = 7.5; n <sub>p</sub> ≥ 7, n <sub>f</sub> = 66
	Rainforest (495-505 m a.s.l.), Grenada.	0.36	-	0.18	0.14	-	n <sub>h</sub> = 22; n <sub>p</sub> ≥ 14; n <sub>f</sub> = 224
	Cloud Forest (695-715 m a.s.l.), Grenada.	0	-	0	-	-	n <sub>h</sub> = 13.5; n <sub>p</sub> ≥ 4; n <sub>f</sub> = 51

<sup>1</sup>ACHU = antillean crested hummingbird; BHHU = blue-headed hummingbird; GTCA = green-throated carib; RBHE = rufous-breasted hermit; PTCA = purple-throated carib. Body mass (g) and culmen length (mm) as in Brown & Bowers (1985). <sup>2</sup>n<sub>h</sub> = number of sampling hours; n<sub>p</sub> = number of sampled plant individuals; n<sub>f</sub> = number of sampled flowers. Note the short sampling effort in the Dominican Rainforest.



FIG. 1. The green-throated carib *Eulampis holosericeus* visiting the yellow morph of *Heliconia caribaea* on Dominica, Lesser Antilles.

Dominica. In Dominica, *H. caribaea* occurs at altitudes from 100-600 m (Temeles & Kress 2003) and overlaps in distribution mostly with the green-throated carib *Eulampis holosericeus* and the antillean crested hummingbird *Orthorhyncus cristatus* (Lack 1973). Of these, the green-throated carib appears to be the more significant pollinator of *H. caribaea* than the antillean crested hummingbird given that we observed it more frequently, but the role compared to the purple-throated carib requires more study. Although the purple-throated carib can be seen at low elevations (Wolf & Hainsworth 1971, Temeles & Kress 2003; pers. obs.), it mainly occurs at mid to high elevations (Lack 1973), overlapping with the distribution of *H. bihai* (Temeles & Kress 2003). In accordance with this and with Temeles & Kress (2003) the only observed visitor to *H. bihai* on Dominica was the purple-throated carib (Table 1).

On Grenada, the southernmost island of the Lesser Antilles, the purple-throated carib is absent. In its place, the large, long-billed rufous-breasted hermit *Glaucis hirsuta* takes over. However, the rufous-breasted hermit occupies only the mid-elevation rainforest and does not occur in the highlands above the rainforest, as the purple-throated carib does on the other Lesser Antillean islands (Lack 1973). Instead,

in Grenada the green-throated carib has expanded its distribution to include the highland as well as the lowland (pers. obs.). Lack (1973) probably observed the rufous-breasted hermit visiting *H. bihai* in the rainforest of Grenada, although he did not specify the *Heliconia* species. In the rainforest of Grand Etang National Park (altitude: 495-505 m), we observed *H. bihai* being visited by all hummingbirds of Grenada (Table 1). Likewise, *H. bihai* on the nearby continental island of Trinidad is also pollinated by the rufous-breasted hermit and small, short-billed hummingbirds (Snow & Snow 1972).

The observations reported here demonstrate that the pollination of *H. bihai* and *H. caribaea* is more complex than previously hypothesized, locally involving several hummingbird species. However, our observations - made in localities other than those of Temeles et al. (2000) and Temeles & Kress (2003) - do not necessarily contradict their co-adaptation hypothesis. There is no doubt that *H. bihai* and *H. caribaea* are functionally specialized (*sensu* Fenster et al. 2004) on pollination by large-sized hummingbirds (Snow & Snow 1972, Temeles et al. 2000, Temeles & Kress 2003, Dalsgaard et al. 2008). The long corollas of both heliconias make it impossible for short-billed hummingbirds to exploit the nectar as efficiently as long-billed hummingbirds (Snow & Snow 1972). Hence, in most localities, short-billed hummingbirds are infrequent visitors of *H. bihai* and *H. caribaea*, therefore playing only a minor role as pollinators and evolutionary partners. In the Lesser Antilles, the large purple-throated carib utilizes the flowers most specialized for hummingbird pollination (Dalsgaard et al. 2008) and, with the obvious exception of Grenada where it does not occur, it is the most frequent visitor to these heliconias (Temeles et al. 2000, Temeles & Kress 2003; Table 1). Hence, *H. bihai* and *H. caribaea* may locally co-adapt with the purple-throated carib, as described by Temeles et al. (2000) and Temeles & Kress (2003). Yet, taking the morphological fit between the large green-throated carib and *H. caribaea* flowers, as well as their overlapping geographic and altitudinal distribution into account, the green-throated

carib may locally also be an important pollinator of *H. caribaea*, at least in some localities in Dominica. Moreover, in the absence of the purple-throated carib on Grenada, the local occurring hummingbirds are important pollinators and thereby evolutionary partners of *H. bihai* on Grenada. It would be interesting to investigate whether *H. bihai* and *H. caribaea* show local co-adaptation toward hummingbirds other than the purple-throated carib. This would further verify the co-adaptation hypothesis described by Temeles et al. (2000) and Temeles & Kress (2003), although locally more hummingbird species have to be added as mutualistic partners, creating a complex geographic mosaic of interactions (*sensu* Thompson 2005). Hopefully, our observations will stimulate further research in the fascinating mutualism between heliconias and Lesser Antillean hummingbirds.

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