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HELICONIA SOCIETY OF PUERTO RICO, INC.

The HSPR Newsletter

The Coevolution of Heliconias and Hummingbirds in the Eastern Caribbean

By W. John Kress and Ethan J. Temeles

A major goal of systematic, evolutionary, and ecological studies is to understand the processes that shape adaptations of organisms to their environment. One approach towards this goal is to use patterns of morphological variation among closely related species to make inferences about the kinds of ecological processes, such as competition, predation, parasitism, or mutualism, through which these characteristics have evolved. This type of study traces back to Charles Darwin and his classic observations in the Galapagos Islands of beak variation and food types among species of ground finches in the genus *Geospiza*.

Since Darwin's time, interactions between flowering plants and their pollinators have provided model examples of hypothesized feeding adaptations, species specialization, and coevolution. However, some investigations suggest that such interspecific interactions are seldom constant throughout a species' range and that populations differ in the traits shaped by the interaction. These observations have resulted in the John Thompson's proposed "*Geographic Mosaic Theory of Coevolution*." Accordingly, studies of co-adaptation between species require an analysis of populations across the broad geographic distribution of the species. Some populations across this geographic landscape are hotspots of reciprocal selection and others are coldspots with little coevolution. We have recently described an interaction between a plant and its hummingbird pollinator found in the Eastern Caribbean that provides an ideal tropical system to test Thompson's theory. Both the pollinators and the plants exhibit character polymorphisms, which can be readily linked to fitness measures, throughout their ranges. Over the last several years and probably for a number of years to come we plan to study co-adaptations in this plant-hummingbird association through extensive observations of both floral and sexual dimorphisms across the island archipelago in the Eastern Caribbean.

The focal system of this research involves the purple-throated carib hummingbird, *Eulampis jugularis*, and its *Heliconia* food plants (Fig. 1), considered one of the strongest examples of ecological causation of sexual dimorphism to date and a

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Dates to Remember

- *HSPR Meeting, 9:30 a.m., Sunday, March 13, 2011. Amphitheater of the Auxilio Mutuo Hospital (9th floor of the main hospital building), Hato Rey, PR.*
- *43rd Aibonito Flower Festival, June 24-July 3, 2011, Aibonito, PR.*

Fig. 1. From left to right, red *Heliconia caribaea* and the purple-throated carib hummingbird, distribution of the hummingbird throughout the Eastern Antilles, and the yellow form of *H. caribaea*.

well-documented plant – pollinator mutualism. Many biology textbooks note that flowers pollinated by hummingbirds have long, tubular corollas matching the size and shape of the birds' beaks. Darwin himself stated that bills of hummingbirds are specially adapted to the various kinds of flowers they visit. Our work has provided evidence for co-adaptation by demonstrating that the purple-throated carib hummingbird is the primary pollinator of *H. caribaea* and *H. bihai*, with flowers of the former corresponding to the short, straight bills of males (the larger sex) and flowers of the latter to the longer, curved bills of females (Fig. 2). Further evidence for co-adaptation comes from a reversal in the floral dimorphism of the *Heliconia* food plants on two islands: on St. Lucia, the female-pollinated *H. bihai* develops a second morph with shorter, straighter flowers matching the bills of males, whereas on Dominica the male-pollinated *H. caribaea* develops a second morph with longer, curved flowers matching the bills of females. The nectar rewards of all *Heliconia* morphs on both islands are consistent with each sex's choice for the morph corresponding to its bill morphology and energy requirements, supporting the hypotheses of ecological causation of sexual dimorphism and co-adaptation.

Our work started nearly a decade ago when one of us (EJT) initiated studies of the purple-throated carib hummingbird, *Eulampis jugularis*, on the island of St. Lucia. The males and females are identical in plumage, but display some of the most extreme sexual dimorphisms of any hummingbird species. First, bills of males average 24.8 mm in length, whereas bills of females average 29 mm in length, a difference of 15 percent. Moreover, bills of males are relatively straight, curving downwards at a 15 degree angle, whereas bills of females are highly curved, curving downwards at a 30 degree angle. These differences in bill morphology were associated with differences in the use of the two *Heliconia* species on the island. Males were associated with a red-bracted morph of *H. caribaea*, which they defended against other males and females. In contrast, females intruded onto male territories to feed and also fed at undefended patches of *H. caribaea*, but more importantly they were the predominant visitor to the other *Heliconia*, a green-bracted morph of *H. bihai*. The morphology of the flowers of the two heliconias reflected this sexual preference by the hummingbirds. Flowers of *H. caribaea* were short and straight, measuring 38 mm in length and 20 degrees in curvature, which approximates the short, straight bills of male purple-throats, their primary pollinator. In contrast, flowers of the green-bracted *H. bihai* were long and curved, measuring nearly 44 mm in length and 31 degree in curvature, which is almost identical to the 30 degree curvature of female bills. The close correspondence between bills of male and female purple-throats and the sizes and shapes of the *Heliconia* flowers they visit argues strongly for reciprocal adaptation. This hypothesis receives additional support from our discovery of a second, red-green morph of *H. bihai* on the island. This red-green morph acts as a geographic replace-

ment of *H. caribaea* and is defended and visited primarily by male purple-throated caribs. Its flowers are both significantly shorter and straighter than flowers of the green-bracted morph visited by females, which is what you would expect given its visitation by males.

We then extended our investigations of this plant-pollinator system to the island of Dominica, located 100 miles north of St. Lucia. Bills of both sexes of purple-throated caribs on this island are slightly longer and slightly less curved than on St. Lucia. As on St. Lucia, however, the primary food plants of these birds are *H. caribaea* and *H. bihai*. But in contrast to St. Lucia which has two morphs of *H. bihai*, green and red-green, on Dominica there is only one morph of *H. bihai* which is red with a yellow stripe. Similarly, whereas there was only a single, red color morph of *H. caribaea* on St. Lucia, on Dominica there are now two: a red morph and a yellow morph.

As on St. Lucia, males associate primarily with *H. caribaea*. Females also visit *H. caribaea* and are the sole pollinator of *H. bihai*. Once again, flowers of the two heliconias correspond closely to the bills of their primary hummingbird visitor. Flowers of *H. caribaea* are short and straight, measuring 36 mm in length and 20 degrees in curvature, which roughly corresponds to the 15-degree bill curvature of males. In contrast, flowers of *H. bihai* measure 48 mm in length and 30 degrees in curvature, a perfect match for the 30 degree bill curvature of females. The flowers of *H. bihai* are 4 mm longer than on St. Lucia which we interpret as a coevolutionary response to the exclusive visitation by female purple-throats with their long bills.

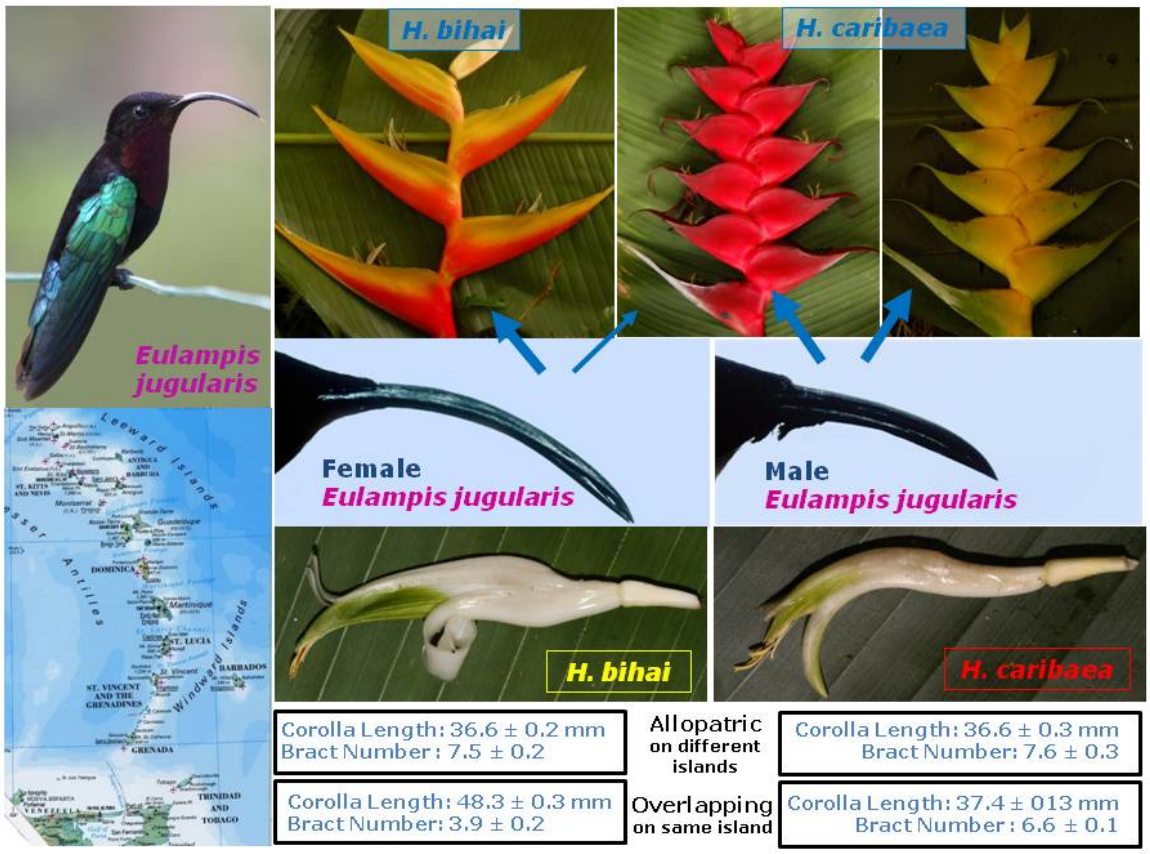

Fig. 2. Polymorphisms in bills of purple-throated carib hummingbirds and inflorescences and flowers of *Heliconia* species in Dominica, W.I.

Vinita Gowda, a graduate student at George Washington University working with us on this project, has provided an important temporal component to our observations. As part of her dissertation, she monitored the flowering times of the heliconias and the visitation

rates of the hummingbirds on three islands: Dominica, St. Kitts to the north, and St. Vincent to the south. On Dominica flowering patterns of *Heliconia bihai* and *Heliconia caribaea* were significantly different: *H. bihai* flowers throughout the year but has a distinct peak flowering season in April, whereas *H. caribaea* has a distinct flowering season from March until September (with a peak in May) and does not produce any flowers the rest of the year. The peak flowering season of the two species did not overlap. With respect to pollinator visitation patterns *H. bihai* shows a clear female dominated interaction throughout the flowering season while *H. caribaea* inflorescences are always strictly defended as territories by males with females often allowed to enter the territories to feed on the flowers during the mating season. Other pollinators that were rarely observed on *H. caribaea* are Green throated Carib hummingbirds (*Eulampis holosericeus*) and Antillean Crested Hummingbirds (*Orthorhyncus cristatus*). Both of these visitors are aggressively chased away by territorial males.

As our studies and observations have spread throughout the archipelago we have tracked the long-distance transition between generalized and specialized plant-pollinator interactions in this heliconia-hummingbird system. What we have found is that one species of plant, *Heliconia bihai*, changes from a generalist strategy in the southern range of the island chain (Trinidad) where its flowers are pollinated by many hummingbird species to a highly specialized pollination strategy in the core of the archipelago (St. Lucia and Dominica) where its flowers are pollinated by one sex of one hummingbird species. We are only now beginning to understand the floral and pollinator traits associated with the transition from generalization to specialization. Where *H. bihai* is pollinated by many hummingbird species with bills of many different lengths, the flowers are 30% shorter in length than on the islands where the flowers are only visited by female purple throated Carib hummingbirds with long-curved bills. We hypothesize that this transition across 300 miles in the Caribbean archipelago results from character release associated with a decrease in the number of species on islands as one moves north farther and farther from the mainland. The number of endemic *Heliconia* species decreases from five on Trinidad to two on St. Lucia and Dominica, whereas the number of hummingbird species decreases from twelve on Trinidad to three on St. Lucia and four on Dominica. This reduction in species diversity may permit *H. bihai* and *H. caribaea* to undergo character displacement where the two heliconias overlap. Similarly, a reduction in competing hummingbird species combined with two abundant and rewarding *Heliconia* food plants may drive the evolution of sexual dimorphism within purple-throated caribs. Our available evidence supports this hypothesis.

These results indicate that a geographic approach can identify populations of plant-pollinator specialization and generalization. Highly-specialized populations may represent hotspots of reciprocal evolution. In this regard, it is significant that the longest flowers of *H. bihai* and the longest bills of female purple-throated caribs occur where it is pollinated exclusively by females. Whether such associations represent coevolutionary arms races requires future study.

We have much more to understand about the mosaic of interactions between the species of heliconia and their hummingbirds pollinators in the Lesser Antilles. Through a grant from the National Science Foundation we have funding support to continue our investigations in the Eastern Caribbean for several more years. Like the Galapagos Islands off the coast of Ecuador, the Eastern Caribbean archipelago is an ideal natural laboratory for understanding the evolutionary processes of adaptation and coevolution.

HSPR thanks collaborators W. John Kress, PhD, Research Botanist and Curator, Department of Botany, MRC-166, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013-7012, USA, and Ethan J. Temeles, PhD, Professor in the Department of Biology, Amherst College, Amherst, MA 01002, USA, for this interesting article.

From Our Last Meeting

Close to 55 persons attended our traditional HSPR Christmas Dinner, held at the charming country house of Gildreth and Bob Castro. This farm is located at Cerro Guilarte, in Adjuntas, and is one of our precious HSI / HSPR Conservation Centers. Bob gave us the official welcome to Siberia –the name by which he calls his farm, among the close friends-, which is situated at 3,200 feet above sea level.

Judy Nelson, from Marín Alto Tropicals, told us of a cheerful anecdote from her last visit to this farm (the June 2008 HSPR meeting). Here is where she found and adopted an adorable stray puppy, which she later named Kathy. She sadly informed us that after 29 years in the tropical cut flower business she, Kelly and Susan plan on retiring to the States. The legendary Marin Alto Tropicals (a heliconia nursery founded by Dr. Harold Kelly Brooks in 1981) is up for sale, including over 200 varieties of heliconias and gingers, which they are currently growing. The 131 *cuerdas*, located next to Torrecilla peak in the mountains of Patillas, are located at 2,300 feet above sea level. From the farm you can see an impressive panoramic view of the turquoise-blue waters of the Caribbean. Interested buyers should contact her at 787-839-2040 or 787-237-8128.

Our Treasurer, Reily Rodríguez, provided us with the report of HSPR's finances. We initially had $2,730.00 in the account. But after paying $1,155.00 for current expenses, we are left with a projected balance of $1,575.00 in the bank. During today's activities, $895.00 was collected. These monies came from: $405.00 from the Raffle, $350.00 from membership dues, $120.00 from a Special Fund and $20.00 from the special invited guests to the dinner. Therefore, we now have approximately $2,470.00 in the bank.

The members were reminded that for our next quarterly meeting (to be held the second Sunday of March 2011), our invited Guest of Honor is going to be Dr. W. John Kress –world authority on heliconias. Dr. Kress is Research Botanist and Curator at the Botany Department of the National Museum of Natural History, Smithsonian Institution, in Washington, D.C. He is also the President of Heliconia Society International. The Meet the Experts Conference will be held at the Amphitheater of the Auxilio Mutuo Hospital, in Hato Rey. This conference was originally scheduled to be held at the University of Puerto Rico's Mayaguez Campus. But, due to the uncertainties related to a possible future student's strike and campus closing, to solve the impasse HSPR member Jorge Matta graciously offered the facilities of the institution where he works at, as an alternative site. A Special Fund was immediately established to help cover the costs associated with Dr. Kress' visit to Puerto Rico. The amount of one hundred and twenty dollars was collected from our members.

From left to right, HSPR President José R. Abreu, HSPR Vice President Héctor Méndez Caratini, and HSI President W. John Kress, at the 2010 Heliconia Society International Conference, held in Singapore.

Dr. Abreu and myself read the names of the three dozens heliconias and more than a dozen different palms (and other precious plants, such as bromeliads) that were available at the Raffle. Among the heliconias that were up for grabs were: H. penduloides Perfect Darling, H. griggsiana Harvest Moon, H. chartacea Columbine, H. temptress, H. curtispatha, H. caribaea Manoa Midnight, H. champneiana Maya Blood, H. orthotricha yellow, H. hirsuta, H. bihai red (from Trinidad), H. bihai Giant Lobster Claw, white torch ginger (also the pink variety) and many, many more. The excitement generated from the Raffle accrued $405.00 for the society. Our sincere thanks goes out to all members who donated plants for the Raffle.

We would like to publicly acknowledge the contagious enthusiasm of young Aaron Jr, who decided to celebrate his eighth birthday among the members of

HELICONIA SOCIETY OF PUERTO RICO, INC.

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HSPR

Promoting Zingiberales in Puerto Rico since 1996.

The Heliconia Society of Puerto Rico, Inc. was founded in 1996. The objectives of the society are to stimulate and promote the enjoyment and understanding of Heliconia *and related plants of the order Zingiberales through education, research and communication, and to interact with the Heliconia Society International and other institutions which share similar interests, purposes or objectives.*

From Our Last Meeting (continued)

HSPR, instead of with his friends of the same age. He was the lucky winner of eight heliconias in the Raffle, to augment his rapidly growing collection. Be on the look out for this kid, who one day promises to be a future leader in our organization. We all wished him a ¡Feliz Cumpleaños!

The members then proceeded uphill, to tour the farm and see the heliconias, gingers and costacaea growing there. Afterwards, a delicious dinner was served with the traditional *lechón asao, pasteles*, *arroz con gandules*, roasted chicken, *guineitos en escabeche* and other gourmet Christmas time delicacies.

During our visit to Siberia we were able to greet old friends, we had not seen in many years, and welcome the new ones. It was an unforgettable meeting, full of camaraderie, enjoyed by those who ventured to drive the tortuous roads of the Cordillera Central and tolerate the coolness of the climate. We are ALL very grateful for our hosts' hospitality, and the great time we had. ¡Muchas Gracias Bob and Gildreth!

Héctor Méndez Caratini
Vice President, HSPR

President's Corner

Greetings in this New Year 2011. The year 2010 was one of persistent "bad weather", according to those who make a living at announcing showers and sprinkles around the Island on radio and TV. To us heliconia enthusiasts I wish 2011 to be another "bad weather" year.

Early this week I was notified by our mutual friend and greatest heliconia enthusiast Héctor Méndez Caratini, that Dr. John Kress had confirmed his visit to Puerto Rico in March. So, during our March 13th meeting we will have the very special, perhaps unique opportunity of enjoying the presence and wise lecturing by the most knowledgeable scientist involved with Zingiberales: Dr. John Kress.

Since this meeting is inside an institution (9th floor Conference Room of the Hospital Auxilio Mutuo, Ponce de Leon Avenue in Hato Rey), please bring clean, containerized rhizomes and plants for the raffle. We want to avoid soiling the space made available to us by the generosity of our member Mr. Jorge Matta. Snacks and eatables are welcome!

See you next March 13th.

José R. Abreu,
President, HSPR