Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird

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Abstract. Matches between the bills of hummingbirds and the flowers they visit have been interpreted as examples of coadaptation and feeding specialization. Observations of birds feeding at flowers longer or shorter than their bills combined with a lack of experimental evidence for foraging trade-offs, however, fail to support these interpretations. We addressed these inconsistencies by considering a seldom-studied dimension of hummingbird–flower relationships, the shape of bills and flowers, through experiments on the Purple-throated Carib, *Eulampis jugularis*, and its major food plant, *Heliconia*, in the eastern Caribbean. Bills of male *E. jugularis* are considerably shorter and straighter than bills of females. We examined foraging performances and trade-offs during visits to natural heliconias and 34 artificial flowers of differing length and curvature. Supporting predictions based on matches between bill and flower morphology, handling times of females were significantly shorter than those of males at the long, curved flowers of a green morph of *H. bihai*. Contrary to predictions, handling times of males were not significantly shorter than handling times of females at the short flowers of *H. caribaea*. At artificial flowers, maximum extraction depths of females were significantly longer than maximum extraction depths of males at all curved flowers, but not at straight flowers. Handling times of females were significantly shorter than handling times of males at the longest artificial flowers for all curvatures, whereas handling times of males were significantly shorter at short, straight, artificial flowers, but only while hover-feeding without a perch. Within each sex, handling times were inversely related to bill length at long flowers for all shapes. Taken together, these performance trade-offs suggest that the long, curved bills of females are adapted for feeding from long, curved flowers, whereas the short bills of males are adapted for hover-feeding from short, straighter flowers. In addition, the finding that differences in feeding performance occur at the extremes of floral phenotypes suggests that the evolution of bill morphology may be driven by a small subset of the flowers visited by a hummingbird species.

Key words: coevolution; Eulampis jugularis; *foraging trade-offs;* Heliconia; *hummingbird; mutualism; Purple-throated Carib; specialization; species interactions; West Indies.*

INTRODUCTION

Evolutionary ecologists have long used patterns of variation in trophic morphology within and between closely related species to make inferences about the kinds of ecological processes that may have produced them (Darwin 1859, Lack 1947, Grant 1984, Dayan and Simberloff 1994). This practice assumes that differences in trophic morphology between individuals reflect both differences in feeding performance and in abilities to use different food resources (e.g., Temeles and Roberts 1993, Kingsolver and Huey 2003). Some experimental and observational studies have provided support for these assumptions (e.g., Benkman and Lindholm 1991, Schluter 1995, Schondube and Martinez del Rio 2002, Muchhala 2007) whereas others have not (e.g., Mont-

gomerie 1984, Temeles and Roberts 1993, Borrell 2005, 2007).

Hummingbirds have been used as textbook examples of feeding specialization (e.g., Raven and Johnson 1996, Freeman 2005) owing to the observed correspondence in size and shape between the bills of the birds and the flowers they visit. Even Darwin (1876:371) was impressed by this match, commenting that "beaks of humming-birds are specially adapted to the various kinds of flowers they visit." Although some studies have documented close matches between hummingbird and floral morphologies (e.g., Snow and Snow 1980, Stein 1992, Temeles et al. 2000), others have reported hummingbird species visiting plant species with flowers substantially longer or shorter than their bills (Feinsinger 1976, Arizmendi and Ornelas 1990, Cotton 1998). The general lack of correspondence between bills and flowers has led some researchers to conclude that present-day interactions between hummingbirds and their food plants have arisen through diffuse coevolu-

tion at best (Feinsinger 1983, Cotton 1998). Similarly, field and laboratory experiments on a variety of hummingbird species have found that longer-billed birds can feed more quickly from longer artificial flowers than shorter-billed birds, whereas shorted-billed birds do not feed more quickly from shorter artificial flowers than longer-billed birds (Hainsworth 1973, Hainsworth and Wolf 1976, Montgomerie 1984, Temeles and Roberts 1993; a similar finding has been reported for other nectar-feeding animals, e.g., hawkmoths [Haber and Frankie 1989] and euglossine bees [Borrell 2005]). The finding that longer bills are equal or better than shorter bills raises the question of why some hummingbird species have short bills (Montgomerie 1984).

One explanation for the apparent mismatches between bill morphology and flower morphology in nectar-feeding birds is that a low availability of preferred foods combined with competition for these foods may result in the incorporation of flowers into the diet that have little correspondence to the forager's feeding morphology (e.g., Temeles et al. 2002). A second explanation is that such mismatches may be an observational consequence of considering hummingbird–flower relationships only in terms of lengths and not other floral characteristics that may substantially affect foraging abilities (e.g., Harder 1985). For example, Temeles (1996) showed that a hummingbird's ability to use flowers that are longer than its bill depended on the diameter of the flower's opening: long flowers with narrow openings excluded short-billed birds, whereas long flowers with wide openings allowed access by short-billed birds.

Another characteristic of bird–flower relationships is shape, especially curvature. Curved bills occur among species within all the major groups of nectar-feeding birds (hummingbirds [Trochilidae], sunbirds [Nectariniidae], honeyeaters [Melaphagidae], and honeycreepers [Drepanidini]) as well as in the flowers of their food plants (e.g., Paton and Collins 1989). Although a number of authors have documented curved bills and flowers in their studies (e.g., Stiles 1975, Feinsinger 1976, Snow and Snow 1980, Kodric-Brown et al. 1984, Stein 1992), few have compared the feeding performances of birds differing in bill shape. Wolf et al. (1972) demonstrated that *Phaethornis longirostris* (= *superciliosus*) with long, curved bills had superior feeding performance than *Thalurania furcata* with straight bills at *Heliconia* species with long, curved flowers. They found the reverse to be true at *Heliconia* species with functionally short, straight flowers. Similarly, Gill and Wolf (1978) found that four sunbird species of differing bill shape differed in the ability to extract nectar from the curved flowers of *Leonotis nepetifolia* as opposed to the straight flowers of *Aloe graminicola*. Straight-billed sunbird species took longer to remove nectar from curved flowers and curve-billed sunbird species took longer to remove nectar from straight flowers.

In this paper, we examine the interaction of bill and flower shape and length on the feeding performance of hummingbirds, specifically, the Purple-throated Carib hummingbird, *Eulampis jugularis*, at flowers of *Heliconia* (Heliconiaceae; see Plate 1). Species of *Heliconia* are found throughout the neotropics, with only two native species present in the eastern Caribbean (Berry and Kress 1991). *Eulampis jugularis* is native to the mid-elevation and montane rainforests of the eastern Caribbean (Raffaele et al. 1998). Although sexes are similar in plumage, males are larger, with wings 8.6% longer and body masses 25% heavier than the smaller females (Wolf 1975). Females, however, have bills that are 30% longer and more strongly decurved than bills of males (Temeles et al. 2000; Appendix A). Feinsinger and Colwell (1978) viewed the dimorphic sexes of *E. jugularis* as an island analog of mainland hummingbird communities in which the short, straight-billed males occupy the mainland role of dominant territorial species and the long, curve-billed females occupy the mainland role of high-reward traplining species (Wolf and Hainsworth 1971, Wolf 1975, Temeles et al. 2005, 2006). Thus, this Caribbean species is a good model for studies of the role of bill morphology on hummingbird feeding performance.

On the island of St. Lucia, West Indies, we determined that each sex of the Purple-throated Carib hummingbird associates primarily with one or the other *Heliconia* species according to its bill morphology and energy requirements (Temeles et al. 2000, Temeles and Kress 2003). Males associate primarily with a red-bracted *H. caribaea* that has short flowers corresponding to their short, straight bills. Females associate primarily with a green-bracted morph of *H. bihai* that has long flowers corresponding to their long, curved bills. At sites where *H. caribaea* is rare or absent it is replaced by an intermediate red-green-bracted morph of *H. bihai*, which has shorter flowers than does the green-bracted morph and is visited mostly by males (Temeles et al. 2000, Temeles and Kress 2003; Appendix A).

Here we examine the feeding performance of male and female *E. jugularis* at the three morphs of *Heliconia* on St. Lucia (*H. caribaea*, green-bracted *H. bihai*, and red-green-bracted *H. bihai*) and at 34 artificial *Heliconia* flowers differing in length, curvature, and diameter. In an initial study on a small sample of birds in an uncontrolled setting (Temeles et al. 2000), it was found that female *E. jugularis* with long, curved bills had shorter handling times at the long flowers of the green-bracted morph of *H. bihai* than at the short flowers of *H. caribaea*. As expected on the basis of their shorter, straighter bills, male *E. jugularis* had shorter handling times at *H. caribaea* than females. Males were observed to visit the green-bracted morph of *H. bihai* so infrequently that no comparison of feeding performance between males and females was possible at this color morph. Thus, one goal of the present study was to repeat these measurements in an experimental setting

with a larger sample of birds, controlling for both nectar volume and concentration, as well as to compare the feeding performance of males and females at the green-bracted morph of *H. bihai*. Based on the previous findings, we predicted that males with short, straight bills should have their shortest handling times at the short flowers of *H. caribaea*, whereas females with long, curved bills should have their shortest handling times at the long flowers of the green-bracted *H. bihai*.

The second part of our study involved experiments using artificial flowers to more precisely characterize the relationships between bill and flower morphology and to understand the floral conditions under which trade-offs in feeding performance might occur. We used two measures of feeding performance: (1) maximum extraction depth of nectar from a flower, which is a measure of how deeply a bird can successfully feed from a flower (Montgomerie 1984, Temeles and Roberts 1993), and (2) handling time, a measure of the time it takes a bird to insert its bill, extract nectar, and withdraw its bill from a flower (Hainsworth 1973, Hainsworth and Wolf 1976, Temeles and Roberts 1993). Based on previous studies (Hainsworth 1973, Hainsworth and Wolf 1976, Montgomerie 1984, Temeles and Roberts 1993, Temeles 1996), we expected longer-billed birds within and between sexes to have greater maximum extraction depths and shorter handling times at the longest flowers relative to shorter-billed birds. The reason for the latter prediction is that at long flowers, a longer-billed bird should be able to insert its bill more deeply than a shorter-billed bird, which would reduce the distance between the bill tip and the nectar supply and thus the distance the tongue must be extended on each lick (Temeles 1996). As a result of shorter tongue extension, licking time is reduced, and thus longer-billed birds would have shorter handling times at long flowers, all other variables being equal.

The novel prediction of our study concerns the effect of flower shape on hummingbird feeding performance. As a flower becomes more or less curved relative to the bird's bill, the shape of the flower would inhibit the insertion of the bill into the flower. Consequently, the bill tip would be farther from the nectar supply, resulting in shorter maximum extraction depths and longer handling times at flowers not corresponding to bill shape. Specifically, we predicted that within and between sexes, individuals should have their greatest maximum extraction depths and shorter handling times with a bill shape closest to that of the flower shape and maximum extraction depths should decrease and handling times should increase as flower shape becomes more dissimilar to the shape of the bill.

In addition to testing these predictions, we examined differences among individuals within a sex to obtain a measure of the phenotypic variation in bill morphology upon which natural selection could act. We discuss the implications of our results for (1) the evolution of sexual dimorphism in bill morphology of hummingbirds, (2) the evolution of curved flowers and curved bills, and (3) generalization and specialization in nectar-feeding birds.

METHODS

Study system

Our study was conducted from 15 May to 8 July 2005 and from 11 May to 7 July 2006 on the grounds of the Fox Grove Inn, Mon Repos, St. Lucia, West Indies. Approximately one month prior to the experiments, *E. jugularis* was attracted to the site by placing six hummingbird feeders filled with 25% sucrose solution (mass : mass) at different locations on the 3-ha grounds of the inn. Birds were then captured using mist nets. Birds were housed individually in $4 \times 3 \times 2.2$ m screened houses erected underneath porches to protect birds from sun and rain and maintained on an ad libitum diet of 25% sucrose solution (mass : mass) and insects. Natural and artificial perches were provided. Birds were given 24 h to acclimate to captivity before being trained to feed from artificial flowers. Following experiments, birds were banded with numbered aluminum bands and plastic, colored bands to prevent reuse and released.

We studied nine birds in 2005 (four males, five females) and 11 birds in 2006 (six males, five females). For each bird, we measured the length of the exposed culmen (in millimeters; from bill tip to the anterior extension of the feathers on the maxillary ramphotheca), total bill length (in millimeters; from bill tip to gape), arc length of the exposed culmen (in millimeters), width and depth of the bill at base (in millimeters), and wing chord (in millimeters). Arc length of the exposed culmen was measured by bending a flexible plastic ruler along the upper curve of the bill from the bill tip to the anterior extension of the feathers on the maxillary ramphotheca. We used two measures to examine the relationship between bill shape and feeding performance: angle of declension (in degrees) and curvature. Angle of declension describes how sharply the bill angles downward from the head of the bird and was measured using a circular protractor by centering the base of the bill on zero and then aligning the bill tip with the degree reading (see Appendix A). We assessed curvature of the bill by relating it to the curvature of a circle. Mathematically, the curvature of a circle, K, is equal to the reciprocal of its radius, R, e.g., $1/R$, and the smaller the value of K, the straighter the object (i.e., straight lines have a curvature of 0; Dodge 1966). The radius of a circle (in millimeters) was determined from the equation $R = (C/2)/\sin A$, where C is the length (chord) of the exposed culmen and A is the angle of declension (in radians; Bell 1956). We then took the reciprocal of the radius, $1/R$, as our measure of curvature, K (in per millimeters). Within each sex, lengths of exposed culmen, total bill length, and arc length of the exposed culmen were highly correlated, as were bill angles and curvatures ($P < 0.01$). We thus used only the measures total bill length and curvature to examine relationships between bill morphology and

feeding performance at the various natural and artificial flowers. Male bills were significantly shorter and straighter than female bills (total bill length, males, 24.8 ± 0.3 mm, females, 29.2 ± 0.3 mm; angle, males, 15.7° ± 0.3°, females, 30.1° ± 0.3°; curvature, males, 0.0260 ± 0.0005 mm^{-1}, females, 0.0397 ± 0.0006 mm^{-1}; $n = 10$ males, 10 females; t tests, all $P < 0.001$).

Natural flower experiments

On the day of the experiment, four to five inflorescences of each of the three *Heliconia* morphs were collected at dawn and placed with stems submerged in water to stay fresh. *Heliconia* flowers last a single day, and only inflorescences with unvisited flowers were selected for experiments (Temeles et al. 2005). Inflorescences of the red-green-bracted and green-bracted morphs of *H. bihai* were collected from Des Cartiers Reserve (13°50′12″ N, 60°58′34″ W), whereas inflorescences of *H. caribaea* were collected along the edge of Mahaut Road (13°50′09″ N, 60°56′46″ W).

Prior to the start of the experiment, the bird was fasted by giving it a 12.5% nectar solution for 12 h and then removing its nectar feeder 1 h before the start of the experiment. For the experiments, we removed a flower's natural nectar and replaced it with either 20 μL (2005) or 10 μL (2006) of 25% (mass : mass) sucrose solution. (The smaller nectar volume was used in 2006 to avoid satiating the birds as a result of the greater number of natural and artificial flowers in our experiments that year.) We covered all other open flowers on the inflorescence such that only a single flower was presented to a bird at a time. The inflorescence was secured to a 1.5-m dowel and placed in with the bird. We then filmed a single feeding visit by the bird to the flower using a Sony Digital Handycam (DCR-TRV730 NTSC; Sony, Tokyo, Japan) mounted on a tripod and controlled by a remote. Following the visit, we sampled the flower for any residual nectar and measured the residual if present (partial feed), and then added another nectar sample to the flower. Each bird was filmed for five separate visits to four flowers of each of the three *Heliconia* morphs. For these natural flower visits, we measured handling time as the total time the bird probed the flower during a visit; i.e., multiple probes of the same flower during a visit were summed into a total handling time. Only trials in which a bird completely removed all nectar were included in analyses of handling time. To avoid pseudoreplication, we first took the mean of all trials for each of the four flowers and then the mean for each of these four means so that we had only one value for each of the three *Heliconia* morphs per bird. The order of presentation of *Heliconia* inflorescences was staggered between birds to avoid any effect that presentation order might have on bird behavior.

Following our measurements of handling times, we conducted choice tests in which the subject was offered choices between two of the three *Heliconia* morphs. The order of presentation was again varied between birds, and choices were repeated until the same bird had been tested on all three choices (i.e., green vs. red-green *H. bihai*, green *H. bihai* vs. *H. caribaea*, red-green *H. bihai* vs. *H. caribaea*). We matched inflorescences in these experiments for both the number of bracts and number of flowers. A positive choice was scored when the bird landed on or began to feed from a flower. A tie was scored when a bird flew to both inflorescences and then returned to its perch.

Once these experiments were completed, we measured the length and angle of declension of each flower used in the experiment and from them calculated the radius of curvature for each flower. Corolla length (in millimeters) was measured from the tip of the flower to the end of the arc of the corolla on its dorsal surface, above the point of insertion of the staminode (delimiting the nectar chamber from the corolla; see Appendix A). Angle of declension was measured by laying the end of the corolla arc on the origin of the protractor and then aligning the tip of the flower with the scale of the protractor (see Appendix A). Radius of curvature was calculated as above for bills from the equation $R = (C/2)/\sin A$, where C is the corolla length (chord) of flower and A is the angle of declension (Bell 1956, Dodge 1966). Flower curvature was thus $1/R = K$ (in per millimeters). Corolla lengths, angles, and curvatures differed significantly between the three heliconias (length, angle, curvature: *H. caribaea*, 37.6 ± 0.2 mm, 38.0° ± 0.8°, 0.0323 ± 0.0005 mm^{-1}, $n = 88$; red-green *H. bihai*, 41.9 ± 0.2 mm, 49.0° ± 0.5°, 0.0354 ± 0.0003 mm^{-1}, $n = 79$; green *H. bihai*, 43.1 ± 0.2 mm, 58.0° ± 0.6°, 0. 0394 ± 0.0003 mm^{-1}, $n = 87$; one-way ANOVAs with Tukey multiple comparisons, $P < 0.05$ overall).

Artificial flower experiments

Studies of natural selection in the wild, as well as studies of feeding performance in captivity, indicate that differences in feeding performance among phenotypes are most often observed at the extremes of resource distributions (e.g., Temeles and Roberts 1993, Grant and Grant 1996, Fenster et al. 2004). Accordingly, artificial flowers were manufactured from clear Lucite and placed in artificial *Heliconia* inflorescences made from fiberglass and approximating the bract size, shape, and color of the red-green morph of *H. bihai* (see Appendix B). Flowers were held within bracts using Play-Doh (Hasbro, Pawtucket, Rhode Island, USA), mimicking the natural orientation of *Heliconia* flowers, and each inflorescence was positioned in a holder on a camera tripod, ~1.5 m from the ground. Birds were fasted prior to the experiment as described in *Natural flower experiments*.

Experiment 1: effect of curvature.—The first experiment was designed to examine the effect of flower curvature on the maximum extraction depths and handling times of male and female *E. jugularis*. For this experiment, we manufactured artificial flowers (internal diameter 4.13 mm) with radii of 50, 35, 30, 25, and 20

mm (smaller radii indicate greater curvatures) corresponding to curvatures (K) of 0.020, 0.029, 0.033, 0.040, an 0.050 mm^{-1} (larger values indicate greater curvatures). For each curvature, we manufactured flowers in lengths of 35, 40, 45, 50, and 60 mm, for a total of 25 different length–curvature combinations. The location of the curve, or bend, in the floral tube was exactly one-third the distance from the base of the flower, approximating the location of the curve of natural *Heliconia* flowers. We used the 60-mm flowers for maximum extraction depth experiments only. Flowers had a tiny fill hole at their dorsal base through which the tip of a gel-loading pipette could be inserted to add or remove sucrose solution.

We trained birds to feed from artificial flowers by removing their feeder at dawn and replacing it with an artificial *Heliconia* inflorescence containing one of the artificial flowers filled to the brim with 25% sucrose solution (mass:mass). Once a bird began to feed from the artificial flower, we began the maximum extraction depth experiment. Each bird was presented with artificial flowers of each of the five different curvatures and 60 mm in length, filled with 25% sucrose solution (mass:mass), one at a time. We conducted three trials at each curvature, and each trial was terminated when the meniscus remained unchanged in its position after three successive feeding attempts by the bird. We then measured the maximum extraction depth as the straight-line distance from the opening of the corolla to the meniscus of nectar, using digital calipers, to the nearest 0.01 mm. The three trials were averaged for each bird at each curvature to give one measure of maximum extraction depth for each of the five curvatures. We staggered the order of presentation of curved flowers among birds to reduce any effect of presentation order on bird performance.

Following the maximum extraction depth experiment, we conducted videotaped trials of birds feeding at artificial flowers of 35, 40, 45, and 50 mm lengths for each of the five curvatures using a digital video camcorder with a remote control. We fasted birds as described in *Natural flower experiments*. We used 20 μL and 10 μL of 25% (mass:mass) sucrose solution in 2005 and 2006, respectively. Each bird was filmed for a single visit to a flower, where one probe (insertion and removal of its bill) qualified as a single trial. Following a visit, an observer would remove and record any residual nectar and then refill the flower. Each bird was filmed for 20 separate feeding visits for each flower length-curvature combination. We staggered the order of presentation of flower curvatures to reduce any effect that presentation order might have on bird feeding performance.

Experiment 2: effect of flower diameter.—As noted above, the artificial flowers used in the first curvature experiment measured 4.13 mm in diameter. Flowers of *H. caribaea* and *H. bihai* do not have a true, fixed opening per se but rather have a slit that the bird separates with its bill to feed. Accordingly, the wide flowers used in the experiment above resulted in birds being able to feed from flowers longer than observed in nature (i.e., 45 to 50+ mm, depending on sex). To obtain a better idea of the degree to which interactions among flower curvature, length, and diameter could limit feeding performance and especially the degree to which such variables could result in resource partitioning between short, straight-billed males and long, curve-billed females, in 2006 only we conducted a second experiment using four narrow Lucite flowers (3 mm internal diameter). The flowers approximated the lengths of *H. caribaea* (38 mm) and the green-bracted *H. bihai* (44 mm) but differed in curvatures ($K = 0.029$ and 0.040 mm^{-1}; see Appendix B). As above, the location of the curve approximated that of natural *Heliconia* flowers, and flowers were secured into bracts using Play-Doh (Hasbro) and positioned in their natural orientation. The remainder of our protocol followed that described above for artificial curved flowers except that we tested birds only at 10 μL of 25% (mass:mass) sucrose solution.

Experiment 3: straight flowers.—The two experiments using artificial flowers above were designed to mimic the foraging behavior of *E. jugularis* at natural *Heliconia* flowers, where the birds generally perch to feed. However, previous studies of hummingbird feeding performance at artificial flowers were conducted under situations in which birds had to hover to feed (e.g., Hainsworth 1973, Montgomerie 1984, Temeles and Roberts 1993, Temeles 1996). In addition, *E. jugularis*, especially males, occasionally hover-feed at flowers in the rainforest canopy (Temeles et al. 2005). To obtain a broader assessment of the relative feeding performances of male and female *E. jugularis* and the conditions under which differences between sexes and morphologies might occur, we conducted a third experiment in 2006 using straight flowers ($K = 0$ mm^{-1}) of five different lengths (35, 40, 45, 50, 60 mm) and 4.13 mm internal diameter. Flowers were presented horizontally from a dowel positioned on a camera tripod 1.5 m above the ground, so that hummingbirds had to hover during visits. In this experiment, we first measured maximum extraction depth as above, taking the average of three successive measurements at a flower 60 mm in length and having a curvature of 0 mm^{-1}. We then conducted handling time experiments as described in *Experiment 1: effect of curvature* using 10 μL of 25% (mass:mass) sucrose solution.

For all experiments using artificial flowers, we selected the 10 fastest handling times in which the bird completely consumed the sucrose solution in a single probe of the flower as measures of maximum performance. To avoid pseudoreplication, we took the mean of these 10 measurements for each flower type per bird for use in the statistical analyses so that we had one measurement per individual bird for each of the artificial flower types.

Statistical analyses

For both the experiments on natural and on artificial flowers, we converted video from analog tape to digital files using Adobe Premiere 4.2 software at 30 frames per second. From these digital files, we measured the number of times the bird probed a flower during a trial, the handling time (in seconds) per probe, and the frequency and duration of bill insertion errors (in seconds; an error involves a bird missing the opening of the flower with its bill; see Temeles 1996). Handling time per probe was measured as the time it took the bird to insert its bill into the flower, lick up nectar, and withdraw its bill from the flower (Montgomerie 1984, Temeles and Roberts 1993). Insertion error time was measured from the moment the bird missed the opening of the flower with its bill to the moment the bird finally inserted its bill into the flower. From these data we also calculated the percentage of feeding visits per flower type in which nectar was only partially consumed (partial feeds).

We used multivariate repeated-measures analyses (MANOVA) from the GLM procedure in SAS (SAS Institute 1999) to examine the effects of sex, flower type, and sex by flower type interactions on handling times, error times, percentage of partial feeds, and maximum extraction depths. Repeated-measures MANOVA avoids violations of the assumption that orthogonal components are uncorrelated and have equal variances that occur when a univariate mixed-model ANOVA is used to analyze repeated-measures data (O'Brien and Kaiser 1985). In all of these MANOVAs, sex was the subject effect. For the experiments on natural *Heliconia* flowers, maximum extraction depths, and straight flowers, we conducted MANOVAs with each of these variables as a single repeated measure. For the experiments on flower curvature and narrow flowers, we conducted MANOVAs with both flower length and flower curvature as repeated measures. We used *t* tests and paired *t* tests with Bonferroni sequential adjustments of *P* values (Rice 1989) to compare means between and within sexes, respectively, and regression analyses to examine relationships between morphological characters of male and female *E. jugularis* and feeding performance at the various flower types. For some analyses, raw data were transformed using log, inverse, or arcsine transformations to conform to assumptions of parametric statistical tests. Because repeated-measures MANOVAs require a balanced design (SAS Institute 1999) and because some males were unable to feed at some flower length–curvature combinations, we used the inverse of handling time for these analyses and assigned zeros to those males that were unable to feed successfully.

Results

Natural heliconias

At both nectar volumes, handling times of male and female *E. jugularis* increased progressively from the short flowers of *H. caribaea* to the long flowers of the green morph of *H. bihai* (10 μL, $F_{2,8} = 46.6$, $P < 0.0001$; 20 μL, $F_{2,6} = 53.4$, $P = 0.0002$; repeated-measures MANOVAs, data log-transformed for analyses; Fig. 1a). Interactions between sex and *Heliconia* morphs were significant at both nectar volumes, and handling times of female *E. jugularis* were significantly shorter than handling times of males at only the green morph of *H. bihai* (10 μL, $F_{2,8} = 6.5$, $P = 0.0213$; 20 μL, $F_{2,6} = 15.4$, $P = 0.0043$; Fig. 1a).

Both sexes made significantly more errors when attempting to insert their bills into either morph of *H. bihai* as compared to *H. caribaea*, and differences between the sexes were significant at green *H. bihai* at low nectar volumes (10 μL, $F_{2,8} = 6.8$, $P < 0.0185$; 20 μL, $F_{2,6} = 33.5$, $P = 0.0006$; repeated-measures MANOVAs, data arcsine-transformed; Table 1). As a result, both males and females spent significantly more time attempting to insert their bills into flowers of either morph of *H. bihai* as opposed to *H. caribaea* (10 μL, $F_{2,8} = 4.9$, $P < 0.0417$; 20 μL, $F_{2,6} = 29.6$, $P = 0.0008$; repeated-measures MANOVAs, data log-transformed, Table 2).

We observed significant differences between the sexes in their ability to completely remove nectar from flowers of the three *Heliconia* morphs. At both high and low nectar volumes, the percentages of feeding visits in which nectar was only partially removed were significantly higher for males at flowers of the green-bracted morph of *H. bihai* than for females (Table 3). Males also made significantly fewer visits to flowers of *H. caribaea* in which they failed to completely remove nectar than to flowers of either morph of *H. bihai* (10 μL, $F_{2,8} = 35.3$, $P < 0.0001$; 20 μL, $F_{2,6} = 10.7$, $P < 0.0105$; Table 3). Males occasionally had difficulty inserting their bills into flowers of the green-bracted morph of *H. bihai*, and flowers from which males failed to completely remove nectar on 50% or more trials had significantly larger angles of declension (10 μL, 62.5 ± 1.2 [mean ± SE], $n = 8$; 20 μL, 62.0 ± 1.2, $n = 6$) than those from which they completely removed nectar more than half of the time (10 μL, 59.0 ± 0.8, $n = 16$, *t* test, $t_{13} = 2.48$, $P = 0.028$; 20 μL, 57.0 ± 0.8, $n = 11$, *t* test, $t_8 = 3.56$, $P = 0.01$). Mean differences in flower lengths and curvatures between flowers from which nectar was partially or completely removed were not significant (*t* tests, all $P > 0.15$). Such comparisons were not possible for males at the other *Heliconia* morphs or for females because of small sample sizes (fewer than three flowers with 50% or more visits in which nectar was partially removed).

Handling times of both male and female *E. jugularis* at flowers of the green morph of *H. bihai* were inversely related to bill length, and at low nectar volumes, these relationships were significant (Fig. 1b). Handling times of males at flowers of the red-green morph of *H. bihai* also were significantly inversely related to bill length at both high and low nectar volumes (Fig. 1c). Handling times of neither sex were significantly related to bill
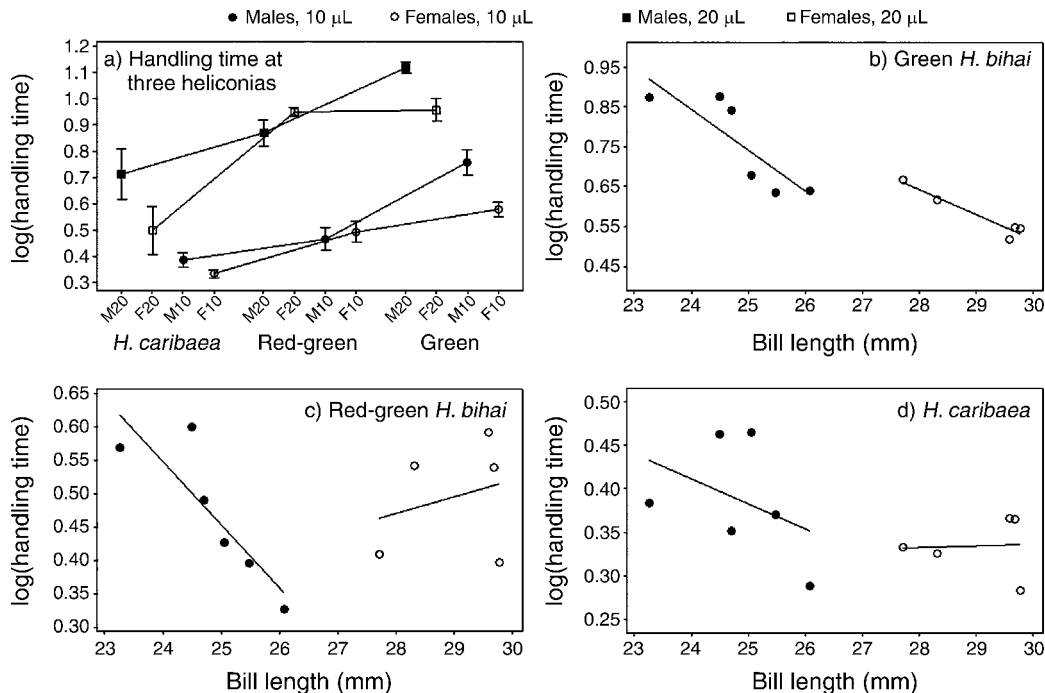
FIG. 1. Handling times (HT, log-transformed) of male (M) and female (F) *Eulampis jugularis* at (a) three St. Lucian (West Indies) heliconias for 10- and 20-μL nectar volumes (mean ± SE) and (b–d) in relation to total bill length (BL, only results for 10 μL are shown). For flowers of green *Heliconia bihai*, handling times of females were significantly shorter than handling times of males at both nectar volumes. Both sexes had significantly shorter handling times at *H. caribaea* than at either morph of *H. bihai* ($P = 0.05$ overall, *t* tests and paired *t* tests with Bonferroni corrections). (b) Relationship between log(handling time) and total bill length of both sexes at green *H. bihai*. Regression statistics are: M10HT = 3.32 − 0.103BL, $r^2 = 70.9\%$, $F_{1,4} = 9.8$, $P = 0.04$, $n = 6$; F10HT = 2.41 − 0.063BL, $r^2 = 93.6\%$, $F_{1,3} = 43.7$, $P = 0.01$, $n = 5$. (c) Relationship between log(handling time) and total bill length of both sexes at red-green *H. bihai*. Regression statistics are: M10HT = 2.81 − 0.094BL, $r^2 = 75.2\%$, $F_{1,4} = 12.1$, $P = 0.025$, $n = 6$; F10HT = −0.23 + 0.025BL, $r^2 = 7.2\%$, $F_{1,3} = 0.23$, $P = 0.66$, $n = 5$. (d) Relationship between log(handling time) and total bill length of both sexes at *H. caribaea*. Regression statistics are: M10HT = 1.10 − 0.029BL, $r^2 = 16.5\%$, $F_{1,4} = 0.8$, $P = 0.42$, $n = 6$; F10HT = 0.28 + 0.002BL, $r^2 = 0.3\%$, $F_{1,3} = 0.01$, $P = 0.94$, $n = 5$. Handling time was measured in seconds.

length at flowers of *H. caribaea* (Fig. 1d), nor did we find any significant relationships between handling time and bill curvature at any of the three *Heliconia* morphs for either sex (all $P > 0.1$). Similarly, relationships between error frequency, error time, and the percentage of partial feeding visits were not significantly related to bill length, angle, or curvature of either male or female *E. jugularis*.

In pairwise choice experiments, nine of 10 females preferred *H. caribaea* to the red-green morph of *H. bihai* with one tie ($P = 0.004$, binomial test), eight of 10 females preferred *H. caribaea* to the green morph of *H. bihai* with two ties ($P = 0.008$), and eight of 10 females preferred the red-green morph of *H. bihai* to the green morph with two ties ($P = 0.008$). Similarly, nine of 10 males preferred *H. caribaea* to the red-green morph of *H. bihai* with one tie ($P = 0.004$), 10 of 10 males preferred *H. caribaea* to the green morph of *H. bihai* ($P = 0.002$), and nine of 10 males preferred the red-green morph of *H. bihai* to the green morph ($P = 0.004$).

Artificial flowers

Maximum extraction depths.—Maximum extraction depths of female *E. jugularis* were significantly greater

than maximum extraction depths of males at all five curved artificial flowers ($F_{1,18} = 42.7$, $P < 0.0001$; repeated-measures MANOVAs, Fig. 2). In contrast, maximum extraction depths did not differ significantly

TABLE 1. Percentages of feeding visits in which male and female *Eulampis jugularis* made errors inserting their bills into flowers of the three morphs of St. Lucian (West Indies) heliconias with 10 or 20 μL of nectar (data were analyzed separately for each nectar volume).

Sex	Volume (μL)	Green *Heliconia bihai*	Red-green *Heliconia bihai*	*Heliconia caribaea*
Female	10	19.7 ± 5.6	15.7 ± 5.3	10.5 ± 3.2
Male	10	57.7[A] ± 10.9	32.0[B] ± 7.4	13.3[B] ± 4.2
Female	20	80.1[C] ± 5.7	85.5[C] ± 2.8	40.1[D] ± 7.6
Male	20	72.6[E] ± 12.0	75.6[E] ± 8.2	32.3[F] ± 11.0

Notes: The higher error frequencies at high nectar volumes were the result of more probes per feeding trial, which increased insertion errors. Values are means ± SE. Within rows, percentages at heliconias having different letters differ significantly ($P = 0.05$ overall; paired *t* tests with Bonferroni sequential adjustment, data arcsine-transformed). Within columns, differences in error frequencies between males and females were statistically significant only at green *H. bihai* at 10 μL of nectar ($P = 0.05$ overall; *t* tests with Bonferroni sequential adjustment, data arcsine-transformed).

TABLE 2. Error times (in seconds) of male and female *Eulampis jugularis* at the three morphs of St. Lucian heliconias with 10 or 20 µL of nectar (data were analyzed separately for each nectar volume).

Sex	Volume (µL)	Green *Heliconia bihai*	Red-green *Heliconia bihai*	*Heliconia caribaea*
Female	10	$0.20^A \pm 0.04$	$0.18^A \pm 0.12$	$0.05^B \pm 0.02$
Male	10	$1.84^C \pm 0.82$	$0.31^D \pm 0.12$	$0.09^D \pm 0.03$
Female	20	$2.00^E \pm 0.57$	$3.21^E \pm 1.00$	$0.17^F \pm 0.04$
Male	20	$3.87^G \pm 2.30$	$2.31^G \pm 1.10$	$0.23^H \pm 0.11$

Notes: The longer error times at high nectar volumes were the result of more probes per feeding trial, which increased insertion errors. Values are means ± SE. Within rows, error times at heliconias having different letters differ significantly ($P = 0.05$ overall; paired t tests with Bonferroni adjustments; data log-transformed). Within columns, differences in error times between males and females were statistically significant only at green *H. bihai* at 10 µL of nectar ($P = 0.05$ overall; t tests with Bonferroni adjustments).

between males and females at straight flowers, even though bills of females were significantly longer than bills of males (t test, $t_7 = 0.87$, $P = 0.4$; Fig. 2). Maximum extraction depths of males were greatest at slightly curved flowers ($K = 0.020$–0.029 mm^{-1}) approximating their bill curvature ($K = 0.026$ mm^{-1}) and declined progressively as flower curvature increased relative to their bills and at perfectly straight flowers (Fig. 2; paired t tests with Bonferroni sequential adjustments, $P = 0.05$ overall). Maximum extraction depths of females were greatest and did not differ significantly at 0.02–0.04 mm^{-1} curvatures (female bill curvatures were ~0.04 mm^{-1}), but were significantly shorter at highly curved (0.05 mm^{-1}) and straight flowers (0 mm^{-1}; Fig. 2; paired t tests with Bonferroni adjustments, $P = 0.05$ overall). For males, maximum extraction depths were positively and significantly related to bill length for all flower curvatures and for straight flowers (Appendix C). Maximum extraction depths of females also were positively related to bill length and were significant for flowers having curvatures of 0.029, 0.040, and 0.050 mm^{-1} (Appendix C). Relationships between maximum extraction depths and bill curvatures were not significant for either males or females ($P > 0.1$).

Curved artificial flowers.—At both high and low nectar volumes, handling times of male and female *E. jugularis* increased as flower length increased (length, 10 µL, $F_{3,7} = 35.2$, $P < 0.0001$; 20 µL, $F_{3,5} = 20.8$, $P = 0.003$; repeated-measures MANOVAs, data inverse-transformed for analyses; Fig. 3). Flower curvature, however, had different effects on the sexes (curvature × sex interaction, 10 µL, $F_{4,6} = 11.5$, $P = 0.0056$; 20 µL, $F_{4,4} = 6.4$, $P = 0.049$). For males, handling times increased progressively with increases in flower curvature and length and were longest at extremely curved, long flowers, consistent with expectations based on our prediction that handling times should increase as flowers become more or less curved relative to the bill (Fig. 3a, c; see *Introduction*). For females, the relationship of handling time to flower length and curvature also was

consistent with expectations based on their maximum extraction depths and bill curvatures, and their handling times were longest at the least and most curved long flowers (Fig. 3b, d). For both sexes at most nectar volumes, handling times were significantly inversely related to bill length (but not to bill curvature), but only at the longest flowers at each curvature (Appendix D). In addition, some males were unable to access nectar at the longest flowers (50 mm) at each curvature, and the ability of males to access such flowers was positively related to bill length, i.e., only males with the longest bills could remove nectar from long, highly curved flowers (Appendix D). The frequencies of feeding visits in which males failed to completely remove nectar were significantly higher than the frequencies for females at 45 mm length × 0.05 mm^{-1} K (males, $80\% \pm 16\%$; females, $0\% \pm 0\%$; $t_4 = 5$, $P = 0.005$; data arcsine-transformed), 50 mm length × 0.05 mm^{-1} K (males, $100\% \pm 0\%$; females, $3\% \pm 2\%$; $t_4 = 19$, $P = 0.001$), and 50 mm length × 0.04 mm^{-1} K flowers (males, $78\% \pm 17\%$; females, $0\% \pm 0\%$; $t_4 = 4$, $P = 0.006$) at low nectar volumes and at 50 mm length × 0.05 mm^{-1} K flowers (males, $100\% \pm 0\%$; females, $10\% \pm 4\%$; $t_3 = 16$, $P = 0.001$) at high nectar volumes. Lastly, we found no significant relationships between error time, error frequency, and flower length and curvature for either sex at either nectar volume ($P > 0.1$ for all variables, repeated-measures MANOVAs).

Narrow artificial flowers.—Both sexes of *E. jugularis* had significantly shorter handling times at short, narrow flowers as opposed to long, narrow flowers, and at straight, narrow flowers as opposed to curved, narrow flowers (length, $F_{1,9} = 75.4$, $P < 0.0001$; angle, $F_{1,9} = 73.0$, $P < 0.0001$; repeated-measures MANOVA, data inverse-transformed; Fig. 4). Females had significantly shorter handling times than males at 0.04 mm^{-1} K × 44 mm long flowers, and only one of six males was able to access nectar from this flower type, which corresponded in length and curvature to flowers of the green morph of

TABLE 3. Percentages of feeding visits of male and female *Eulampis jugularis* at the three morphs of St. Lucian heliconias in which the bird failed to completely remove 10 or 20 µL of nectar (data were analyzed separately for each nectar volume).

Sex	Volume (µL)	Green *Heliconia bihai*	Red-green *Heliconia bihai*	*Heliconia caribaea*
Female	10	13.2 ± 2.7	9.3 ± 3.9	10.1 ± 1.7
Male	10	$46.4^A \pm 7.1$	$20.4^B \pm 5.0$	$3.4^C \pm 1.5$
Female	20	17.2 ± 3.5	11.5 ± 3.1	9.9 ± 2.7
Male	20	$44.3^D \pm 8.3$	$19.3^E \pm 7.0$	$7.8^F \pm 1.8$

Notes: Values are means ± SE. Within rows, percentages at heliconias having different letters differ significantly ($P = 0.05$ overall; paired t tests with Bonferroni sequential adjustment, data arcsine-transformed). Within columns, differences in percentage of partials between males and females were statistically significant at both nectar volumes of green *H. bihai* and at 10 µL of nectar at *H. caribaea* ($P = 0.05$ overall; t tests with Bonferroni sequential adjustment, data arcsine-transformed).
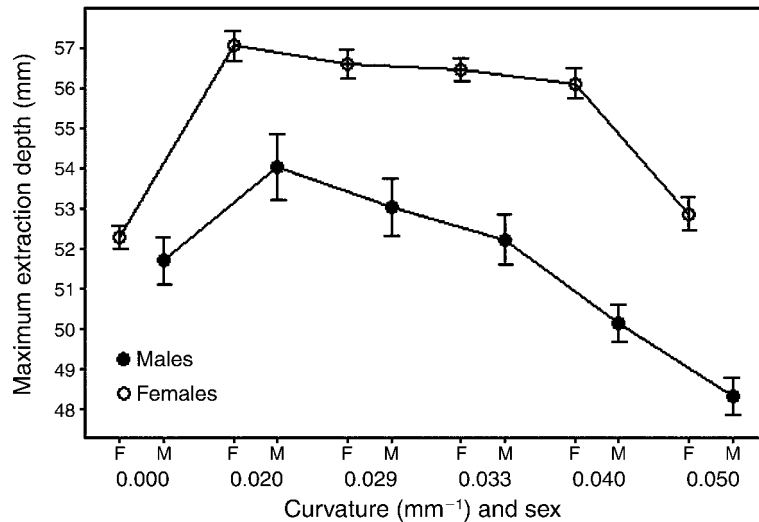
FIG. 2. Maximum extraction depths (mean ± SE) of male (M) and female (F) *Eulampis jugularis* at artificial flowers of increasing curvature (K) from 0 (straight) to 0.050 mm^{-1} (highly curved), where $K = 1$/radius (in mm). For males, differences in maximum extraction depths were significant between all curvatures from 0.02 to 0.05 mm^{-1}, whereas maximum extraction depth at the 0 mm^{-1} flowers was significantly shorter than at 0.02 mm^{-1} flowers and significantly longer that at 0.05 mm^{-1} flowers ($P = 0.05$ overall, paired t tests with Bonferroni sequential adjustments). For females, maximum extraction depths at curvatures of 0 and 0.05 mm^{-1} were significantly shorter than at all other curvatures ($P = 0.05$ overall, paired t tests with Bonferroni adjustments). Comparing sexes, maximum extraction depths of males were significantly shorter than those of females at all curvatures except 0 mm^{-1} ($P = 0.05$ overall, t tests with Bonferroni adjustments). Bill curvatures of males and females averaged 0.026 and 0.040 mm^{-1}, respectively.
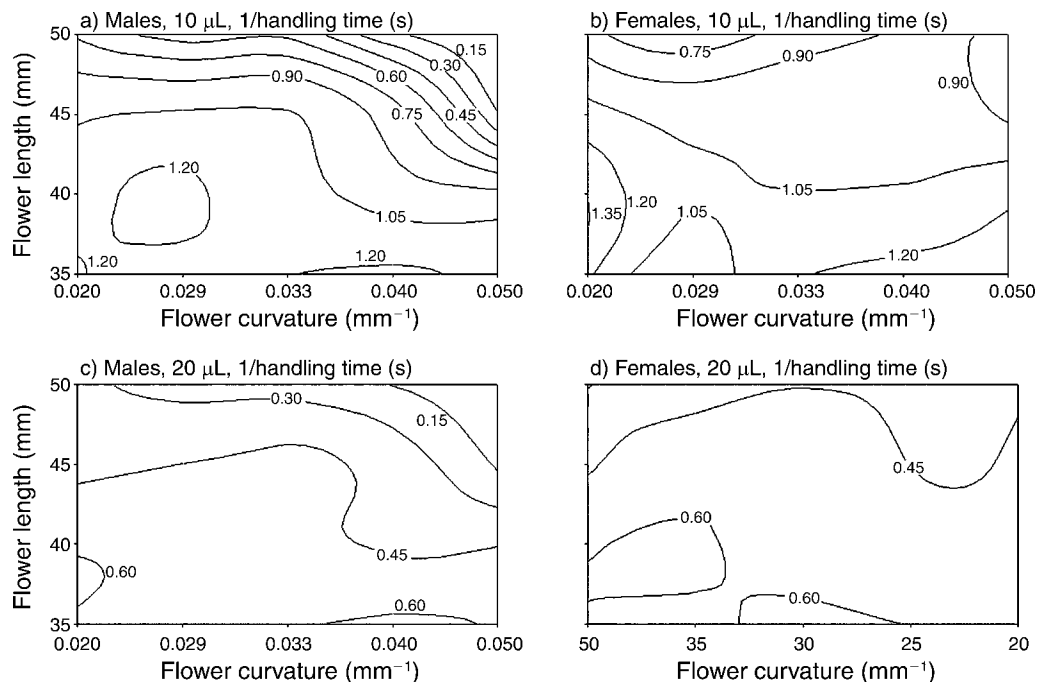

FIG. 3. Contour plots of handling times (mean ± SE, inverse-transformed) of male and female *Eulampis jugularis* at artificial flowers of increasing curvature (K) from 0.020 (slightly curved) to 0.050 mm^{-1} (highly curved), where $K = 1$/radius (in mm), and of increasing length from 35 to 50 mm, for 10- and 20-μL nectar volumes. Numbers on contours are 1/handling time in 0.15 decrements. Handling times increased significantly with curvature and length for both sexes ($P < 0.01$, repeated-measures MANOVAs). Handling times of males were significantly shorter than those of females for 50-mm lengths at $K = 0.033$, 0.040, and 0.050 mm^{-1} and for the 45 mm length at $K = 0.050$ mm^{-1} ($P = 0.05$ overall, t tests with Bonferroni adjustments). Bill curvatures of males and females averaged 0.026 and 0.040 mm^{-1}, respectively.
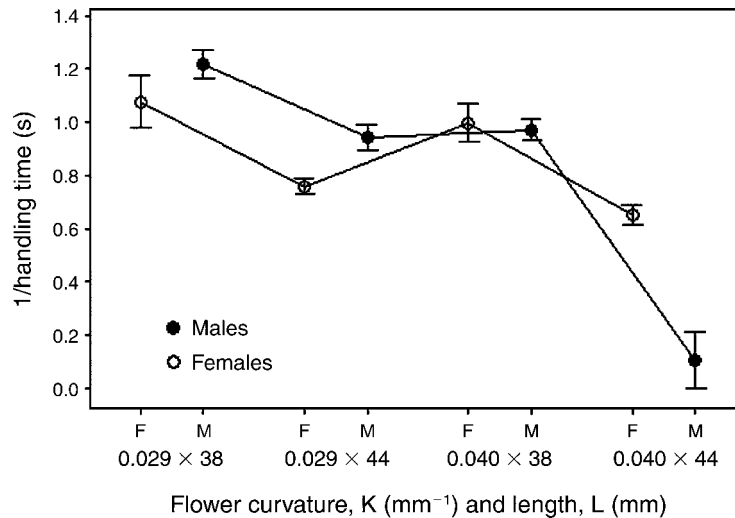
FIG. 4. Handling times (mean ± SE, inverse-transformed) of male (M) and female (F) *Eulampis jugularis* at narrow (3 mm) artificial flowers measuring 38 mm and 44 mm in length (L) and having curvatures (K) of 0.029 and 0.040 mm^{-1}, where curvature = 1/radius (in mm) (given in labels as $K \times L$). All flowers contained 10 μL of nectar. For both sexes, handling times increased with both increasing corolla length and increasing curvature (all $P < 0.01$, repeated-measures MANOVAs). Handling times of females were significantly shorter than handling times of males at 0.040 mm^{-1} × 44 mm long flowers, and only one of six males could extract nectar from this flower type ($P = 0.05$ overall, t tests with Bonferroni adjustments).

H. bihai. Consequently, the frequency of feeding visits in which males partially removed nectar from 44 mm × 0.04 mm^{-1} K flowers was significantly higher than for females (males, 86% ± 14%; females, 1% ± 1%, $t_5 = 6.9$, $P = 0.001$, data arcsine-transformed). At long flowers of both curvatures, handling times of both males and females were inversely related to total bill length, but not curvature, and relationships were marginally significant ($P \leq 0.1$; Appendix E). Relationships between error

time, error frequency, and flower types were not significant ($P > 0.2$ for all variables, repeated-measures MANOVAs).

Straight artificial flowers.—We found significant effects of sex and flower length on handling times of male and female *E. jugularis* at straight, artificial flowers (sex, $F_{1,9} = 6.4$, $P = 0.03$; length, $F_{3,7} = 48.3$, $P < 0.0001$; repeated-measures MANOVA, data inverse-transformed, Fig. 5). In contrast to our studies at curved flowers, males had
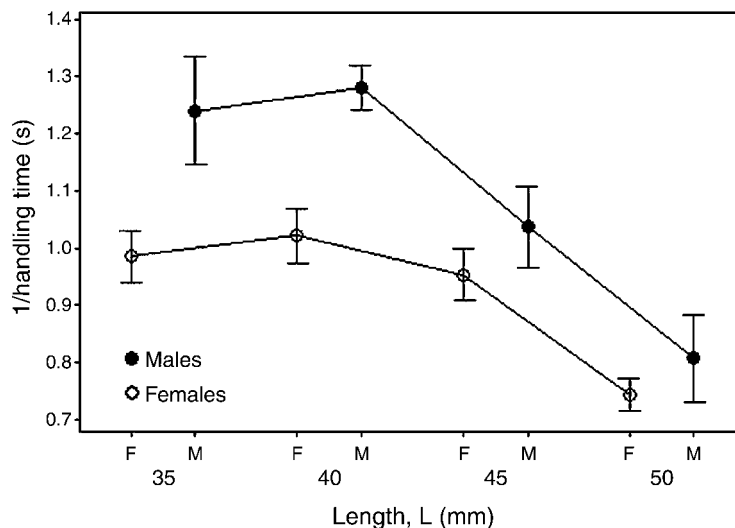

FIG. 5. Handling times (mean ± SE, inverse-transformed) of male (M) and female (F) *Eulampis jugularis* at straight artificial flowers (curvature, $K = 0$ mm^{-1}) measuring 35, 40, 45, and 50 mm in length (L), with 10 μL of nectar. For both sexes, handling times were significantly longer at 50-mm flowers than at shorter lengths ($P = 0.05$ overall, paired t tests with Bonferroni adjustments). Handling times of males were significantly shorter than handling times of females at 35-mm and 40-mm flowers ($P = 0.05$ overall, t tests with Bonferroni adjustments).

shorter handling times than females at all lengths of straight flowers and significantly shorter handling times than females at 35-mm and 40-mm flowers (Fig. 5). At all lengths of straight flowers, handling times of females were inversely related to bill length and were marginally significant at 40-mm lengths (Appendix F). In contrast, handling times of males were inversely related to bill length only at 35 mm long flowers and were positively related to bill length at longer flowers and significantly so at the longest lengths (Appendix F). For both sexes, handling times were not related to bill curvature at any of the flower lengths. Likewise, we found no significant relationships between error time, error frequency, flower length, and sex (all $P > 0.2$ for all variables, repeated-measures MAN-OVA).

DISCUSSION

Females of *Eulampis jugularis* with long, curved bills are able to feed at longer flowers of any curvature than males with short, straight bills. The bill morphology of males prevents the complete removal of nectar from long, curved artificial flowers and access to nectar in some extremely long, curved, natural flowers of *Heliconia*. While males and females are able to feed equally well from short flowers whether straight or curved, males are able to feed more quickly than females from short, straight flowers accessible only by hovering. Here we discuss the implications of our results for the evolution of feeding specialization and sexual dimorphism in bills of hummingbirds as well as for the evolution of curved bills and flowers.

Evolution of sexual dimorphism in hummingbird bills

Sexual dimorphism in bill length is common in hummingbirds (Bleiweiss 1999, Colwell 2000). In the hermit hummingbirds (subfamily Phaethornithinae), males tend to have longer bills than females, whereas in the non-hermits (subfamily Trochilinae, which includes *Eulampis*) the reverse is true, although exceptions occur in both subfamilies. Bleiweiss (1999) suggested that females of species in the Trochilinae have longer bills than males because dominant males exclude subordinate females from preferred flowers. Under these circumstances, longer bills are advantageous by allowing females to feed not only from the same plants as males but also from plants with longer flowers outside of the males' feeding niches. Our observations of *E. jugularis* support this hypothesis. As shown here, both sexes prefer the rich nectar found in the short flowers of *H. caribaea*, but under natural conditions, larger, dominant males exclude smaller, subordinate females from the most rewarding patches of *H. caribaea* (Temeles et al. 2000, 2005). As a result of this competitive exclusion, females are the most frequent visitor to the green-bracted morph of *H. bihai* on St. Lucia, which is not defended by males and has larger flowers (Temeles et al. 2006). We suggest that over evolutionary time, this
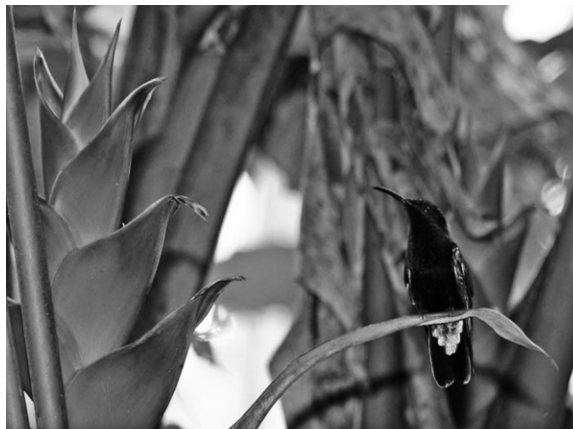

PLATE 1. Male *Eulampis jugularis* at *Heliconia caribaea*. The short, straight bill of this bird measures 25 mm in length and 0.026 mm^{-1} in curvature, corresponding closely to the dimensions of *Heliconia caribaea*, its preferred food plant. Photo credits: (top) E. J. Temeles and (bottom) W. J. Kress.

competitive exclusion may have led to the evolution of extreme bill dimorphism in *E. jugularis*.

The partitioning in floral characters of the heliconias on St. Lucia may have been reinforced by differences in energy requirements and foraging costs of sexes of *E. jugularis* (Hainsworth and Wolf 1970, Wolf and Hainsworth 1971). Models of foraging patterns have shown that the larger, more energetically demanding males would be unable to meet their daily energy requirements by foraging at the highly dispersed flowers of the green-bracted morph of *H. bihai* with low nectar volumes (Temeles et al. 2005). In these models, equal handling times by males and females at the green-bracted morph were assumed. However, the present study has demonstrated that significant differences exist in handling times of males and females at the green-bracted morph (Fig.

1a). These differences in handling times combined with the inability of males to remove nectar from 30% of the flowers of the green-bracted morph due to incompatibilities between flower and bill shape indicate that feeding at the flowers of the green-bracted morph by females may be even more exclusive than previously suggested by the models. The differences in floral morphology between *H. caribaea* and *H. bihai*, as predicted by our scenario for the evolution of bill dimorphism in Purple-throated Carib hummingbirds, conform remarkably well to results of recent theoretical models for the evolution of morphological differences between nectar-feeding animals and their food plants as a result of resource competition (Rodríguez-Gironés and Santamaría 2006, 2007).

Our present finding that handling times of females and males of *Eulampis jugularis* do not significantly differ from one another at the short flowers of *H. caribaea* contradicts an earlier study (Temeles et al. 2000) in which it was reported that males had shorter handling times than females at this *Heliconia*. This discrepancy may be due to that fact that in the earlier study, there were no controls for differences in nectar volume or concentration, nor social context (i.e., scanning for territorial defenders), all of which may affect handling times (e.g., Montgomerie 1984). If longer bills are not disadvantageous when feeding from short flowers, our current results raise the question of why male *E. jugularis* have shorter, straighter bills than females. One answer may be that short, straight bills are an advantage in feeding at short, straight flowers when the bird is hovering (Fig. 5). Although males of *E. jugularis* perched to feed from most of the flowers of *H. caribaea* on St. Lucia, flowers of this species are significantly shorter on Dominica and St. Kitts (Temeles and Kress 2003; E. J. Temeles, *unpublished data*), and such shorter flowers may be more easily accessed and efficiently visited via hover-feeding than perch-feeding. In addition, *H. bihai* is in flower throughout the year on St. Lucia, but *H. caribaea* is not. For this reason males subsist at certain times of the year when *H. caribaea* is not in flower by hover-feeding from flowers of other plant species (Temeles et al. 2005). Other factors that may affect bill size are certain aspects of a male's behavior, such as territorial fighting, which may favor short bills, and aspects of a female's behavior, such as nest-building, which may favor long bills. Nonetheless, the available evidence suggests that the short, straight bills of males of *E. jugularis* are primarily an evolutionary response to the availability of short, straight flowers accessed by hover-feeding, whereas the long, curved bills of females certainly seem to be a response to the long, curved flowers of *H. bihai*, which constitute their major reliable food source throughout the year on St. Lucia.

In their reviews of sexual dimorphism in hummingbirds, both Bleiweiss (1999) and Colwell (2000) examined bill length, but not bill shape. In the case of *Eulampis jugularis*, a distinguishing feature of sexual dimorphism

is bill shape (see Appendix A). Sexual dimorphism in bill shape is present in other hummingbird species within the Trochilinae (e.g., some *Campylopterus* and *Lafresnaya* species) and the Phaethornithinae (e.g., *Glaucis*, *Threnetes*, and some *Phaethornis* species; Schuchmann 1999). In nearly all of these species, bills of females are more strongly decurved than bills of males. In a study of one species of hermit hummingbird in Costa Rica, males of *Phaethornis guy* with straight bills visited the straight flowers of *Heliconia beckneri* and females of the same species with curved bills visited the curved flowers of *H. tortuosa* (Taylor and White 2007). Whether these sexual differences in resource use by *P. guy* are driven by social dominance and competition as in *E. jugularis* or by dimorphic niches resulting from a lek mating system (Bleiweiss 1999) requires additional study. The widespread sexual dimorphism in bill morphology of hummingbirds, however, makes them ideal for studies of both resource partitioning by the sexes and ecological mechanisms for the evolution of sexual dimorphism.

Evolution of curved bills and curved flowers

Curved bills and flowers are widespread in nectar-feeding systems, having evolved on all continents (Spieth 1966, Stiles 1975, Gill and Wolf 1978, Johnsgard 1983, Paton and Collins 1989). To some extent, "shape" is both a consequence of evolutionary history and developmental constraints (e.g., Endress 1994). Nonetheless, the evolution of one flower shape from another in related species and the geographic variation in degree of curvature within a species (e.g., McDade 1992, Temeles and Kress 2003) suggest that shape per se is subject to natural selection and evolutionary change and merits hypotheses on causal factors determining bill and flower curvature.

Westerkamp (1990) argued that evolution of curvature in "bird-flowers" depended largely on whether flowers were accessed by hovering or from a perch. Under this hypothesis, plants with flowers visited by hover-feeding birds could exclude such visitors simply by lengthening the floral tube. In plants with floral perches a simple lengthening of the floral tube would be less effective because very long tubes perpendicular to a perch might be out of reach of the bird. A curved corolla would permit access as well as specialization by a perching bird (Westerkamp 1990). Our results provide support for Westerkamp's hypothesis: males of *E. jugularis* were unable to insert their bills into approximately a third of the highly curved flowers of the green-bracted morph of *H. bihai*. The birds perch on the bracts of the heliconias and twist their heads downward to feed (see Appendix A). The straight bills of males were simply unable to negotiate the curvature and angle of the floral tubes of some flowers of this species, whereas in the flowers of *H. caribaea*, the short corollas permit access by their short, straight bills, as well as by the longer, curved bills of females.

The results of our studies of the relationships between bill and flower shape allow us to make some predictions that we hope will stimulate future work. First, exclusiveness and specialization can be easily achieved by the host plant through an increase in floral length, such as that observed between *Passiflora mixta* and *Ensifera ensifera* (Snow and Snow 1980). Further specialization can be achieved by altering the shape of the flower, such as by increasing curvature, as well as by varying the position of this curvature along the length of the bill or corolla. For example, the primary curve of the flowers of *Heliconia* that we studied occurs approximately one-third of the distance from the base of the flower. As a result, the distal two-thirds of the length of the flower is comparatively straight, which facilitates access by birds with relatively straight bills. We would thus predict that flowers with a curvature positioned near the flower opening where the bill is inserted would be specialized for a pollinator with a highly curved bill, whereas flowers with a curvature positioned near the base of the flower tube would be visited by birds with either curved or straight bills.

Second, our finding that short, straight-billed males of *E. jugularis* are able to feed successfully from curved artificial flowers of short to moderate lengths, but are excluded from long, curved flowers, suggests that curvature as a mechanism for pollinator specialization in nectar-feeding birds may be restricted to extremes of floral and bill lengths. This prediction as well as our hypothesis on the position of the floral curvature are testable through phylogenetic analyses of bird–plant coevolution. The extensive interspecific variation in length and curvature of flowers in the genus *Heliconia* (Berry and Kress 1991, Kress et al. 1999) and the corresponding variation in bill length and curvature of their hummingbird pollinators (Stiles 1975, Schuchmann 1999) provide an ideal case study to test these predictions (W. J. Kress and E. J. Temeles, *unpublished data*).

Third, we found that male and female *E. jugularis* did not differ significantly in maximum extraction depths at straight flowers, even though bills of females averaged 4 mm longer than bills of males. The similarity in maximum extraction depths of males with short, straight bills and females with long, curved bills at straight flowers implies that females are disadvantaged by their curved bills when feeding at straight flowers and shows that bill length alone does not unequivocally predict feeding depth. For species or sexes of hummingbirds with equivalent bill lengths but differing bill curvatures, variation in feeding performance may be greater.

Lastly, we found that male Purple-throated Caribs were often unable to access the nectar in a long, curved artificial flower with a narrow diameter, but were successful at a flower of similar length and curvature, but with a wider diameter. This result suggests that flower diameter may mediate relationships between bill and flower curvature in a manner analogous to relationships between bill and flower lengths (Temeles 1996, Temeles et al. 2002). Thus, we predict that as flower diameter decreases, curved flowers should become more specialized on birds with correspondingly curved bills.

Specialization, generalization, and coevolution

As noted in our introduction, observations of hummingbirds feeding at flowers both shorter and longer than the lengths of their bills have caused some researchers to conclude that present-day interactions between hummingbirds and flowers can only result from diffuse coevolution (Feinsinger 1983, Cotton 1998). Our mechanistic analyses of hummingbird feeding performance offer a research template for understanding the ecology and evolution of such interactions. Our finding that short, straight-billed and long, curve-billed male and female *E. jugularis* do not differ significantly in handling times across a range of short to moderately curved flowers shows that observational mismatches between bill and floral phenotypes do not necessarily correspond to functional mismatches (also see Collins 2008). To put it another way, both types of bill morphologies may work equally well at these floral phenotypes, and such floral phenotypes may exert little natural selection on bill morphologies. More importantly, our finding that differences in feeding performance primarily occur at the extremes of floral phenotypes in relation to bill morphologies suggests that only a small subset of the flowers of different plant species visited by a given hummingbird may drive the evolution of its bill morphology (e.g., "drivers" in the context of diffuse coevolution between plants and insect herbivores; Agrawal 2005). We recognize that the feeding mechanics of hummingbirds may be intrinsically simpler at experimental Lucite tubes mimicking flowers than at natural flowers. Other factors, such as the internal parts of flowers as well as energetics, food availability, and competition, may equally contribute to the evolution of hummingbird bill morphology (Temeles et al. 2002, Rodríguez-Gironés and Santamaría 2006). For example, females of *E. jugularis* preferred the short, straight flowers of *H. caribaea* to the long, curved flowers of *H. bihai* in our choice experiments. As predicted from these choice tests, during April and May in St. Lucia when *H. caribaea* is at its peak flowering, both females and males forage extensively at this species. From September to December when *H. caribaea* is no longer in flower, females rely primarily on the less-preferred species *H. bihai* and males forage extensively at flowers of various species in forest and secondary growth (e.g., *Hibiscus, Ipomoea, Inga*). Thus, the bill morphology of male and female Purple-throated Caribs may be driven, and reflect, the food plants available to them at critical periods during their life cycle and not their preferences throughout the year. We suggest that future studies, in addition to focusing on the range of plant species visited by a hummingbird species, also embrace mechanistic

considerations between form and function. The most important factors of natural selection on hummingbird bill morphology may not be the range of plant species visited, but rather the frequency of visits to plant species with extreme phenotypes in length, diameter, and curvature and their abundances relative to other food plants, especially at critical times of year when food is limited.

LITERATURE CITED

Agrawal, A. A. 2005. Natural selection on common milkweed (*Asclepias syriaca*) by a community of specialized insect herbivores. Evolutionary Ecology Research 7:651–667.

Arizmendi, M. C., and J. F. Ornelas. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. Biotropica 22:172–180.

Bell, J. 1956. Tangent, chord theorem. Mathematical Gazette 40:211–212.

Benkman, C. W., and A. K. Lindholm. 1991. An experimental analysis of the advantages and evolution of a morphological novelty. Nature 349:519–520.

Berry, F., and W. J. Kress. 1991. *Heliconia*: an identification guide. Smithsonian Institution Press, Washington, D.C., USA.

Bleiweiss, R. 1999. Joint effects of feeding and breeding behaviour on trophic dimorphism in hummingbirds. Proceedings of the Royal Society B 1437:2491–2497.

Borrell, B. J. 2005. Long tongues and loose niches: evolution of euglossine bees and their nectar flowers. Biotropica 37:664–669.

Borrell, B. J. 2007. Scaling of nectar foraging in orchid bees. American Naturalist 169:569–580.

Collins, B. G. 2008. Nectar intake and foraging efficiency: responses of honeyeaters and hummingbirds to variations in floral environments. Auk 125:574–587.

Colwell, R. K. 2000. Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. American Naturalist 156:495–510.

Cotton, P. A. 1998. Coevolution in an Amazonian hummingbird–plant community. Ibis 140:639–646.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London, UK.

Darwin, C. 1876. The effects of cross and self fertilization in the vegetable kingdom. John Murray, London, UK.

Dayan, T., and D. Simberloff. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. Ecology 75:1063–1073.

Dodge, C. W. 1966. The circular functions. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Endress, P. K. 1994. Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge, UK.

Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. Ecological Monographs 46:257–291.

Feinsinger, P. 1983. Coevolution and pollination. Pages 282–310 *in* D. J. Futuyma and M. D. Slatkin, editors. Coevolution. Sinauer, Sunderland, Massachusetts, USA.

Feinsinger, P., and R. K. Colwell. 1978. Community organization among Neotropical nectar-feeding birds. American Zoologist 18:779–795.

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. Annual Review of Ecology and Systematics 35:375–403.

Freeman, S. 2005. Biological science. Second edition. Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.

Gill, F. B., and L. L. Wolf. 1978. Comparative foraging efficiencies of some montane sunbirds in Kenya. Condor 80:391–400.

Grant, B. R., and P. R. Grant. 1996. High survival of Darwin's finch hybrids: effects of beak morphology and diets. Ecology 77:500–509.

Grant, P. R. 1984. Ecology and evolution of Darwin's finches. Princeton University Press, Princeton, New Jersey, USA.

Haber, W. A., and G. W. Frankie. 1989. A tropical hawkmoth community: Costa Rican dry forest Sphingidae. Biotropica 21:155–172.

Hainsworth, F. R. 1973. On the tongue of the hummingbird: its role in the rate and energetics of feeding. Comparative Biochemistry and Physiology 46A:65–78.

Hainsworth, F. R., and L. L. Wolf. 1970. Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. Science 168:368–369.

Hainsworth, F. R., and L. L. Wolf. 1976. Nectar characteristics and food selection by hummingbirds. Oecologia 25:101–113.

Harder, L. D. 1985. Morphology as a predictor of flower choice by bumble bees. Ecology 64:198–210.

Johnsgard, P. A. 1983. The hummingbirds of North America. Smithsonian Institution Press, Washington, D.C., USA.

Kingsolver, J. G., and R. B. Huey. 2003. Introduction: the evolution of morphology, performance, and fitness. Integrative Comparative Biology 43:361–366.

Kodric-Brown, A., J. H. Brown, G. S. Byers, and D. F. Gori. 1984. Organization of a tropical island community of hummingbirds and flowers. Ecology 65:1358–1368.

Kress, W. J., J. Betancur, and B. Echeverry. 1999. Heliconias—Llamaradas de la Selva Colombiana. Cristina Uribe Editores, Bogotá, Colombia.

Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge, UK.

McDade, L. A. 1992. Pollinator relationships, biogeography, and phylogenetics. BioScience 42:21–26.

Montgomerie, R. D. 1984. Nectar extraction by hummingbirds: response to different floral characters. Oecologia 63:229–236.

Muchhala, N. 2007. Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. American Naturalist 169:494–504.

O'Brien, R. G., and M. G. Kaiser. 1985. MANOVA method for analyzing repeated measures designs: an extensive primer. Psychological Bulletin 97:316–333.

Paton, D. C., and B. G. Collins. 1989. Bills and tongues of nectar-feeding birds: a review of morphology, function and performance, with intercontinental comparisons. Australian Journal of Ecology 4:473–506.

Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, New Jersey, USA.

Raven, P. H., and G. B. Johnson. 1996. Biology. Fourth edition. McGraw-Hill, New York, New York, USA.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Rodríguez-Gironés, M. A., and L. Santamaría. 2006. Models of optimal foraging and resource partitioning: deep corollas for long tongues. Behavioral Ecology 17:905–910.

Rodríguez-Gironés, M. A., and L. Santamaría. 2007. Resource competition, character displacement, and the evolution of deep corolla tubes. American Naturalist 170:455–464.

SAS Institute. 1999. SAS/STAT user's guide. Version 8. SAS Institute, Cary, North Carolina, USA.

Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. Ecology 76:82–90.

Schondube, J. E., and C. Martinez del Rio. 2002. The flowerpiercers' hook: an experimental test of an evolutionary trade-off. Proceedings of the Royal Society B 27:193–198.

Schuchmann, K.-L. 1999. Family Trochilidae (hummingbirds). Pages 468–680 in J. del Hoyo, A. Elliott, and J. Sargatal, editors. Handbook of the birds of the world. Volume 5. Barn owls to hummingbirds. Lynx Edicions, Barcelona, Spain.

Snow, D. W., and B. K. Snow. 1980. Relationships between hummingbirds and flowers in the Andes of Columbia. Bulletin of the British Museum of Natural History 38:105–139.

Spieth, H. T. 1966. Hawaiian honeycreeper, Vesteria coccinea (Forster), feeding on Lobeliad flowers, Clermontia arborsescens (Mann) Hillebr. American Naturalist 100:470–473.

Stein, B. A. 1992. Sicklebill hummingbirds, ants, and flowers. BioScience 42:27–33.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecology 56:285–301.

Taylor, J., and S. A. White. 2007. Observations of hummingbird feeding behavior at Heliconia beckneri and H. tortuosa in southern Costa Rica. Ornitologia Neotropical 18:133–138.

Temeles, E. J. 1996. A new dimension to hummingbird–flower relationships. Oecologia 105:517–523.

Temeles, E. J., R. S. Goldman, and A. U. Kudla. 2005. Foraging and territory economics of sexually-dimorphic purple-throated caribs, Eulampis jugularis, at three heliconias. Auk 122:187–204.

Temeles, E. J., and W. J. Kress. 2003. Adaptation in a plant–hummingbird association. Science 300:630–633.

Temeles, E. J., Y. B. Linhart, M. Masonjones, and H. D. Masonjones. 2002. The role of flower width in hummingbird bill length–flower length relationships. Biotropica 34:68–80.

Temeles, E. J., I. L. Pan, J. L. Brennan, and J. N. Horwitt. 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. Science 289:441–443.

Temeles, E. J., and W. M. Roberts. 1993. Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. Oecologia 94:87–94.

Temeles, E. J., K. C. Shaw, A. U. Kudla, and S. E. Sander. 2006. Traplining by purple-throated carib hummingbirds: behavioral responses to competition and nectar availability. Behavioral Ecology and Sociobiology 61:163–172.

Westerkamp, C. 1990. Bird-flowers: hovering versus perching exploitation. Botanica Acta 103:366–371.

Wolf, L. L. 1975. Female territoriality in the purple-throated carib. Auk 92:511–522.

Wolf, L. L., and F. R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52:980–988.

Wolf, L. L., F. R. Hainsworth, and F. G. Stiles. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. Science 176:1351–1352.

APPENDIX A

Photographs of bills of Eulampis jugularis, flowers and inflorescences of Heliconia species on St. Lucia, West Indies, orientation of birds during feeding visits to heliconias, and measurements of bill and flower chords and angles (Ecological Archives E090-075-A1).

APPENDIX B

Artificial Heliconia inflorescences and flowers: instructions for their construction, dimension, and images (Ecological Archives E090-075-A2).

APPENDIX C

Figures and regression statistics for relationships between total bill lengths and maximum extraction depths of male and female Eulampis jugularis at artificial flowers of increasing curvatures (Ecological Archives E090-075-A3).

APPENDIX D

Figures and regression statistics for relationships between handling times and total bill lengths of male and female Eulampis jugularis at artificial flowers of increasing curvature and long lengths (Ecological Archives E090-075-A4).

APPENDIX E

Figures and regression statistics for relationships between handling times and total bill lengths of male and female Eulampis jugularis at narrow artificial flowers (Ecological Archives E090-075-A5).

APPENDIX F

Figures and regression statistics for relationships between handling times and total bill lengths of male and female Eulampis jugularis at straight artificial flowers (Ecological Archives E090-075-A6).