

Attempts to posteriorize digital identity by enhancing ID BMP levels with exogenous BMP2 and BMP4 were unsuccessful. BMP2- and BMP4-loaded beads were implanted in ID2 and ID3, over a wide range of concentrations and developmental time (11). In agreement with previous reports (17, 18), we observed combinations of truncations, joint deletions, and cartilage dysmorphologies (96%, $n = 160$) that precluded assessment of digit respecification. However, several developing tissues exhibit markedly different responses to treatment with specific combinations of homo- and heterodimeric BMP ligands (19–21). Thus, although application of homodimeric BMP2 and BMP4 can only elicit the above dysmorphologies, we agree with the recently proposed possibility that other combinatorial repertoires of homo- and heterodimeric BMP ligands may regulate digital identity (4) during normal development.

As an alternative approach, we assessed the effects of reduced ID BMP levels. Noggin-loaded beads applied to ID3 (Fig. 4F) and ID2 (Fig. 4G) caused the transformation of d3 to d2 (23%, $n = 48$) and d2 to d1 (21%, $n = 14$), respectively. Noggin-mediated transformations correlated with reduced ID *Bmp2*, *Bmp4*, and *Bmp7* expression, whereas *HoxD10–12* expression was not affected [$n > 10$ for each probe (7)], further suggesting that the *HoxD* complex does not play a primary role in establishing digit identity. These results confirm previously reported *Bmp4*, *HoxD11*, and *HoxD13* expression in the IDs of chick leg buds with inhibited BMP signaling due to ectopic expression of a dominant negative *BmpR1b* receptor (*dnBmpR1b*) (22). Interestingly, figure 1B of (22) shows a *dnBmpR1b*-expressing foot with apparent anterior transformations of digital identity (23).

Combined with, and in the context of, our embryological and molecular analyses, published data can be interpreted to suggest that experimental modulation of ID BMP signaling can cause both anterior and posterior transformations of digit identity, with higher BMP levels necessary (22) and sufficient (4, 15) for the development of more posterior identities. Therefore, it is of interest that Noggin-mediated inhibition of mandibular arch BMP signaling causes homeotic transformations of tooth identity (24). We suggest that differential BMP signaling may represent a conserved mechanism for specifying discrete identities among meristic structures within a developmental field.

Our results indicate that A/P identity is not an inherent property of digital primordia, but is specified by the ID mesoderm prior to its regression. We show that more posterior IDs specify more posterior digital identities, and that digital fate is determined by the most posterior ID cues a primordium receives. We further demonstrate that digit identity can be trans-

formed through experimental modulation of ID BMP signaling, suggesting the BMP family plays a role in regulating digital identity. These data represent an important advance in understanding how autopoietic mesoderm organizes A/P positional information downstream of ZPA signaling and directs the skeletal patterning of the digital arch [for a schematic model, see (11)]. By extension, this study highlights the importance of understanding the intermediary molecular mechanisms that convert early ZPA signals into the interdigitally compartmentalized arrangement of A/P positional information present at later stages.

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23. Figure 4B of Zou and Niswander (22) shows the cartilage pattern of a *dnBmpR1b*-expressing chick foot relative to the unmanipulated control foot. In the normal foot, d4 has five phalanges and d3 has four. In the infected foot, d4 appears to have four phalanges, whereas d3 appears to have three. Zou and Niswander suggest that *dnBmpR1b* expression causes distally incomplete digits to develop; however, these digits exhibit perfectly formed distal claws. Alternatively, we interpret this phenotype as *dnBmpR1b*-mediated digital fate transformations (d4 to d3 and d3 to d2) due to inhibited ID BMP signaling.
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Evidence for Ecological Causation of Sexual Dimorphism in a Hummingbird

Ethan J. Temeles,* Irvin L. Pan, Jillian L. Brennan, Jedediah N. Horwitt

Unambiguous examples of ecological causes of animal sexual dimorphism are rare. Here we present evidence for ecological causation of sexual dimorphism in the bill morphology of a hummingbird, the purple-throated carib. This hummingbird is the sole pollinator of two *Heliconia* species whose flowers correspond to the bills of either males or females. Each sex feeds most quickly at the flower species approximating its bill dimensions, which supports the hypothesis that floral specialization has driven the evolution of bill dimorphism. Further evidence for ecological causation of sexual dimorphism was provided by a geographic replacement of one *Heliconia* species by the other and the subsequent development of a floral dimorphism, with one floral morph matching the bills of males and the other of females.

Sexual dimorphism in size and morphology is widespread in animals. Charles Darwin drew attention to these differences and offered three explanations for their evolution that were based on mechanisms of sexual selection, fecundity selection, and ecological causation (for example, resource partitioning) (1). Although empir-

ical studies have demonstrated that the first two mechanisms operate in natural populations (2), unambiguous examples of ecological causation of sexual dimorphism are absent from the literature, an exception being some mosquito species, in which the mouthparts of males are adapted for drinking nectar and the mouthparts

of females for drinking blood (3). A major obstacle has been the difficulty of showing that sexual dimorphisms are due to differences in resource use and ecology, because sexual differences in the size of feeding structures scale positively with body size in many animal species (4). The positive relationship between body size and feeding morphology makes it unclear whether ecological differences between the sexes are the cause or the consequence of sexual dimorphism (4).

Darwin was aware of the problem of attributing sexual dimorphisms to ecological causes, and in suggesting divergence in food use as a cause, he noted that such sexual differences should be confined to the feeding apparatus (1). The example Darwin used to illustrate this putative cause of sexual dimorphism was the New Zealand huia (*Neomorpha acutirostris*), now extinct. The sexes were similar in body size and plumage, but the bill of the male was short, thick, and straight, whereas the bill of the female was longer, slender, and decurved (5). The second example Darwin used to illustrate sexual dimorphism due to differences in food use was hummingbird bills. The relationship between sexual differences in the bills of hummingbirds and patterns of flower visitation, however, has received little attention in studies of natural hummingbird populations. Here we present evidence for ecological causation of sexual dimorphism in the bill morphology of the purple-throated carib hummingbird *Eulampis jugularis*

from the island of St. Lucia, West Indies.

Several features of *E. jugularis* make it an excellent candidate for studies of food-based hypotheses for the evolution of sexual dimorphism. First, although the wings and body masses of males average 8.6 and 25%, respectively, larger than those of females, the bills of females are on average more than 30% longer than those of males (6), which is one of the most extreme bill dimorphisms of any hummingbird (7). Moreover, the bills of females are curved downward at an approximately 30° angle, whereas the bills of males are much straighter and are curved downward at only a 15° angle (Fig. 1). Second, mapping sexual dimorphism in wing and bill length onto a time-calibrated DNA-hybridization-based phylogeny yields no consistent pattern among *E. jugularis* and its closest relatives, which suggests that behavioral and ecological factors have had some role in the evolution of sexual dimorphisms within this group (8). Third, the expression of sexual dimorphism in *E. jugularis* is inconsistent with patterns of sexual selection for larger male size, where bill length should scale positively with male size rather than negatively. Hence, *E. jugularis* fulfills Selander's criterion that the only reliable evidence for ecological causation of sexual dimorphism is a modification of feeding structures in a direction that is inconsistent with sexual selection and is greater than would be expected on the basis of body size differences alone (4, 5).

Our fieldwork (May through June 1999) encompassed periods when the birds were actively nesting and rearing young. We censused understory food plants within 100 m of either side of trails passing through four rainforest reserves

(9). The only understory food plants available during the months of May and June were a red-bracted *Heliconia caribaea* and an endemic green-bracted *H. bihai* (10). To determine whether the sexes of *E. jugularis* differed in their use of these two *Heliconia* species, we conducted watches at "dense" and "sparse" patches of *H. caribaea* and *H. bihai* in Quillesse Reserve (11). *Eulampis jugularis* was the sole pollinator of *H. caribaea* and *H. bihai*. Males were associated with dense patches of *H. caribaea*, which they defended against intruding conspecifics, although they occasionally fed at flowers of *H. bihai* on the periphery of their territories. Females intruded into dense patches of *H. caribaea* that were defended by males, and they also trapline-foraged in sparse patches of *H. caribaea* and *H. bihai* and dense patches of *H. bihai*, which they occasionally defended. Censuses of the reserves support the results of patch watches: 15 of 15 males, but only 7 of 18 females, were observed feeding in patches of *H. caribaea* ($P < 0.001$; $\chi^2 = 13.75$, $df = 1$).

To examine the relationship between flower use and bill dimensions, we measured flower lengths and curvatures of *H. caribaea* and *H. bihai* in the three reserves having both *Heliconia* species (Table 1). At all three sites, the flowers of *H. caribaea* were significantly shorter and straighter than were the flowers of *H. bihai* [$P < 0.05$; t tests with sequential Bonferroni adjustments (12)]. Differences in nectar production and concentration between the two species were not significant ($P > 0.05$; t tests with sequential Bonferroni adjustments).

The striking correspondence between flower lengths and curvatures shown in Table 1 and hummingbird bill lengths and curvatures suggests that the bills of males are specialized for feeding from flowers of *H. caribaea*, whereas the bills of females are specialized for feeding from flowers of *H. bihai*. If bills of each sex are specialized for feeding from a certain species of flower, each sex should have faster feeding times at the flower species most approximating its bill size and shape and should have slower feeding times at the flower species least approximating its bill size and shape (13, 14). The feeding times of females were significantly shorter at the longer, more curved flowers of *H. bihai* (mean $\pm$ SE = 3.4 ± 0.4 s) than at the shorter, straighter flowers of *H. caribaea* (mean $\pm$ SE = 4.4 ± 0.8 s; paired t test, $t = 2.32$, $P = 0.034$, $n = 6$ females, 278 feeding visits). In contrast, the feeding times of males (mean $\pm$ SE = 2.7 ± 0.5 s) were significantly shorter than the feeding times of females (3.8 ± 0.8 s) at flowers of *H. caribaea* (paired t test; $t = 4.53$, $P = 0.023$, $n = 3$ males and females at the same patches, 143 feeding visits). Because males were so overwhelmingly in association with *H. caribaea*, we observed too few visits by males to *H. bihai* for use in statistical comparison. Although nectar volumes were not con-

Department of Biology, Amherst College, Amherst, MA 01002, USA.

*To whom correspondence should be addressed. E-mail: ejtemeles@amherst.edu

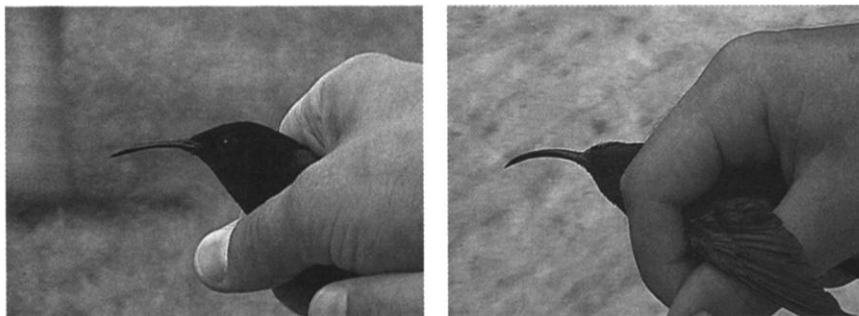


Fig. 1. Sexual dimorphism in bill length and curvature of male (left) and female (right) purple-throated caribs, *E. jugularis*. The sexes are monomorphic in plumage, and males are 25% heavier than females. Nonetheless, the bills of females are 30% longer and 100% more curved than the bills of males.

Table 1. Flower lengths and curvatures (mean $\pm$ SE) of *H. caribaea* and *H. bihai* from three St. Lucian rainforest reserves. The number of flowers measured is shown in parentheses.

<i>Heliconia</i> species	Flower length (mm)			Flower curvature (degrees)		
	Barre de L'Isle	Des Cartiers	Quillesse	Barre de L'Isle	Des Cartiers	Quillesse
<i>H. bihai</i>	44 $\pm$ 0.5 (15)	44 $\pm$ 0.6 (18)	43 $\pm$ 0.4 (20)	30 $\pm$ 1.2 (16)	32 $\pm$ 1.0 (18)	31 $\pm$ 0.6 (25)
<i>H. caribaea</i>	38 $\pm$ 0.6 (10)	37 $\pm$ 1.2 (8)	40 $\pm$ 0.6 (10)	20 $\pm$ 0.9 (9)	21 $\pm$ 1.6 (8)	21 $\pm$ 1.2 (10)

trolled in these observations, the feeding time estimates support the hypothesis that the bills of males and females are specialized for feeding from flowers of *H. caribaea* and *H. bihai*, respectively.

Additional support for the hypothesis of floral specialization by males and females comes from Forestière Reserve, which lacks *H. caribaea*. At this site, we found a red-and-green-bracted morph of *H. bihai* (15). At Forestière, we observed males feeding at, and defending, flowers of the red-green— but not the green-bracted *H. bihai*. The red-green morph had significantly shorter and straighter flowers than the green-bracted morph [$P < 0.05$, t tests with Bonferroni adjustments (Table 2)], but the two *Heliconias* did not differ in nectar production or concentrations.

We interpret the red-green—bracted morph at Forestière Reserve as an ecological replacement of the red-bracted *H. caribaea* specialized on by male purple-throated caribs. We also recorded the red-green morph at the other three reserves. In support of the hypothesis of ecological replacement, the red-green morph increased in frequency where the red-bracted morph of *H. caribaea* was rare, and vice versa (Table 3) ($P < 0.001$, $\chi^2 = 70$, $df = 6$) (16). Additional support for this interpretation is provided by a comparison of flowers at Des Cartiers, where the red-green morph was common, and at Quilèsse, where it was rare (Table 3). At Des Cartiers, we also observed males defending patches of the red-green morph. At this reserve it had significantly straighter flowers ($25^\circ \pm 1^\circ$ of curvature, $n = 23$ flowers) than the green-bracted morph ($32^\circ \pm 1^\circ$ of curvature, $n = 18$ flowers; $P < 0.05$, t test with Bonferroni adjustments). Standing crops and concentrations of nectar did not differ between the two flower morphs. In contrast, at Quilèsse, the red-green

morph was quite rare and consisted of one small patch used exclusively by female purple-throated caribs but not by males. No significant differences in flower curvature, nectar standing crop, or nectar concentration were recorded between the red-green— and the green-bracted *H. bihai*, although the red-green morph's flowers were significantly longer (47 ± 0.6 mm, $n = 10$ flowers) than flowers of the green-bracted *H. bihai* (43 ± 0.4 mm, $n = 28$ flowers; $P < 0.05$, t test), which is consistent with expectations based on the exclusive use by females of the red-green morph at this site.

Our study provides unambiguous evidence that sexual differences in bill length and bill curvature are associated with sexual differences in *Heliconia* use by male and female *E. jugularis*. The variation in the red-green morph's flower morphology among reserves, however, raises the question of which party in the association has evolved to match the other. The bill morphology of *E. jugularis* differs significantly between islands, which suggests that bill dimorphism of *E. jugularis* on St. Lucia is not merely a consequence of past adaptation and evolution (17). The two *Heliconia* species are the major food plants of *E. jugularis* from January to July, during the period before, during, and after breeding (18, 19). Selection might be particularly intense during this period because the birds are constrained to the use of these *Heliconia* plants owing to nesting and mating activities. These data suggest that both the birds and the flowers may be targets of reciprocal selection.

Because males and females were defending territories against conspecifics, food competition between the sexes is the most likely explanation for sexual differences in resource use. Nonetheless, sexual selection also may be involved, because the same floral resource that males defend for food also serves for mate attraction (20). Larger size has been shown to be an advantage in contests for territories both within and between hummingbird species (21, 22), and we suggest that both food and mate competition may have selected for larger male body size and partitioning of *Heliconia* species on the basis of patch reward [*H. caribaea* inflorescences bear two to three times as many flowers as *H. bihai* (20)]. Once resource partitioning on the basis of patch rewards was established, natural selection may then have acted on the bill dimensions of males and females. Controlled studies involving experimental manipulation of patch rewards and measurements of feeding times of males and females with known bill sizes and shapes will be necessary to determine the relative roles of these mechanisms underlying sexual differences in flower use (2).

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7. This statement of extreme bill dimorphism is based on a comparison of *E. jugularis* to 107 hummingbird species from (23, 24).
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10. Corresponding to the cultivars "Purpurea" and "Emerald Forest" (27).
11. A dense patch consisted of 65 or more stalks of *Heliconia* and a sparse patch consisted of 13 or fewer stalks. Six watches at each patch type were conducted from approximately 0800 to 1400 hours. We recorded the species and sex of each hummingbird pollinator and whether the hummingbird fed from and defended flowers.
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16. For both *H. caribaea* and the red-green morph, three of four cells in Table 3 deviate significantly from independence at $P < 0.00001$, and deviations of the remaining cells are either significant or approach significance ($P < 0.02$ for the red-green morph; $P = 0.08$ for *H. caribaea*). Only one of the four cells of the green morph deviated significantly from independence. For statistical methods, see (28).
17. This statement is based on measurements of bill lengths of specimens collected from the Lesser Antillean Islands of Dominica, Guadeloupe, Martinique, St. Kitts, and St. Lucia. Significant differences in the bill lengths of females, but not of males, were obtained for 6 of the 10 island pairs (Tukey multiple comparisons, $P = 0.05$ overall).
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Table 2. Flower lengths and curvatures (mean $\pm$ SE) of the green- and red-green—bracted morphs of *H. bihai* at Forestière Reserve, St. Lucia. The number of flowers measured is shown in parentheses.

<i>Heliconia</i>	Flower length (mm)	Flower curvature (mm)
Green	42.0 $\pm$ 0.4 (21)	29.0 $\pm$ 0.8 (21)
Red-green	39.5 $\pm$ 0.9 (23)	25.5 $\pm$ 0.9 (22)

Table 3. Frequencies of *H. caribaea* and the green and red-green morphs of *H. bihai*, at four St. Lucian rainforest reserves (numbers refer to plants with bracts).

Site	<i>H. caribaea</i>	Green	Red-green
Barre de L'Isle	156	166	25
Des Cartiers	18	615	188
Forestière	0	290	105
Quilèsse	193	917	10