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Douglas L. Altshuler and Christopher James Clark

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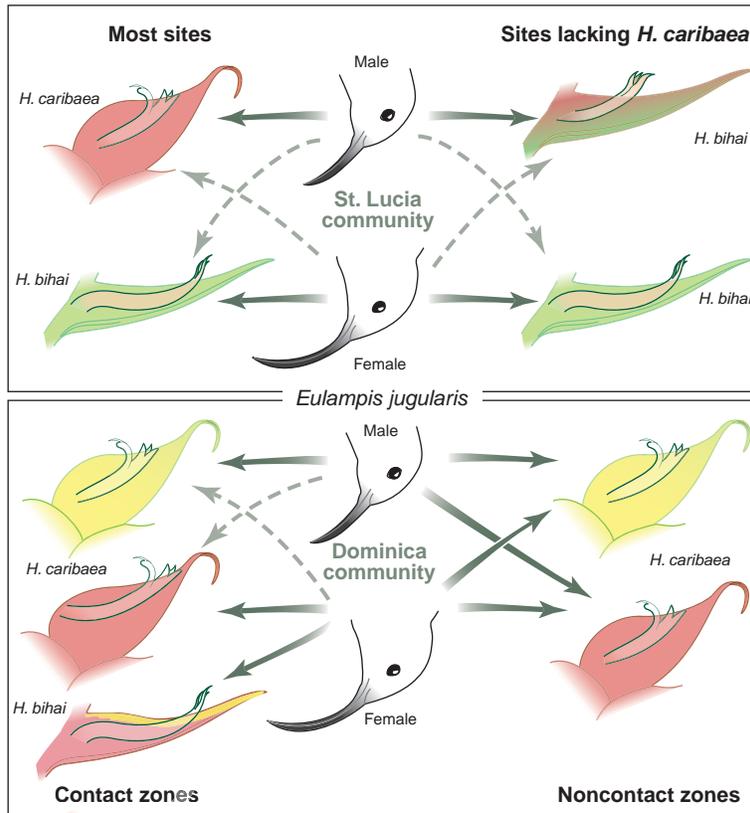
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Darwin's Hummingbirds

Douglas L. Altshuler and Christopher James Clark

Islands have had a long association with evolutionary biology ever since Darwin observed the myriad variations in species from the Galápagos and other archipelagos and used them to formulate his theory of evolution by natural selection. The simplicity of island flora and fauna and the replicate series of study sites that islands provide enable contemporary biologists to identify how ecological processes such as competition and predation have shaped evolution within communities (1, 2). On page 630 of this issue, Temeles and Kress (3) present a comparative study of hummingbirds and their *Heliconia* food plants from islands of the Lesser Antilles. Their study provides evidence for reciprocal evolution (coevolution) between species, in this case hummingbirds and *Heliconia*. In addition, they elucidate how ecological pressures shape the different morphologies of males and females (sexual dimorphism) within a species, evidence that has been difficult to obtain from studies on mainland fauna.

Hummingbirds consume flower nectar using sustained hovering when feeding, a highly specialized behavior. Although all hummingbirds display this behavior, they show wide variations in their body mass, and in the size and shape of their bills and wings (4). Another curious feature of hummingbirds is the pronounced difference in color (5), bill shape (6), and body size between males and females. For example, females tend to be larger in small species and



A dance between hummingbird and *Heliconia*. The feeding relationships between the Caribbean purple-throated hummingbird, *Eulampis jugularis*, and different morphs of two species of *Heliconia* (*H. caribaea* and *H. bihai*) on the islands of St. Lucia and Dominica. Solid lines indicate that hummingbirds regularly feed from that flower morph, whereas dashed lines indicate rare or occasional feeding forays.

males tend to be larger in large species (7). A central challenge for comparative biologists is to understand the sources of this remarkable variation.

Sexual dimorphism arises through one of three mechanisms: sexual selection, fecundity selection, and ecological causation. Darwin noted that ecological causes should be associated with the feeding apparatus and even suggested hummingbirds as an example (8). However, finding proof of ecological causation is very challenging because sexual dimorphism of feeding structures usually correlates positively with differences in body size. In previous work, Temeles *et al.* (9) demonstrated ecological causation of bill size dimorphism in the hummingbird *Eulampis jugularis* from the Caribbean island of St. Lucia. In this

species, males are larger than females but have shorter and less curved bills (see the figure), thus exhibiting a reversal in the dimorphism between bill and body size.

On St. Lucia, the hummingbirds feed primarily on two species of *Heliconia*: *H. caribaea* characterized by a red bract (the hardened structure that protects the flower's corolla) and *H. bihai*, which has a green bract (see the figure). Male hummingbirds defend patches of *H. caribaea* and feed on the flowers, which have relatively straight and short corollas, closely matching the shape of the male bill. In contrast, females imbibe nectar from the longer and more curved corolla of *H. bihai* flowers and forage over greater distances among undefended plants, a behavior known as "traplining." In sites where *H. caribaea* is rare or absent, there appears an additional red-green-bracted morph of *H. bihai* with a corolla that is straighter and shorter than that of the green-bracted variety. The corolla of the *H. bihai* red-green morph has evolved a similar shape and size to that of the absent *H. caribaea*, and this altered morphology matches the shape of the *E. jugularis* male bill. The close match between bill morphology and flower shape demonstrates that feeding ecology can drive bill dimorphism.

These findings in St. Lucia hummingbirds strongly suggest that bill dimorphism stems from ecological causes. In their new study on the neighboring island of Dominica, Temeles and Kress (3) report that the male and female hummingbirds split floral resources in a new way, providing even stronger evidence that ecological pressures can induce bill dimorphism. Although the same *Heliconia* species are present on Dominica, there are two *H. caribaea* morphs (red- and yellow-bracted) and only one *H. bihai* morph (red with a yellow stripe). On St. Lucia, the corolla of the *H. bihai* red-green-bracted morph matches the shape of the male bill, but on Dominica it is the red-bracted *H. caribaea* corolla that has become longer and more curved to match the shape of the female

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bill (see the figure). Males prefer the yellow-bracted *H. caribaea*, which has a shorter and straighter corolla than the red-bracted morph. At some sites where only the two *H. caribaea* morphs are present, their corollas do not differ and both sexes of hummingbird feed equally from both flower morphs.

On both islands, the energetic rewards of the flower morphs correspond to the body sizes of male and female hummingbirds. Because males are larger than females, it follows that they require more energy (10). If the flower morphs offer the same amount of energy, then the same hummingbird body size would be optimal for nectar extraction, and we would reject the hypothesis that foraging ecology drives size dimorphism. On both islands, *H. bihai* offers slightly less nectar than *H. caribaea*, corresponding to the difference in body size of the male and

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female hummingbirds that feed on the two different morphs. Similarly, on St. Lucia, the red-green replacement morph of *H. bihai* offers more nectar than the green morph, whereas on Dominica the red replacement morph of *H. caribaea* offers less nectar than the yellow morph.

The Antillean islands of St. Lucia and Dominica provide two striking examples of ecological environments that produce sexual dimorphism in hummingbirds. The rearrangements of flower morphology and nectar productivity are surprisingly plastic. Hummingbird and *Heliconia* engage in a coevolutionary dance, with flower shape evolving in response to hummingbird bills, and bill shape evolving in response to



The morphs of *Heliconia* on St. Lucia. (Left) *H. bihai* green morph, (middle) *H. bihai* red-green morph, (right) *H. caribaea* red morph. [From (3)]

flower shape. By offering nectars containing different amounts of energy, *Heliconia* species select for different body sizes. Although this is not evidence that size dimorphism in *E. jugularis* evolved solely in response to foraging ecology, it casts doubt on assumptions that sexual dimorphism is a measure of sexual selection (11).

On the islands of St. Lucia and Dominica, this coevolutionary dance is finely tuned. These island ecosystems provide a natural laboratory for further studies of reciprocal evolution. The hummingbirds are clearly benefitting from the plants: Males control an energy-rich accessible food source and females have nearly exclusive use of an alternative food source. On the other side of the equation, how do differences in animal feeding behavior and efficiencies affect plant fitness (12)? Gene flow is clearly available to plants with trampling pollinators but how do plants with territorial pollinators accomplish ge-

netic outcrossing? Also, does the consumption of insects by hummingbirds directly influence hummingbird morphology (13) and indirectly influence flower morphology? Once again, islands may provide the ideal setting for answering these questions.

References

1. P. R. Grant, *Ecology and Evolution of Darwin's Finches* (Princeton Univ. Press, Princeton, NJ, 1986).
2. J. A. Endler, *Trends Ecol. Evol.* **10**, 22 (1995).
3. E. J. Temeles, W. J. Kress, *Science* **300**, 630 (2003).
4. K. L. Schuchmann, in *Handbook to the Birds of the World*, J. del Hoyo, A. Elliott, J. Sargatal, Eds. (Lynx Edicions, Barcelona, 1999), vol. 5, pp. 468–680.
5. R. Bleiweiss, *Evol. Ecol.* **11**, 217 (1997).
6. ———, *Proc. R. Soc. London Ser. B* **266**, 2491 (1999).
7. R. K. Colwell, *Am. Nat.* **156**, 495 (2000).
8. C. Darwin, *The Descent of Man, and Selection in Relation to Sex* (Murray, London, 1871).
9. E. J. Temeles, I. L. Pan, J. L. Brennan, J. N. Horwitt, *Science* **289**, 441 (2000).
10. J. H. Brown, W. A. Calder III, A. Kodric-Brown, *Am. Zool.* **18**, 687 (1978).
11. J. J. Wiens, *Trends Ecol. Evol.* **16**, 517 (2001).
12. D. R. Campbell, N. M. Waser, M. V. Price, *Ecology* **77**, 1463 (1996).
13. F. G. Stiles, *Condor* **97**, 853 (1995).

PALEOCLIMATE

Toward Integrated Reconstruction of Past Climates

Kevin E. Trenberth and Bette L. Otto-Bliesner

Climate involves interactions among the atmosphere, the oceans, the land surface and its vegetation and hydrology, and the cryosphere. It naturally varies on time scales ranging from interannual (El Niño) to millennia or longer. The instrumental record of a hundred years or so is clearly inadequate to help us understand these processes.

Paleoclimate reconstructions fill this

void. Made up of estimates of climate variables at times long before the instrumental record, they are based on proxy indicators known to be sensitive to climate. Examples include cores from long-lived trees, ice sheets in Greenland and Antarctica, glaciers at high elevations in the tropics, sediments, and corals. With considerable ingenuity, these proxies have been used to derive information about past climates, natural variability, and global climate change.

The reconstruction of a time series of temperature or precipitation at a single location is no mean achievement. To synthe-

size results from previous reconstructions is even more difficult and has only recently been credibly achieved after considerable work, especially in statistical analysis (1). However, it is becoming clear that a synthesis of data with more physical credibility requires collaboration between paleoclimate and climate dynamics experts (including modelers).

Two difficulties faced by climate reconstructions concern chronological dating and what a proxy is really measuring. For example, oxygen isotopes (measured by the $\delta^{18}\text{O}$ isotopic ratio) in corals are affected by both temperature and salinity of the seawater in which the coral grows, resulting in an inherent ambiguity. Other methods are based on trace element ratios normalized to calcium (such as Sr/Ca and Mg/Ca) in the skeletons of corals and shells. It is assumed that the trace metals are incorporated into the skeleton at concentrations that depend on growth temper-

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