Adaptive Radiation in Hawaiian Honeycreepers

The Hawaiian Islands are the most isolated archipelago on the planet. Here, we are more than 2,000 miles away from the nearest continent and some 1,000 miles away from the closest Pacific atolls. Because of this isolation, over millions of years, relatively few plant and animal species arrived on the islands. The "three Ws" (wind, waves, and wings) are used to describe the means by which species arrived here. From a small collection of "founding species" descended all of the animals and plants that are native to Hawaiʻi. The Hawaiian rain forest is a hotbed of "endemism." Of its native inhabitants, a large proportion are unique to these islands.

In contrast to "indigenous" species, Hawaiian endemic species evolved into a new species after arriving here from somewhere else. Indigenous species have remained relatively unchanged since their arrival and are not unique to Hawaiʻi. Among the endemic forest birds, most species belong to a group known as the Hawaiian honeycreepers. All of the honeycreeper species are thought to have evolved from a single finch species that arrived on the islands more than 15 million years ago. This process of "adaptive radiation" has, over time, resulted in honeycreepers that are very different from each other and adapted to many different environments.

The oldest of today's main islands, Kauaʻi, is only about five million years old. So much of the early evolution of the honeycreepers probably happened on other, older islands in the chain. Through a process called "interisland dispersal," the ancestors of the honeycreeper species we know today colonized the new islands, even as their old homelands were being slowly eroded away. These new islands may have offered different habitat for the birds, which over time could have further radiated into new species.

In the 1970s, paleontologists began in earnest to collect partially fossilized bird remains from sand dunes, lava tubes, caves, and sinkholes in the Hawaiian Islands. This fossil record revealed many species of honeycreepers that were already extinct by the time Western scientists had started identifying and describing Hawaiian birds. Most of these extinctions were most likely a result of the impacts of the Hawaiian people: competition or predation by Polynesian introductions, conversion of lowland habitats into agricultural areas, and killing of birds for food and other human uses.

In addition to uncovering evidence of bird extinctions, fossil research has helped to shed new light on the true extent of adaptive radiation

Hawaiian Honeycreepers at a Glance

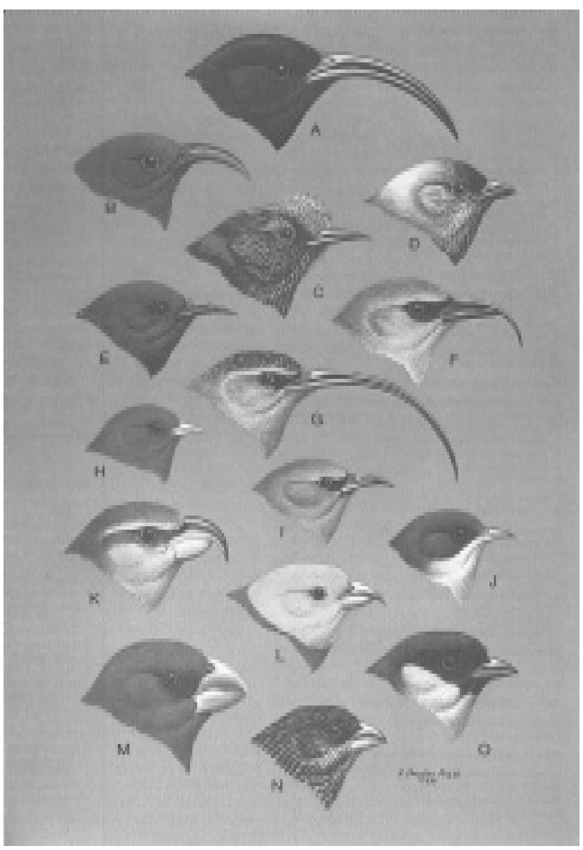
- Thought to have evolved from a single species of finch.
- Fifty-seven species are thought to be part of the Hawaiian honeycreeper subfamily.

Eighteen species, known only from fossil record, were probably extinct by 1778.	32 percent
Twenty-Two species have gone extinct since 1778.	39 percent
Ten surviving species are classified as endangered.	18 percent
Seven surviving species are not classified as endangered.	12 percent

in Hawaiian honeycreepers. From the single ancestral finch species, at least 57 honeycreeper species are known to have evolved. What caused this remarkable formation of new species?

Adaptive Radiation

Adaptive radiation is often thought of as being driven by the need or opportunity for plants or animals to live in habitats other than the ones to which they are best adapted. It is easy to see how such needs and opportunities could arise for birds arriving on the Hawaiian Islands from other parts of the world. The Hawaiian honeycreepers evolved into species with different primary food sources: nectar, hard seeds, soft fruit, and insects and larvae. Some honeycreeper species have diets made up of combinations of these food sources. Their beak structure and even their leg and facial muscles reflect their diet and how they forage for food.



Variations in bill morphology of selected Hawaiian honeycreepers

(Illustration: H. Douglas Pratt, Jr.)

Some nectar-eating honeycreepers have beaks that are shaped to fit specific flowers. This is evidence of coevolution, in which honeycreepers and flowering plants evolved together, the birds feeding on the nectar and in turn spreading pollen from flower to flower. Birds and flowers evolved specialized relationships, of which the *ʻiʻiwi* and Hawaiian lobeliad plants are an excellent example. The long, curved bill of the *ʻiʻiwi* is perfectly suited to gathering nectar from the long, tubular, curved flowers of many lobeliad species.

Many factors are thought to have influenced adaptive radiation in Hawaiian honeycreepers, including the following:

Isolation and Dispersability

Populations of a bird species that remain isolated from each other can, over time, evolve into separate species. In general, birds can easily disperse from one place—or island— to another by flying. But the pattern of species and island-specific subspecies of honeycreepers suggests that some species were more likely to do so than were others.

Some scientists believe that insect-eating honeycreepers have a more reliable source of food than do species that feed on fruit or nectar. They hypothesize that “frugivorous” (fruit-eating) and “nectivorous” (nectar-feeding) birds are more likely to fly between islands looking for food in lean years. Because the “insectivores” (insect-feeders) had less reason to move around, they remained more isolated and developed into more species and subspecies.

Other scientists believe that there is not such a clear link between eating habits and interisland dispersal. Instead, they distinguish between common “generalists” such as the *ʻapapane* and *ʻamakihi* that are widespread across the islands on the one hand, and specialized seed eaters and nectivores on the other hand. Generalists are able to feed on a variety of food types. The more specialized eaters, some scientists maintain, would have been more likely to stay where their food source was and further evolve in that place. The generalists would have been more likely to fly from island to island.

Adaptation to Food Resources

Birds can rapidly adapt to new types of food or changes in the abundance of food sources. Over time, these adaptations (physical or behavioral changes) can result in the emergence of new species. In 1984 and 1985, studies of endangered Laysan finches that had been introduced in 1967 to Pearl and Hermes Reef, showed significant differences had already developed between the Pearl and Hermes finches and their ancestors on Laysan. The differences appeared to be a response to differences in food availability. If those differences turn out to be genetically linked, then evolutionary change had occurred among these birds in fewer than 20 generations.

Intraspecies Food Competition

Competition for food among members of the same species can lead to “adaptive shifts” or changes. Less competitive members of the species may shift to feeding on a different size or type of food, and over time this division of food can lead to bills that are specialized to this available food source.

ʻIʻiwi (Photo: Eric Nishibayashi)

Other Rain Forest Examples of Adaptive Radiation

- The Hawaiian *Drosophila* flies: Over 500 species of flies in the Drosophilidae family have been identified in Hawaiʻi, all of which evolved from a single common ancestor species. Nearly one-quarter of the known species in this family are found in Hawaiʻi, including many that are “narrowly endemic.” That means that they occur in only a very small area.

- Hawaiian lobeliads: Six of seven genera of this group of plants are endemic to Hawaiʻi. The 126 species in the genera *Cyanea, Clermontia, Delissea,* and *Rollandia* are considered by many scientists to be the largest group of Hawaiian plants to have evolved from a single immigrant species.

Evolution is Not Over

Evolutionary changes in Hawaiian honeycreepers did not end at some time in the past. In fact, there is evidence that rapid evolutionary changes have occurred within the past 100 years, in response to human-induced extinctions and habitat changes. Given the fact that the honeycreepers evolved over *millions* of years, to measure significant changes in *one hundred* years indicates rapid natural selection.

Here is an example of such a rapid shift:

In the early 1990s, a group of biologists compared body measurements of live *ʻiʻiwi* with museum specimens collected prior to 1900 (Smith, et al., 1995). Early studies of the *ʻiʻiwi*—prior to 1900—reported that the long, curved flowers of Hawaiian lobeliads were this bird’s preferred food. Now, however, *ʻiʻiwi* feed mainly on the open flowers of *ʻōhiʻa*, which do not have tubular, curved flowers.

What might have caused this change in diet?

Researchers point to two factors. The first is that the lobeliads, once a prominent part of the understory of Hawaiian rain forests, are now rare. During the 20th century, habitat degradation and grazing by feral ungulates induced the extinction of 25 percent of Hawaiian lobeliad species. Most of the species that remain are rare or endangered. So the preferred food of the *‘i‘iwi* is greatly reduced.

Researchers suggest the second factor influencing this dietary shift was the extinction of the *‘ō‘ō*. The *‘ō‘ō* was a Hawaiian honeyeater, another native Hawaiian bird not related to the honeycreepers. This bird was behaviorally dominant over the *‘i‘iwi*, keeping the *‘i‘iwi* from feeding heavily in the favored trees of the *‘ō‘ō*: the *‘ōhi‘a*. By 1900, the *‘ō‘ō* was extinct, and as the lobeliads declined over the course of the 1900s, the *‘i‘iwi* shifted its foraging emphasis to *‘ōhi‘a* flowers.

Birds that feed most efficiently on *‘ōhi‘a* flowers, such as the *‘apapane* and the *‘ākohekohe*, have short bills to exploit this food source. Researchers hypothesized that a shift in diet away from the long, tubular, curved lobeliad flowers to the open *‘ōhi‘a* flowers would have resulted in selective pressures which favored shorter bills over longer bills.

The biologists tested this hypothesis by comparing bill measurements and other body measurements of live *‘i‘iwi* with museum specimens collected prior to the extinction of the *‘ō‘o*. Evaluating the data they collected, they found that the upper mandible (beak portion) became shorter, while overall body size stayed the same. The results of their analysis suggest “the longer billed birds, presumably due to lower feeding effiencies on *‘ohi‘a,* were lost over time as selection favored shorter and possibly straighter bills.”

As human-induced extinctions and declines of native species continue, the structure of Hawaiian natural communities is changing rapidly. These changes open the possibility for rapid evolutionary shifts, such as the one that appears to be happening with the *‘i‘iwi*.

Ongoing Threats

Of the 17 known surviving species of Hawaiian honeycreepers, 1 is considered threatened, 10 are considered endangered, and some of these may already be extinct. What is contributing to this loss of species today?

- Habitat destruction: The Maui parrotbill is an illustrative example of the impact of habitat destruction. By the 1890s, it was already rare in the remaining *koa*-dominated rain forests. These *koa* forests were destroyed, largely by wildfires, browsing by introduced animals, and logging. Today, the parrotbill survives only in higher-elevation *‘ōhi‘a* forests, where it is an extremely rare bird.

- Avian malaria and other diseases: Like many Hawaiian honeycreepers, the rare *‘ākohekohe* is thought to be highly susceptible to avian malaria, a disease introduced early this century with nonnative birds. The disease is transmitted by a nonnative mosquito and is believed to prevent honeycreeper populations from surviving in lower-elevation forests. Mosquitos rarely occur above 1200 meters (3936 feet) elevation. Many native birds escape infection only while they remain in upper-elevation forests. Although a raise in temperature due to climate change is a factor in reducing these disease free forests.

- Predation by cats, mongooses, and rats: These animals eat native bird eggs and chicks, and sometimes even adult birds, especially those tending their young.

These pressures are happening at a rapid rate, much more quickly than many bird species can adapt. The honeycreepers that are faring the best tend to be those that can adapt to a broad range of habitats. The most common honeycreepers on Maui and in Hawai‘i are the *‘apapane* and the *‘amakihi*. Both of these birds range from the rain forests into upper-elevation shrublands and even into planted forests. As the *‘i‘iwi* shows, however, rapid evolutionary shifts are possible, and that possibility—along with efforts at habitat protection, feral animal control, and research into avian diseases—may spell survival for some of the remaining Hawaiian honeycreeper species.

Sources

Freed, L. A., “Extinction and Endangerment of Hawaiian Honeycreepers: A Comparative Approach,” in Landweber, L. F., and A. P. Dobson (eds.), *Genetics and the Extinction of Species*, Princeton University Press, Princeton, New Jersey, 1999, pp. 137-162.

Freed, L. A., S. Conant, and R. C. Fleisher, “Evolutionary Ecology and Radiation of Hawaiian Passerine Birds,” in Kay, E. A. (ed.), *A Natural History of the Hawaiian Islands, Selected Readings II*, University of Hawaiÿi Press. Honolulu, 1994, pp. 335-345.

Givnish, T. J., K. J. Sytsma, J. F. Smith, and W. J. Hahn, “Molecular Evolution, Adaptive Radiation, and Geographic Speciation in *Cyanea (Campanulaceae, Lobelioideae)*,” in Wagner, W. L., and V. A. Funk (eds.), *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*, Smithsonian Institution, Washington, DC, 1995, pp. 288-337.

Juvik, James O., “Biogeography,” in Juvik, Sonia P., and James O. Juvik (eds), *The Atlas of Hawai‘i*, 3rd ed., University of Hawaiÿi Press, Honolulu, 1998, pp. 103-106.

Medeiros, Arthur C., and Lloyd L. Loope, *Rare Animals and Plants of Haleakala National Park*, Hawai‘i Natural History Association, Hawaiÿi National Park, Hawaiÿi, 1994.

Smith, T. B., L. A. Freed, J. K. Lepson, and J. H. Carothers, “Evolutionary Consequences of Extinctions in Populations of a Hawaiian Honeycreeper,” *Conservation Biology*, Vol. 9, No. 1, 1995, pp. 107-113.

Adaptive Radiation in Hawaiian Honeycreepers: Questions on the Reading

1) Define adaptive radiation, and explain its relationship to endemic species. Give one example of adaptive radiation in Hawaiian species other than honeycreepers.

2) Why are fossil records valuable sources of information to scientists studying the evolution of native bird species?

3) Is the shift in the size of *'i'iwi* bills over the last 100 years an example of adaptive radiation in action? Explain your answer.

4) Using what you have learned about evolution and adaptation, explain why extinctions of rain forest bird species have happened—and continue to occur—so rapidly in the face of human-caused changes to native Hawaiian rain forests.