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S15-2 Food specialization and radiation of Hawaiian honeycreepers

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Abstract Hawaiian honeycreepers are renowned for adaptive radiation and diet specialization. Specialization arose from competition for the relatively few resources available in this remote archipelago and because arthropod prey sufficient to satisfy nestling protein requirements could only be captured by highly modified bills. Historically, most species fed their nestlings with larvae of the widespread geometrid moth genus, *Scotorythra*; but other invertebrates were important also. Thus the palila, *Loxioides bailleui*, a specialist on potentially toxic *Sophora chrysophylla* seeds, feeds its nestlings on *Cydia* moth larvae found inside *Sophora* seeds. *Sophora* seeds are also fed to the nestlings, and seed availability largely determines the timing and extent of breeding. By this and other means, food specialization contributed to reproductive isolation in *Loxioides* and possibly other honeycreepers. Alien threats to insect prey affect *Loxioides* populations and have hastened the extinction or decline of other specialized Hawaiian birds.

Key words Adaptive radiation, Food specialization, Hawaiian honeycreepers, Moth larvae

1 Introduction

Hawaiian honeycreepers (Fringillidae: Drepanidinae) are renowned both for the extinction crisis that endangers them and for the great diversity of bills that demonstrate so spectacularly their specialization on invertebrates, nectar, fruits, and seeds. Food is provided from among 960 flowering plant species (Wagner et al., 1999), 5 500 insect species, 310 spider species (Nishida, 2002), and about 750 land snails (Cowie et al., 1995), although very few single taxa are abundant throughout the archipelago. For example, the canopies of Hawaiian forests are dominated by less than 15 tree genera, and few of these provide staple food for honeycreepers (Perkins, 1903). Although birds find food on many shrubs and lianas, full trophic relationships are difficult to reconstruct because the feeding habits of many honeycreepers are poorly known and native plant communities, especially at lower elevations, have changed markedly since Polynesian colonization (Burney et al., 2001).

We consider that diet specialization evolved in response to competition for a limited variety of plant and invertebrate resources, and because invertebrate prey could be obtained readily when specialty foods became scarce. Certain Lepidopteran larvae (caterpillars) were accessible to birds whatever their bill shape, and they affected reproduction because they provided essential nutrients for nestling growth. Caterpillars and other easily-captured prey, therefore, were critical to the radiation of nectar, fruit, and seed specialists and to insectivores with extreme bill forms. We illustrate ecological processes involved in the honeycreeper radiation by examining aspects of divergent natural selection, competition, and reproductive isolation in the palila (*Loxioides bailleui*), the most thoroughly studied species (Banko et al., 2002a). Palilas forage primarily on the seeds of the widespread mãmane (*Sophora chrysophylla*, Fabaceae), through which they provide a living example of the evolution and consequences of food specialization.

2 Evolution of Hawaiian honeycreepers

Hawaiian honeycreepers began diverging from a cardueline finch ancestor after the emergence of the oldest large island, Kauai, 5.1 MYA (Fleischer and McIntosh, 2001). Earliest among the species to radiate were seedeaters, including the palila (Fleischer et al., 2001), in contrast to nectar specialists which first appeared 2–3 MYA (Fleischer and McIntosh, 2001). The early prevalence of finch-billed species is not surprising, given the presumed seed-eating habit of their cardueline ancestor.

A diverse array of bill forms demonstrates that many honeycreepers were food specialists. Birds with heavy, conical bills specialized on seeds that required great force to extract or crush; birds with long or short curved bills probed flowers for nectar; and others had bills of various form for extracting invertebrate prey by probing, prying, hammering, and crushing. Not all honeycreepers, however, evolved extreme bills or exploited foods that were difficult to obtain. Some, like the extant *Himatione sanguinea* and *Hemignathus* spp., have relatively short, utilitarian bills that allow them to exploit a variety of foods, including nectar and small, agile arthropod prey (Baldwin, 1953). Of the 57 or more honeycreeper species, 37% had conical, finch-like bills and foraged on seeds that were produced abundantly for many months by widespread plant species (James and Olson, 1991). Heavy-billed birds, such as the palila, specialized on seeds found within hard shells or tough, fibrous coverings. Snails (Mollusca) are also eaten by finch-billed honeycreepers, such as *Melamprosops phaeosoma* (Baldwin and Casey, 1983), and may once have been major prey for other finch-billed species.

Regardless of dietary specialization, honeycreepers relied on caterpillars, especially those of widespread *Scotorythra* spp. (Geometridae), both for nestling and adult survival (Perkins, 1913: clii). Perkins (1903) drew attention to the significance of *Scotorythra* caterpillars for 16 honeycreeper species that represent all foraging guilds and occur on all major islands. Some of the other 958 described native species of Hawaiian moths (Nishida, 2002) were also heavily exploited. For example, the palila relish a native crambid caterpillar (*Uresiphita polygonalis virescens*) found on mãmane trees (Perkins, 1903: 436), demonstrating that common caterpillar species 1) may have subsidized bird populations when specialized foods became temporarily scarce, and 2) would have been readily caught by birds with disparate bill forms and foraging behavior.

Scotorythra moths probably originated before Kauai arose from the sea (Heddle, pers. comm.), so preceding the origin of honeycreepers. Their 38 species (Nishida, 2002) were abundant and occurred on many host plants used by foraging birds (Perkins, 1913: cl-clii). Just as caterpillars influence timing and extent of breeding in Darwin's finches on the Galapagos (Grant and Grant, 1989), so *Scotorythra* and other caterpillars may have profoundly influenced honeycreeper reproduction and demography. Not only would caterpillars have provided protein needed by nestlings (Newton, 1973), but their abundance would have subsidized fledglings with poorly-developed foraging abilities as well. Indeed, specialization on nectar and fruit, which are low in protein, might not have evolved had caterpillars or other protein-rich invertebrate prey not been readily obtainable by birds with bills better suited to other foods.

Apart from caterpillars, spiders (Araneida) were also major prey for honeycreepers, especially for the smaller species (Perkins, 1913:xxxii; Baldwin, 1953: 314). Not surprisingly, some honeycreepers depend primarily on caterpillar and spider food, despite their cardueline origin. Those that do are species of *Oreomystis*, *Paroreomyza* and *Loxops*, which have relatively short, narrow bills and were historically among the most common insectivores (Perkins, 1903: 416, 418). Although some species of *Scotorythra* were periodically superabundant (Perkins, 1913: cli) and arthropods generally available year-round (Baldwin, 1953), there may have been highs and lows in prey abundance, the highs coincident with new leaves on host plants (Coley, 1983). Therefore, seeds, nectar, and fruits that were abundant for much of the year should have been attractive, such that not all honeycreepers became strictly insectivorous.

3 Case study in food specialization: the palila

Examining food specialization in the palila provides insight into the adaptive radiation of honeycreepers generally. The bill of the palila is adapted for removing mãmane pods from trees and extracting the soft embryos. After biting through the tough stem and while holding the pod with one foot against its perch, the bird bites and pulls sideways to tear apart the pod and expose the seeds (Banko et al., 2002a). Palilas forage in mãmane trees >90% of the time, and though seeds are eaten by all age classes, younger birds are initially inept and often select alternative foods provided by mãmane or other sources. In addition to seeds, caterpillars found inside mãmane pods and on foliage are important sources of protein, especially for nestlings.

Although once widespread in coastal habitats (Burney et al., 2001), palilas are now restricted to upper altitudes. They are concentrated today on the western slope of Mauna Kea, where a substantial elevation gradient results in an altitudinal wave of pod production from higher to lower levels, and so prolonged seed availability (Banko et al., 2002b). Palilas track pod ripening by moving up and down the slopes (Hess et al., 2001). Where the range of elevation is small, pods are available in shorter seasonal pulses, and palila populations there have disappeared or are declining.

Although crambid caterpillars were major prey of palilas a century ago (Perkins, 1903), they are now rare in palila habitat and have been superseded in the diet by caterpillars of *Cydia* spp. (Tortricidae), which are found within mãmane pods (Banko et al., 2002a). Parents feed *Cydia* to their young until 3–4 months after fledging, but independent juveniles, which survive at lower frequencies than adults, consume few *Cydia*. Because *Cydia* caterpillars are cryptic within mãmane pods, juvenile palilas may be naive at identifying pods that contain the caterpillars. Both mãmane seeds and *Cydia* caterpillars are rich in lipid and protein, but the seeds also contain high levels of potentially toxic alkaloids, including cytisine (Banko et al., 2002c). Palilas forage selectively on the pods of particular trees, presumably because their seeds contain lower levels of alkaloids. *Cydia* caterpillars do not sequester alkaloids from mãmane seeds and are nutritious and relatively safe for palilas of all ages.

Specialization on mãmane pods has limited the palila reproductively, as indicated by slow growth, prolonged parental dependency, courtship feeding, and close correlation between pod availability and breeding effort. Even on a nutritious diet of seeds, flower parts, and caterpillars, nestlings still require 26 days to fledge, possibly because digestion is slower for a seedeater but also because alkaloids are physiologically costly to detoxify. For example, mãmane seeds are fatally toxic to house finch (*Carpodacus mexicanus*; Carduelinae) nestlings (Banko et al., 2002c). This suggests that if hybrid nestlings were produced in a speciation scenario, they might not survive their first serving of mãmane seeds: since both sexes feed the brood, the palila parent would eventually deliver a potentially toxic meal.

Nevertheless, hybridization between palilas and other species is unlikely because mãmane seeds are fed to females by courting males. If females assess male quality by the alkaloid level of seeds fed to them during courtship, sexual selection and intra-specific competition may have accelerated differentiation and permitted sympatric speciation. At least one extinct species of finch with a bill similar to *Loxioides* was sympatric with the palila on Mauna Kea (H. James, pers. comm.), and *T. persecutrix* co-occurred with the palila on Kauai (Burney et al., 2001).

The availability of mãmane pods strongly affects the timing and frequency of palila nesting (Banko et al., 2002a). Annual pod production is highly variable, but when pods are abundant, palilas may nest for over 8 months, many pairs attempting to nest and some attempting two broods. When pods are less abundant or available for shorter periods, the nesting season is abbreviated and fewer pairs attempt to nest or re-nest.

4 Consequences of specialization for conservation

Two-thirds of all endemic Hawaiian bird species and subspecies are extinct (Banko et al., 2001). About half of all taxa disappeared within the last 1 500 years, and 24 vanished after 1825. Thirty-two of the 47 remaining taxa are endangered, and 11 of these have little or no prospect of survival. Avian malaria, avian pox, and introduced rats and feral cats have devastated the Hawaiian avifauna. It is the most specialized species that have become extinct or are seriously threatened; those with more generalized foraging habits, in contrast, tend to be more common. The conservation dilemma for extreme food specialists should be obvious.

Destruction of lowland habitats accelerated the disappearance of forest birds because many trees flowered and fruited at different times in accord with elevation (Perkins, 1903: 393). It prevented birds from tracking food availability along the original, full gradient of elevation. This phenomenon certainly applies to palila populations on the eastern and northern slopes of Mauna Kea, where mãmane forests were destroyed at lower elevations by cattle grazing (Banko, 2002b). Because forest still extends over a large range of elevation on the western slope of Mauna Kea, palilas are still able to survive there. Yet it represents only the extreme upper portion of their historic range.

Nearly all other Hawaiian forest birds have become restricted to upper elevations as well, not only because habitats and resources have been destroyed in the lowlands, but also because disease-transmitting mosquitoes are scarce above 1 500 m. Moreover, many species of parasitic and predatory insects were imported to Hawaii a century ago to protect sugar cane and other crops from caterpillar outbreaks. These biocontrol agents and other introduced pests, such as ants, spread rapidly into native forests and have decimated native caterpillars and other natural invertebrate prey of the birds (Perkins, 1913). *Cydia* caterpillars, for example, are heavily parasitized by four species of wasps, only one of which may be native (Brenner et al., 2002). Similarly, *Scotorythra* caterpillars found on mãmane foliage are heavily parasitized by five alien species of wasps and flies (Banko et al., 2002b). The incidence of parasitism is related to elevation, and at higher elevations, where palilas forage and nest more frequently, parasitism of *Cydia* is lowest (Banko et al., 2002b).

5 Conclusions

The variety of potential bird foods in the remote Hawaiian Archipelago was limited, until human arrival, by infrequent colonization by plants and invertebrates. Natural selection nevertheless produced a remarkably divergent range of bill morphologies and food specializations among the honeycreepers. The assortment of foraging opportunities arising from habitat heterogeneity may have partly overcome the potential ecological and evolutionary constraints of a limited resource base on birds. Dynamic geological processes that created the archipelago, and the resulting physiographic diversity of individual islands, influenced the evolution of many Hawaiian taxa (Carson and Clague, 1995).

Competition initially centered on seeds, reflecting the finch ancestry of the honeycreepers and preponderance of species with finch-like bills. Strong competitive pressures are suggested by the specialization of the palila on potentially toxic seeds, and the preference of other finch-billed species for seeds that, although abundant, were difficult to extract. Species probably became reproductively isolated in various ways, such as through song, other behavioral mechanisms, and allopatric differentiation (Grant and Grant, 2002). Specialization on particular foods also isolated species as populations became dependent on the phenology and distribution of preferred resources, especially those which subsidized reproduction or promoted courtship.

Reproductive isolation of the papila, for example, would be difficult to breach by species not adapted to toxic foods, such as mãmane seeds. Abundant arthropod prey sustained diet specialization when preferred foods became temporarily scarce or were nutritionally unsuitable for nestlings (e.g., nectar, fruit). *Scotorythra* caterpillars and spiders were key components of the diets of many honeycreepers (Perkins, 1913), probably because they were frequently abundant and could be captured by birds with a bill of any form. From this evidence, we infer that arthropod prey played an important role in the radiation of the honeycreepers. Survival of the extant species depends upon the continued availability of native caterpillars, as well as preferred seed, nectar, and other invertebrate resources.

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