

S15-1 An overview of feeding specialization and generalization on islands

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Abstract Land birds on small, remote islands sometimes feed in unexpected and diverse ways. Observations such as these have given rise to the idea that islands are difficult to reach; the first lucky colonists to arrive enter a competitor-free environment, to take advantage of extra resources and diversify their diets. They become generalists by responding to new opportunities. They may be driven by natural selection to generalize because resource variety, like bird diversity, is reduced on islands. Species in archipelagos are different. Evolutionary patterns are more complex than on solitary islands, more multidirectional than unidirectional. Some species display generalist behavior while others are impressively specialized. We know most about evolution in archipelagos from the study of two spectacular adaptive radiations: the honeycreepers (finches) in the Hawaiian archipelago and Darwin's finches on the Galápagos islands. Adaptation to feeding in a specialized manner on a narrow range of food resources has been facilitated by strong isolation on the archipelagos and the rarity of colonization by other bird species. Environmental change has played a largely unknown part in creating new niche possibilities. The appearance of behavioral novelties, such as tool-using by the Galápagos woodpecker finch (*Cactospiza pallida*), reflects an unpredictable element in the evolution of feeding specializations. To place feeding specializations and generalizations in an evolutionary context, a phylogeny is needed. This work has only just begun, and presents some stimulating challenges to quantify modern diets and to reconstruct ancestral ones.

Key words Foraging diversity, Specialized beaks, Novel behavior, Phylogeny, Radiations

1 Introduction

Some birds on islands are strange, and do strange things. I shall start with a bird that everyone knows but no one has seen alive: the dodo. It was a pigeon built like a goose without the power of flight. It illustrates three fundamental points about birds on islands: (1) change in feeding niche, (2) morphological trends, in this case towards massive body size and flightlessness, and (3) vulnerability to extinction. Its feeding behavior cannot be observed because it became extinct centuries ago; but contemporary island species do strange things also, and these can be observed today. We can observe tool-using behavior in the woodpecker finch (*Cactospiza pallida*) on the Galápagos islands, or the rolling, breaking and eating of booby eggs by the sharp-beaked ground finch (*Geospiza difficilis*) on the same islands, or, in the very same population, blood-drinking from wounds that the finches inflict at the base of booby wing feathers (Bowman and Billeb, 1965).

Observations such as these and many more, together with island biogeography theory, have given rise to the idea that, for birds, islands are difficult to reach. The first lucky colonists to arrive enter a competitor-free environment, and there take advantage of extra resources and diversify their diets (Grant, 1998). They may start out as generalists (Ricklefs and Cox, 1972), although there seems to be no obvious trend (Schluter, 2000), or they become generalists by responding to new opportunities. They may be driven in

the same direction by natural selection because resource variety, like bird diversity, is reduced. This is especially likely to happen if occasional temporal fluctuations in resources make food-finding difficult at times. More than a century ago, Grayson (1871) made this point when interpreting his surprising finding that hawks, owls and wrens on Socorro in the Revilla Gigedo group of Mexican islands fed largely on land crab meat.

2 Generalists on solitary islands

Species on such islands become generalists in two ways (Grant, 1999). Either all individuals are generalists in the same way (type 1a) or they are specialized in somewhat different ways (type 1b), according to age, sex, beak morphology etc. There is no good theory that tells us when and where to expect each type, probably because factors inherent within species are as important as extrinsic (environmental) factors. Nevertheless, both types of generalists exist.

2.1 Type 1a generalization

Members of this group are exemplified by the white-eyed vireo (*Vireo griseus*) on Bermuda. Crowell (1962) performed a pioneering field study by comparing the foraging characteristics of three bird species on Atlantic island, Bermuda, with their foraging behavior in similar habitats on the North American mainland. By using the information

theory statistic H as a measure of foraging niche diversity, he found that only one of the three species, the vireo, was more generalized in its foraging on Bermuda. Type 1a generalization is expressed by the absence of conspicuous foraging differences among individuals in the island population. The study also produced the insight that niche expansion involves an increase in the use of marginal resources rather than the acquisition of entirely new ones by adoption of new foraging techniques. This may be the usual mode by which niche expansion begins, perhaps by trial-and-error learning and exploitative responses to local foods within the behavioral repertoire of the birds. Later the repertoire changes.

2.2 Type 1b generalization

The alternative type 1b generalization has been described by Jiro Kikkawa and colleagues (1975) in silvereyes (*Zosterops lateralis*) on Heron Island, Australia, and more recently quantified by Werner and Sherry (1987) in a study of the Cocos finch. The distantly isolated Costa Rican island of Cocos is occupied by a single species of Darwin's finch (*Pinaroloxias inornata*) and only three other, and unrelated, species of land birds. By banding 89 individual finches and quantifying their foraging in nine types of probing and gleaning, Werner and Sherry showed that none of them fed in all nine ways. Rather, 62 spent more than 50% of their foraging activity on a single foraging behavior. The finches are individually specialized and, importantly, different individuals are specialized on different food resources or to different ways of exploiting them. The same has been found in some of their Galápagos relatives (Grant, 1999).

Despite these two well-investigated examples, there are very few comparative studies of diet diversity and foraging behavior in island populations and their mainland relatives (Grant, 1964; Morse, 1971; Martin, 1992). Even so, the direct evidence for trends towards diet generalization on islands is complemented by indirect evidence from morphology. Maximum food size is a function of beak size. As beak size increases among populations or species, maximum food size increases faster than minimum food size, with the result that the potential range of food sizes in the diet increases. Birds on islands, especially small species (Clegg and Owens, 2002; Owens et al., this symposium), tend to become larger in beak as well as body size and, by inference, their diets broaden.

3 Generalists and specialists in archipelagos

Species in archipelagos are different. They show no such trends. Evolutionary patterns are more complex than on solitary islands, more multidirectional than unidirectional. Some display generalist behavior while others are impressively specialized. Most is known about evolution in archipelagos from the study of two spectacular adaptive radiations: honeycreepers (finches) in the Hawaiian archipelago and Darwin's finches on the Galápagos islands. The

honeycreeper radiation has been extremely rapid (Schluter, 2000; Fleischer and McIntosh, 2001). From a cardueline finch ancestor, they have diversified morphologically in a manner that not only duplicates a range of passerine morphologies in other families, but also goes beyond them into novel morphological space (Lovette et al., 2002). Darwin's finch morphologies are also diverse; 14 species evolved in the last 2–3 MY, and are much more varied than extant mainland relatives (Sato et al., 1999, 2001; Burns et al., 2002). Diets diversified as well.

For understanding the evolution of diets and foraging niches, a phylogeny is needed. A simple overview of diet evolution can be gained by examining variation in diets across a phylogeny, such as the microsatellite-based phylogeny of Darwin's finches (Petren et al., 1999) or one that is mtDNA-based (Sato et al., 1999). Both show that specialized and generalized diets are interspersed among the lineages, implying multiple evolutionary origins for both.

To improve detail, quantitative data are needed. Diets of the four most recently derived ground finch species have been well characterized on the small Galápagos island of Daphne Major. Two species are specialists and two are generalists, as reflected in their positions on axes of variation of seed size and flower exploitation (Grant and Grant, 1996). Interestingly, one of the generalists, the cactus finch (*Geospiza scandens*), specializes on cactus (*Opuntia*) products when overall food supply declines to low levels (Boag and Grant, 1984). This makes it clear that the generalized diet of the other generalist, the medium ground finch (*G. fortis*), is derived, because the species itself is phylogenetically derived (Petren et al., 1999). In this case, a specialist species has given rise to a generalized one, reminiscent of the trend on solitary islands.

Schluter and colleagues have used more powerful statistical inference procedures to estimate ancestral diets in Darwin's finches and other groups of organisms (Schluter et al., 1997). Results vary to some extent, depending on the algorithm used when transition rates are constrained to be equal or not. The results are also dependent on adequate characterization of diets of all species. In terms of the theme of specialization and generalization, adequate characterization has not yet been realized for any monophyletic group of birds on islands. The analyses, limited by uncertainty, show a way forward but not a destination reached.

Substituting beak sizes and shapes for diet is an alternative to diet analysis for reconstructing ancestral states. Beak morphologies are easier to assess and better known. For example, among the Hawaiian honeycreepers, there are two specialized beak morphologies, one thin and down-curved, the other very deep. The first is a tool for probing flowers for nectar, or cracks and crevices in bark for cryptic arthropods. With its extreme evolution, some aspects of food acquisition and crushing in the basic honeycreeper diet must have been relinquished as new techniques were acquired. The deep blunt beak of the Kona finch (*Chloridops kona*) exemplifies the other bill form. It was

apparently used in a specialized way to crack the hard seeds of *Myioporium* (Perkins, 1903). The deep but narrow and hooked beak of the parrotbill (*Pseudonestor xanthophrys*) is also used to break twigs and small branches to reach cryptic insect larvae by brute force. Similar adaptations are found in mainland avifaunas, and in other island settings as well, reflecting repeated and convergent evolution from different starting points. For example, sickle-shaped beaks are possessed by the neotropical woodcreepers, Dendrocolaptidae (Raikow and Bledsoe, 2000) as well as by one of the vangids, the sickle-billed vanga (*Oriolia bernieri*) on Madagascar (Yamagishi et al., 2002).

In contrast to predictable convergence, the woodpecker finch on the Galápagos represents the idiosyncratic, unpredictable, element in evolution. In its diet, it is similar to the cryptic arthropod-exploiters of Hawaii, such as the extinct akialoa, *Hemignathus obscurus* (Perkins, 1903); but the manner in which it obtains its prey could not be more different. Rather than developing an attenuate, probing bill for grasping prey, its behavior is modified to bring the prey within reach: a twig or cactus spine is used by the bill as a tool to provoke emergence of insect larvae from their galleries deep within branches. Such a change in foraging niche through the acquisition of a new skill is very different from the marginal expansion described by Crowell (1962) and referred to earlier. It also differs from the blood-eating of the sharp-beaked ground finch, which appears to be derived from the more prosaic habit of eating ectoparasitic hippoboscids and ticks (Bowman and Billeb, 1965). Rather, it has more in common with egg-exploitation in the ground finch because egg-eating has no obvious antecedents.

How did tool-using behavior arise? According to one explanation, a twig was picked up in the trial-and-error phase of early learning and crudely manipulated, yielding some food reward. Tool-use may have improved through subsequent trials with errors and successes, and other finches may have observed and copied the behavior. Mutation affecting a genetic predisposition to behave in this way is another explanation, with social learning perhaps playing a secondary role. By experimenting with captive young woodpecker finches in the presence of tutors that did or did not use tools, Tebbich and colleagues (Tebich et al., 2001) have supported the second explanation by showing that social learning is not required for the expression and development of tool-using behavior. Trial-and-error learning, nevertheless, occurred during the development of tool-using skills in the experimental birds. This pioneering study opens up new possibilities for examining the evolution of specialized behaviors, both feeding and reproductive, on islands.

Long-term stability presumably facilitates specialization, which is why the strongly isolated Hawaiian and Galápagos archipelagos have more specialists, apparently, than the less isolated Solomon and Bismarck archipelagos (Mayr and Diamond, 2001).

4 The importance of environmental change

There is another, different problem and challenge confronting attempts to understand the evolution of feeding ecology on islands. It lies in reconstructing ancestral environments to place the reconstructed ancestral states of island birds in their correct paleo-environmental context (Grant, 2001). I illustrate the point with a single example. According to allozyme and mitochondrial DNA evidence, Darwin's finches colonized the Galápagos about 2 MYA, possibly as much as 3 MYA, at a time when the archipelago was simpler than it is now (Grant, 1999). As new islands were formed through volcanic activity under modern Fernandina, the number of islands increased and their heights and degrees of isolation changed. Moreover, global, and presumably local, climate changed from hot to cooler, then oscillated back and forth during the last million years of glacial-interglacial dynamics. Sea level fell and rose repeatedly, causing coastlines to expand and contract. Vegetation changed, possibly from Cocos island-like rainforest at all elevations to the seasonally arid vegetation at low elevations and moist forest in the highlands present today.

Throughout this period new species of plants and animals probably invaded and colonized the islands, while others became extinct. The adaptive radiation of Darwin's finches happened in the past and therefore should be interpreted in terms of the past, that is, against this backdrop of strong environmental change. For example, the recently evolved ground finches and tree finches may have evolved only after small hard seeds became abundant under a climate of seasonal aridity at low elevations and the development of *Scalesia* forests in the highlands. Presumably when that happened, some of their predecessors became extinct, for the same reason: a change in the food supply.

It is an open question whether a knowledge of past environments in a changing landscape is merely desirable or essential for understanding the evolution of birds and their foraging niches on islands. To what extent are the features of those birds explicable solely in terms of current adaptive landscapes? What is the residual variation whose explanation has to be sought in past events? I suspect the residual variation is not negligible when we ask why birds feed in some ways and not in others.

5 Conclusions

Generalized and specialized feeding of birds on islands has been reviewed here largely in the context of feeding opportunities arising from food availability. Direct quantitative data on diets are surprisingly scarce, and one obvious need is for more data on a variety of birds on many islands. Another need is for more phylogenetic reconstruction and better methods of analysis to permit stronger inferences about the evolutionary pathways of dietary diversification and change. A third need is to determine how much of the features of island birds is explicable solely in terms of

current adaptive landscapes, and how much requires a knowledge of past events.

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