

CHAPTER TEN

Reconstructing the Radiation of Darwin's Finches



This is the process grandly exemplified in the thinning out and increasing divergence and specialization of the various lines of descent in an adaptive radiation.

(Simpson 1949, p. 208)

INTRODUCTION

ADAPTIVE RADIATION is as much an ecological as an evolutionary phenomenon (Schluter 2000), as implied by the adjective “adaptive.” It results in an accumulation of ecologically diverse species through repeated speciation. In chapter 3 we referred to a graphical representation of speciation (Fig. 3.1) as an abstraction designed to capture the essence of the process from a mass of particulars. In this chapter we pay attention to the particulars that have been left out so far. They vary from one speciation cycle to another, as does the environment, which partly accounts for the diversity and helps us to understand why, for example, tree finches were ultimately derived from warbler finches and not vice versa.

As described in chapter 2, the Galápagos environment has undergone fluctuations in temperature and sea level, but with long-term trends of cooling, aridification, and increase in number of islands. The radiation of finches unfolded with an increase in number and diversity of species in a changing environment: an increase in number of islands increased the opportunities for speciation and thereby the *number* of species (Figs. 2.2 and 2.4), and a change in climate and altered vegetation increased the opportunities for *new types* of species to evolve. The net result, the product of the evolutionary process, is a heterogeneous array of species in a heterogeneous archipelago; the larger and higher the island, the more habitats it supports and the more numerous and diverse are the finch species (Abbott et al. 1977).

RECONSTRUCTING THE RADIATION

Since the exercise of interpreting the past is retrospective with limited scope for verification, several aspects of the radiation raise more questions than can be answered at present. Moreover, a study of adaptive radiation without fossils is a study of the survivors, not the whole of the radiation, unless there has been no extinction, which seems very improbable in the light of the fossil record in general (Valentine 1985, 2004). Episodic extinction is almost inevitable in a seismically and volcanically active environment like the Galápagos. Missing data on extinctions are the largest limitation on what can be achieved in attempts to interpret evolutionary history. Extinctions have been aptly described by Williams (1969) as “invisible history.”

Discussion of some parts of the radiation is therefore unavoidably speculative. We view the past through the lens of the present, and the lens is clouded and distorted. Using what is known from paleoclimatology, geology, evolution, ecology, and biogeography, we do our best to recreate the past in order to understand the present. We adopt a uniformitarian principle from geology in assuming that processes occurring in the past were fundamentally the same as those we observe today—natural selection, adaptation, competition, and introgressive hybridization. Environmental circumstances were different, however.

THE SHAPE OF THE RADIATION

Species that evolved early in the radiation differ in three ways from those that evolved relatively late: they display (a) almost the complete generic, morphological (Fig. 10.1) and ecological diversity of the whole group, yet (b) no species diversity within genera, and therefore (c) no possibilities for sympatry within genera. The early set of species comprises a warbler finch species (*Certhidea*), the Cocos finch (*Pinaroloxias*), one ground finch (*G. difficilis*), and one vegetarian finch (*Platyspiza*). Five tree finch species and an additional five ground finch species constitute the late set, and they occur in various sympatric combinations.

The sharp contrast between the early and late sets gives the radiation a structure. The structure is not expected from a simple model of species accumulation with time. In such a model the earliest species would have the greatest opportunity to produce new species similar to themselves. For example, there are five species of tree finches, hence there has been enough time for at least five (older) vegetarian finch species to evolve, differing in beak size or

CHAPTER TEN

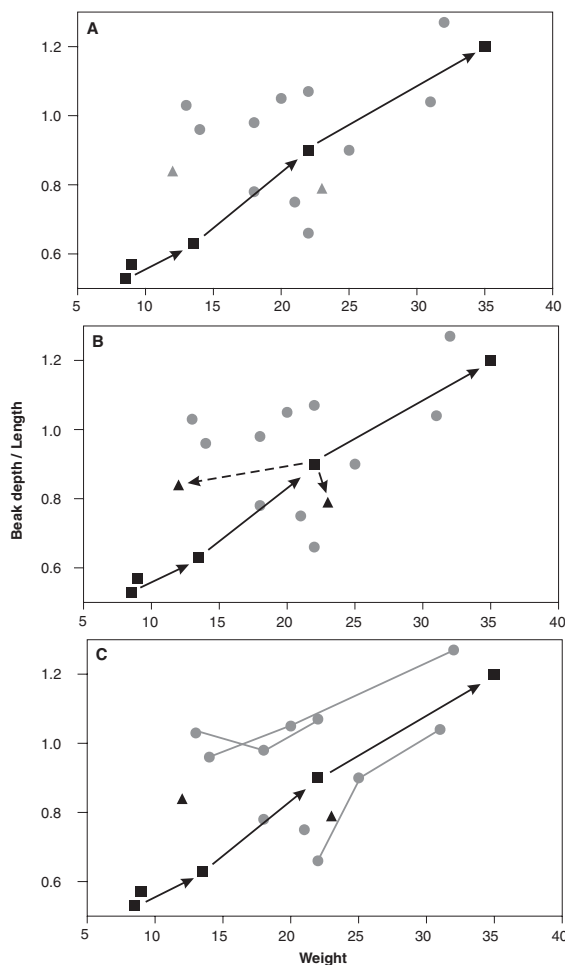


Fig. 10.1 Accumulation of morphological diversity (disparity) among Darwin's finch species on the Galápagos in three stages, A, B, and C. Upper: the early set of species span the full range of body sizes and beak shapes. The species are connected by a line on the basis of their microsatellite DNA relationships and branching points in Fig. 2.1; arrows give an evolutionary interpretation of the time course. Middle: the central point represents the highland populations of *G. difficilis*, and is connected with broken arrows to later evolving conspecific populations on the two northernmost islands and on Genovesa. Lower: triplets of related species in the late set of species are connected by lines to show that their variation is roughly parallel to the early set. For a given body size they have relatively pointed or robust beaks. Beak proportions have been calculated from mean measurements of males from Lack (1947). Weights are from Grant et al. (1985).

shape and diets and coexisting in various combinations. And yet there are no sympatric vegetarian finches, or warbler finches, or sharp-beaked ground finches, or Cocos finches. How can we account for the differences between the early and late set of species?

The singular Cocos finch is a special case and is easily explained. Isolated on a single island, it has no opportunity to diversify in separate locations. The species has been present long enough to have given rise to other species (Fig. 2.1), and its environment is varied enough to support a variety of feeding types in the population (Werner and Sherry 1987), and yet it has remained a single species under conditions suitable for sympatric, but not allopatric, speciation. These facts have been used as an argument against sympatric speciation of Darwin's finches (Lack 1947, Grant 1999, Coyne and Price 2000).

SPECIATION AND EXTINCTION

Accumulation of species is the net result of two opposing processes, speciation and extinction. If speciation and extinction can be likened to birth and death processes within populations, and their rates are assumed to be constant but not necessarily equal in a given time interval, one can use the temporal pattern of species origins derived from molecular data to see if overall speciation has proceeded at a constant or differing rate (Nee 2006, Rabosky 2006, Weir 2006, Price 2007). The Darwin's finch radiation, analyzed in this way, has been temporally heterogeneous: assuming extinction rate to have been constant, speciation was slower in the first half than in the second (Schluter 2000). Figure 10.2 illustrates the accumulation of species. After the warbler finches split into two lineages there was an apparently long time before the next two Galápagos species, the sharp-beaked ground finch and vegetarian finch, were formed.

Possible causes of low speciation rate early in the radiation are not difficult to identify. The archipelago was less heterogeneous then than now: fewer islands, less habitat diversity, fewer food types. It is more difficult to interpret the strong morphological and ecological differences among the early set in terms of contemporary evolution. In contrast, the late evolving set are easy to understand because species transformations among them were small. We discuss effects of low speciation and high extinction on the early set, first separately and then together.

CHAPTER TEN

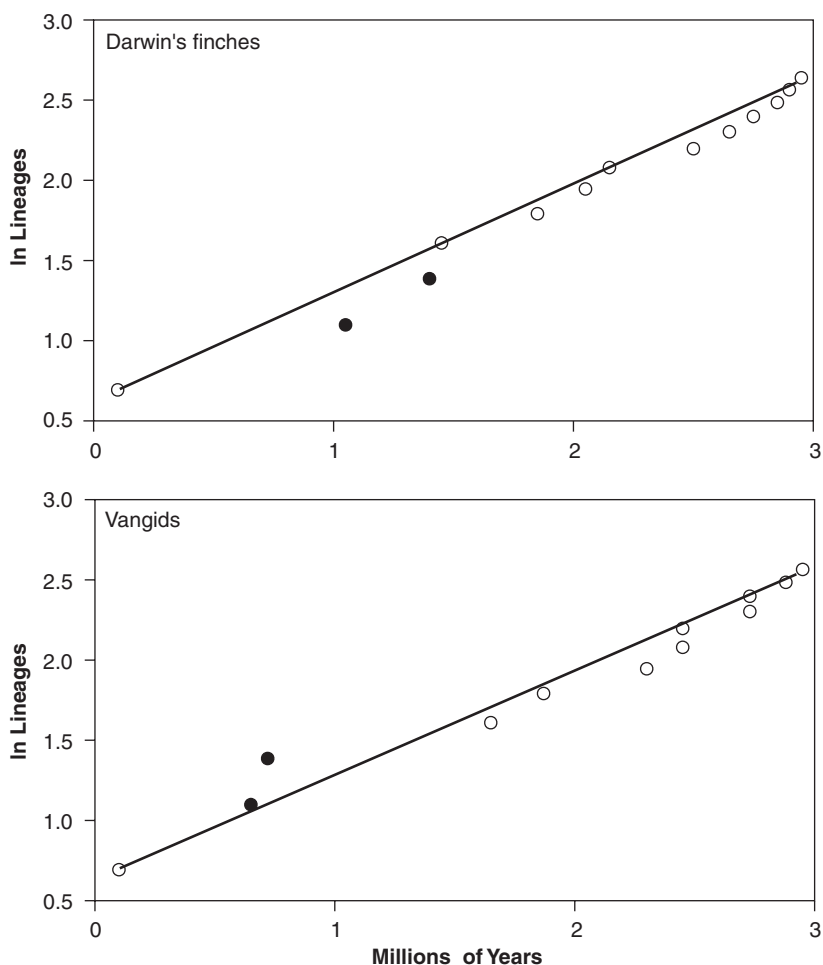


Fig. 10.2 Accumulation of species through time. After the first division of Darwin's finches into two lineages of warbler finches (bottom left in upper diagram), an unexpectedly long time appears to have elapsed before the origin of the next two species on Galápagos; points for these two (solid symbols) fall below the line drawn to illustrate a regular exponential increase in number of species. The radiation of vangids on Madagascar (lower diagram), discussed in the next chapter, displays a contrasting pattern of accumulation of species that is more rapid early than late. Based on Fig. 2.1 and RNA sequence data in Fig. 8-6 of Yamagishi and Honda (2005).

Speciation

Warbler finches, vegetarian finches, and highland sharp-beaked ground finches occupy very different niches, far apart in a hypothetical landscape of adaptive peaks and valleys. At one time under warm and wet conditions (ch. 2) these may have been the only species of finches on the Galápagos. Morphological diversification could have proceeded very rapidly and extensively as is often claimed for other radiations (e.g., Foote 1997, Harmon et al. 2003, Valentine 2004, Gavrillets and Vose 2005, Ruta et al. 2006, Seehausen 2006; see also the vangids in Fig. 10.2), but not accompanied by much speciation. Or diversification was slow and gradual, episodic rather than continuous (chs. 5 and 6), through long-term adaptive change within each lineage after reproductive and ecological isolation had evolved—so-called phyletic evolution beyond speciation (Simpson 1949). Thus, for example, vegetarian finches might have acquired their present, distinctive features either a long time ago, rapidly, or more recently, gradually.

The problem posed by both alternatives but especially by the first is to explain the large morphological gaps between species: why did evolutionary diversification not stop after a minimally sufficient difference for coexistence had arisen? After all, pronounced diversification is not inevitable, as shown by the minimal difference in morphology between the two *Certhidea* lineages. Lacking a detailed knowledge of paleocommunities of plants and arthropods, we have no answer to the question. The second alternative of gradual change seems more plausible than the first when taking into account how ecological communities generally develop by speciation and immigration (Ricklefs and Schluter 1993).

Immigration of new plants and arthropods would have aided both speciation and directional adaptive change after speciation by periodically producing new ecological opportunities for consumers. Perkins (1903) offered a similar explanation for the buildup of the honeycreeper finch fauna in the Hawaiian archipelago in terms of evolutionary responses to opportunities provided by the radiation of lobelias and an expansion of the insect fauna. On the Galápagos, climatic change permitted the establishment of arid-adapted plants, and their inferred influx provides a plausible explanation for the high speciation rate of tree finches and ground finches. The highland populations of the sharp-beaked ground finch played a pivotal role in this expansion (Fig. 10.1, middle). Originating relatively early in the history of Darwin's finches in *Zanthoxylum* forests, and somewhat generalized in morphology, they gave rise to new, arid-adapted populations (Fig. 2.1) as well as to a mini-radiation of ground finch

species, possibly also to the tree finches. Morphologically these new species diverged above and below the initial evolutionary trajectory towards blunt beaks and large size.

These ideas on the effects of new immigrants need to be tested with molecular phylogenies of key plants such as *Zanthoxylum* and *Opuntia*. There are no molecular phylogenies of Galápagos plants. All that is known at present is that *Opuntia* arrived fairly recently: Ecuadorean mainland and Galápagos *Opuntia* scarcely differ in allozymes (Browne et al. 2003).

Extinction

Extinction of species with intermediate morphologies provides an explanation for wide morphological gaps between species and for the slow rate of species accumulation in the early part of the Darwin's finch radiation. High rates of extinction among the early-formed species could give a spurious impression of slow speciation, and invalidate the approach used above. The paleontologist G. G. Simpson interpreted repeated patterns in the fossil record as a result of a "thinning out" of the species first formed in a radiation (see quotation at head of chapter). The modern view from the world of fossils is that extinction is both diversity-dependent, and environment-dependent. It tends to increase as the diversity of species increases, and is especially pronounced when the environment changes (Valentine 2004).

Extinction of some members of the early set could have been caused by habitat change associated with increasing aridity. Competition, both among the early species and with the tree and ground finch species that proliferated in the late phase, could have contributed to extinction. The later species are likely to have been more versatile ecologically, because their environments were more unpredictable, and more adaptable to a changing constellation of foods. For example, anthropogenic removal of the *Zanthoxylum* forests on the islands of Santa Cruz and Floreana resulted in the extinction of sharp-beaked ground finch populations that were largely restricted to forests dominated by this species (Grant 1999). Other ground finch species and tree finches now exploit the transformed and degraded habitat on these islands.

Extinction in recent times sheds a little light on extinctions in the past. A change in habitat is likely to have been the cause of the only known extinction of a Darwin's finch population in the absence of human influence. The

population of mangrove finches restricted to small patches of mangroves on the east coast of Fernandina became extinct in the twentieth century (Grant and Grant 1997d). The apparent cause was seismic activity, land elevation, drying of the soil, and death of the favored old individuals of white mangroves and black mangroves. There is no reason to believe that competition with other finch species was involved. For example, there are no tree finches in the mangroves on this island. Thus extinction of populations has occurred in modern times when habitat has been lost either naturally or anthropogenically (Grant et al. 2005b).

Putting these ideas together, we suggest that changing habitat conditions and competitive exclusion jointly eliminated the species in the early set most similar ecologically to those in the later set. Some species became extinct through loss of the resources they were adapted to exploit during the transformation of Galápagos vegetation from rainforest to current, heterogeneous, and partly arid-adapted, forest. The early species surviving to the present are ecologically and morphologically the most different from the late species and from each other: the smallest species of a possible set of warbler finches and the largest of a possible set of vegetarian finches (Fig. 10.1). As a consequence there is only one species per genus, hence no sympatric combinations of congeneric species.

Implications for Phylogeny

The likelihood of extinction casts a different light on the phylogeny. The representation in Figure 2.1 is the simplest estimation of history, given the genetic data of existing species. In other words it is visible history, and it assumes no distorting influences from the invisible history of missing species (extinction). However, as we have suggested, extinction of some of the early-formed species is probable, and the *Tiaris*-like ancestral species (ch. 2) itself may have been one of the casualties.

Taking extinction into consideration we suggest the following sequence. The first new species to evolve on one of the five Galápagos islands was the warbler finch. A second species originated from one of the ancestral populations, and not from the warbler finch. It was either the species that later became the Cocos finch—a proto-Cocos finch—the sharp-beaked ground finch, or a species that gave rise to both. Cocos Island was then colonized, and some time later the source population on Galápagos became extinct. Its extinction

on Galápagos is sufficient to explain the apparently long lag in speciation after the warbler finch was formed (Fig. 10.2).

The suggested relationships make sense of the plumage features of the Cocos finch, which are black in the male and brown in the female, as in *Tiaris*, other continental and Caribbean relatives, and ground finches, but unlike the green warbler finches. Furthermore, the Cocos finch and some populations of sharp-beaked ground finches share a unique rusty color in wing and under-tail coverts (Lack 1947), and have similar songs (Grant et al. 2000). In terms of microsatellite DNA, the genetically most similar populations to the Cocos finch are sharp-beaked ground finches on Pinta and Santiago.

This revised view of early phylogeny conflicts with the apparent derivation of all species from the *fusca* lineage of warbler finches. The conflict is resolved by relaxing the assumption of genetic independence after two species separated from one, an assumption that is clearly violated by hybridization of modern species (Figs. 8.6 and 8.7) and encouraged by depiction of their relationships in sharply dichotomous branching patterns (Fig. 2.1). Introgressive hybridization, a second element of invisible history, can distort the reconstruction of history if gene exchange is asymmetrical, and if some pairs of species exchange genes more than others. History is most prone to distortion when estimated from mitochondrial DNA, because it is only a single molecule, maternally inherited. We suggest introgression of alleles occurred from the *fusca* lineage of warbler finches into the proto-Cocos finch and the sharp-beaked ground finch early in their history, causing some degree of genomic blending and reticulate evolution. Phylogenetically, one lineage captured another through introgression (Fig. 10.3).

The apparently anomalous position of the Genovesa population of sharp-beaked ground finches in the phylogeny may have a similar explanation: it may be the result of a combination of a high rate of extinction of earlier species along one branch, a high rate of speciation recently, and gene exchange among the products (Figs. 2.1 and 5.4).

ADAPTIVE LANDSCAPE

Our thesis is that changes in resources, and competition for them, opened up opportunities for speciation but also caused some extinctions. Jointly they helped to give the radiation its shape. The conceptual framework of an adaptive

RECONSTRUCTING THE RADIATION

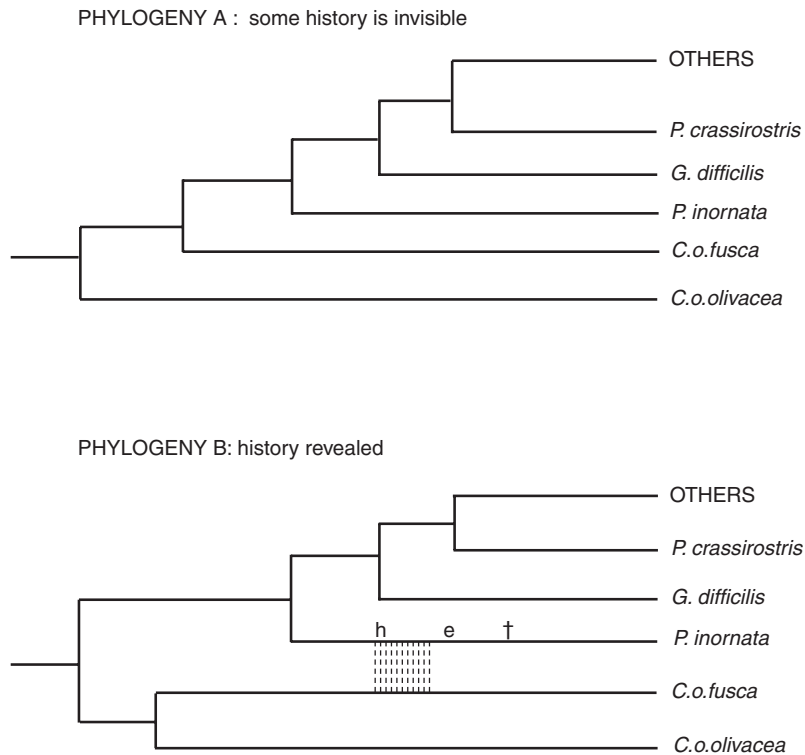


Fig. 10.3 Phylogeny with hybridization and extinction. Phylogeny A depicts the conventional representation of relationships among early-formed species of Darwin's finches in a branching diagram based on genetic similarities (Fig. 2.1). Actual branching sequences may have been different. Phylogeny B illustrates one possibility. The Cocos finch (*P. inornata*) may have hybridized (h) with one group of warbler finches, as indicated by broken lines, before some individuals emigrated (e) and colonized Cocos island; extinction (†) of the species on Galápagos occurred later. As a result *P. inornata* appears in phylogeny A to have evolved from *C. olivacea*.

topography or landscape (Fig. 10.4) exemplifies the main ideas and allows further exploration of them.

Sewall Wright (1932) initially constructed the landscape in terms of gene combinations, then Simpson (1944) modified it to deal with phenotypes. The basic idea is that the N-S and E-W axes of a landscape represent variation in two morphological characters suitable for exploiting food or other resources. The third, vertical, axis is fitness. There are fitness peaks in the landscape

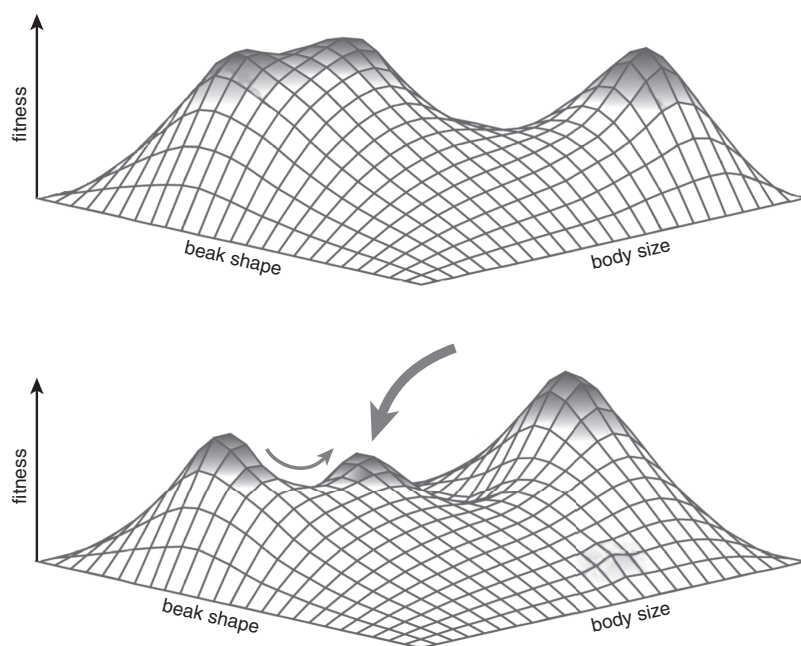


Fig. 10.4 An adaptive landscape, in which various combinations of body size and beak shape confer different fitnesses on individuals in a single island environment. A landscape with two occupied fitness peaks (upper) is converted to one with three peaks (lower) by a change in food supply. The new peak in the middle can become occupied in three ways: (a) the original population on the left-hand peak splits into two, and disruptive selection maintains them as two separated sub-populations (peak split), (b) colonization occurs from the left-hand peak (shown by a thin arrow) by a combination of genetic drift and selection (peak shift), and (c) colonization occurs by immigration from another island, as in the allopatric model of Fig. 3.1 and shown by a thick arrow (peak colonization). For this process to result in a distinct species on the middle peak, mating must be restricted to the occupants of each peak, either from the outset (c) or through evolution (a and b). If the landscape changes in reverse of the sequence shown, i.e., from lower to upper, then introgressive hybridization may be enhanced, as happened on *Daphne* (ch. 8), or a bimodal population becomes unimodal (ch. 9; but see ch. 3). Based on Grant and Grant (2002a).

owing to non-uniform distributions of resources and optimal combinations of morphological character values for exploiting them. Ascent of a population to a peak in fitness in the adaptive landscape is caused by natural selection; therefore, valleys between two peaks represent a barrier. Wright invoked random genetic drift to account for the crossing of the valley. Alternatively, according to the speciation model in Fig. 3.1 a new peak is colonized by immigrants from an island with a somewhat different adaptive landscape.

The adaptive landscape has been made operational by using seed resources on several islands to construct a general relationship between maximum density profiles (fitness) and beak sizes for all of the granivorous species of Darwin's ground finches combined (Fig. 10.5). Then, mean beak sizes of populations on each of 15 islands were predicted from peaks in the density profiles that were generated from resource distributions on each of those islands (Schluter and Grant 1984a, Schluter et al. 1985). There were two main results from this exercise. First, with few exceptions, observed average beak sizes were generally close to what they were predicted to be. Second, no more than one species was associated with a peak. One factor affecting the closeness of fit was the presence or absence of a similar competitor species. The presence of only one species in each feeding niche quantitatively defined by seed measurements is evidence for competitive exclusion. Statistically it is highly improbable that the pattern could have arisen by chance.

Adaptive landscapes are not static; they change when the environment changes. To emphasize change, Merrell (1994) coined the term "adaptive seascape" for an ever-changing configuration of fitness maxima! Not all fitness peaks existed on Galápagos islands when the ancestral species arrived. Peaks increased in number with the arrival of new plants and arthropods. As resources increased, decreased, or changed in proportions, peaks would have increased or decreased in height, shifted in position, been deformed by accretion of new resources to existing peaks, become established in new locations somewhere between existing ones or far from them, split into two (Fig. 10.4), or disappeared altogether. Such dynamics would have created new opportunities for diversification of the finches. Hybridization (chs. 8 and 9) could have contributed to the responses to those opportunities.

There are other implications of this viewpoint. First, some peaks may not be occupied because they are too far from existing peaks, despite the dynamics of peak positions, or because a previous occupant has become extinct. Unrecorded extinction may prevent us from understanding how a species became isolated

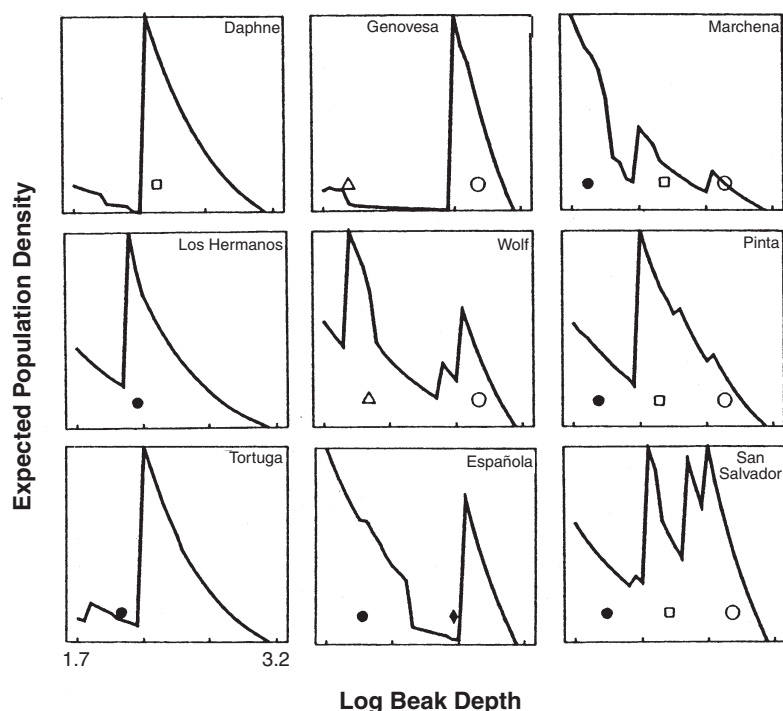


Fig. 10.5 An adaptive landscape for finches, with strong peaks, is revealed by calculating fitness as the expected population density of a solitary seed-eating finch with a particular average beak size (across the range of beak sizes) from the food supply on each island. Actual beak sizes on each island are indicated by symbols for *G. fuliginosa* (solid circle), *G. difficilis* (open triangle), *G. fortis* (open square), *G. conirostris* (solid diamond), and *G. magnirostris* (open circle). Nine examples are shown from the 15 in Schluter and Grant (1984a).

on its peak, such as appears to be the case with warbler finches. Second, the resources that determine the peaks are not entirely independent of their finch consumers: consumers and their resources coevolve. A possible example of coevolution is shown by the particularly large form of *G. magnirostris*, restricted to the only two islands, San Cristóbal and Floreana (Fig. 9.3), where the seeds of one of their food plants, *Opuntia* cactus, are exceptionally large and hard (Grant and Grant 1982). The evolution of large seed size as a result of directional evolutionary pressure exerted by the finches would have fed back on the finches, resulting in a selective favoring of large finches that could crack them.

In theory this evolutionary mechanism could have contributed to peak splitting (Fig. 10.4).

The adaptive landscape was developed by Wright (1932) as a metaphor for the evolution of a population in a heterogeneous environment. Although not intended for this, it can also stand as a metaphor for adaptive radiations that begin when a mountain barrier, valley, or sea is crossed and a substantially new realm of peaks—an archipelago of peaks—becomes accessible.

A PATTERN OF ECOLOGICAL SEGREGATION

As species accumulate in an adaptive radiation, competitive interactions are likely to increase and become more intense (Perkins 1903, Simpson 1949) unless the diversity of resources increases through immigration at a faster rate than does the diversity of consumers. Competition between species is minimized by occupation of different habitats, or specialization on different food types or food sizes within a habitat through evolutionary change in beak morphology (Perkins 1903, Lack 1947, Amadon 1950, Pratt 2005). Thus the question arises, is there predictability in the order in which ecological segregation evolves in a radiation? Diamond (1986) concluded from a study of montane birds in New Guinea that habitat separation of closely related species precedes the evolution of dietary differences. Some support has been found from other studies of birds (Richman and Price 1992; also, Richman 1996, Price et al. 2000) as well as lizards (Losos 1994, Losos et al. 1998).

In one respect the Darwin's finch radiation is consistent with this pattern. Species formed early in the radiation occur together less often than later ones do. Warbler finches occur either in moist upland forest (*olivacea* lineage), or mid-elevation and lowland forest (*fusca* lineage). Vegetarian finches occur mainly in transition forest at middle elevations, and the sharp-beaked ground finches occupy *Zanthoxylum* forest above the transition forest (Plate 7). However, species in the early set are separated also by food type and food size, therefore determining which of these segregating modes came first is not possible. Once again, extinction has possibly deprived us of the missing links that would help to answer the question of which came first. As for the late set of species, tree finches are concentrated in the moist highlands where different species co-occur, and ground finches are concentrated in arid lowlands and occur together, but members of the two genera can be found in the same habitat in

CHAPTER TEN

the breeding season, for example on the top of the highest island, Fernandina. They are ecologically segregated by habitat to some extent, but conspicuously segregated by food type and size. If the ecology of recently formed species reflects the early and now missing stages of diversification, segregation by niche precedes segregation by habitat. This has been found in a recent analysis of some plant species (Ackerly et al. 2006).

SPECIALIZATION

Perkins (1903) developed the idea that the Hawaiian honeycreeper finch radiation proceeded by successive specializations in beak morphology to the foods provided by lobelias and arthropods. Simpson (1949) believed that increasing specialization is one of the most widespread features of evolution, and Lack (1947) applied the idea to Darwin's finches when interpreting the adaptive radiation. In fact there is no clear pattern among the finches, although the subject has not been investigated as fully as possible. On the one hand, the species with the most specialized feeding habits evolved somewhat late in the radiation. The woodpecker finch is the best example. It uses a cactus spine or twig as a tool to extract cryptic arthropod prey (Plate 29). Sharp-beaked ground finches are another example. On the island of Wolf they peck at the developing wing feathers of seabirds and drink the blood (Plate 14). On the other hand, there is a tendency for the early set of species to be restricted to a single habitat more than the later set. Some early specialists may have become extinct; specialists are more vulnerable to ecological disturbance than generalists. Schluter (2000) analyzed several sets of data from different adaptive radiations including Darwin's finches and concluded that there is no quantitative support for the proposed trend. Simpson's statement about "divergence and specialization" would be better recast as divergence and adaptation to new resources.

THE BUILDUP OF COMPLEX COMMUNITIES

The contemporary avian community on Galápagos has been built up from a simpler one by evolutionary generation of diversity of finches and mockingbirds (*Nesomimus* spp.), together with immigration of nine other terrestrial species from the continent. Apart from the yellow warbler (*Dendroica petechia*),

the others—dove (*Zenaida galapagoensis*), cuckoo (*Coccyzus minor*), martin (*Progne subis*), hawk (*Buteo galapagoensis*), flycatchers (*Myiarchus magnirostris* and *Pyrocephalus rubinus*), and owls (*Tyto alba* and *Asio flammeus*)—are ecologically very different from finches and mockingbirds, and from each other. This may reflect selective establishment of immigrant species from among those that have reached the Galápagos islands. In other words, food supply, habitat requirements, and competition have guided the development of the whole terrestrial avian community, and not just the Darwin's finch component.

A reduction and simplification of the environment could set this process in reverse. Conversion of forests to agriculture and introduction of alien vertebrates have jointly resulted in the extinction of some populations of finches (Grant et al. 2005b). And now there is deep concern over the possible effects of avian malaria (*Plasmodium*), should it arrive, in the light of experience in Hawaii, where it has had a major impact on the endemic honeycreeper finch fauna (van Riper et al. 1986). The mosquito vector, *Culex quinquefasciatus*, is already present in Galápagos (Whiteman et al. 2005). Perhaps more seriously, *Philornis downsi*, a nest parasitoid, is more than a potential threat, it is a real threat. The larvae of this dipterous fly kill finch nestlings, and have had a large impact on reproduction of finch populations in both highlands and lowlands of large islands (Fessl and Tebbich 2002, Fessl et al. 2006). This shows all too clearly that community buildup in the past depended on the presence of suitable habitat and the absence of enemy organisms.

SUMMARY

In this chapter we attempt to interpret the radiation of Darwin's finches by paying attention to the ecological circumstances in which different speciation cycles took place. The radiation unfolded with an increase in number and diversity of species in a changing environment, and it was molded by natural selection, introgressive hybridization, and extinction. An increase in number of islands increased the opportunities for speciation and thereby the *number* of species. A change in climate and altered vegetation increased the opportunities for *new types* of species to evolve. Species that evolved early in the radiation differ in three ways from those that evolved relatively late: they display (a) almost the complete generic, morphological, and ecological diversity of the whole group, yet (b) no species diversity within genera, and hence (c) no

CHAPTER TEN

sympatry within genera. These differences can be accounted for either by low speciation rates or by a high rate of extinction of early species. It is not possible to distinguish their separate effects because neither is directly known. Nevertheless, there are reasons to suggest that both processes have been at work: speciation was probably slow in the early stages of the radiation because ecological opportunities were limited, and extinction of some of the early products of the radiation was caused by the combined influence of competitors and changing habitat conditions. There is no clear pattern of increasing specialization, in contrast to an earlier suggestion that increasing specialization is typical of adaptive radiations. A recurring theme of the chapter is that extinction, both anthropogenic and natural, obscures some aspects of the radiation. Extinction, like introgressive hybridization early in the radiation, is invisible history. Allowance for both extinction and introgression alters the interpretation of the early sequence of the radiation given in chapter 2.