

What Darwin's Finches Can Teach Us about the Evolutionary Origin and Regulation of Biodiversity

B. ROSEMARY GRANT AND PETER R. GRANT

Darwin's finches on the Galápagos Islands are particularly suitable for asking evolutionary questions about adaptation and the multiplication of species: how these processes happen and how to interpret them. All 14 species of Darwin's finches are closely related, having been derived from a common ancestor 2 million to 3 million years ago. They live in the environment in which they evolved, and none has become extinct as a result of human activity. Key factors in their evolutionary diversification are environmental change, natural selection, and cultural evolution. A long-term study of finch populations on the island of Daphne Major has revealed that evolution occurs by natural selection when the finches' food supply changes during droughts. Extending this finding to the past, we discuss how environmental change has influenced the opportunities for speciation and diversification of finches throughout their history: The number of islands has increased, the climate has cooled, and the vegetation and food supply have changed.

Keywords: adaptation, natural selection, speciation, song learning, Galápagos history

B iologists are increasingly interested in diversity. One major source of interest is the conservation of biodiversity in a world threatened with anthropogenic habitat destruction and environmental pollution. A second major source of interest is the regulation and maintenance of existing biodiversity by natural processes and the functioning of this biodiversity in units that vary from small communities to large ecosystems. Finally, the biodiversity puzzle has a third piece, without which our understanding is bound to be incomplete: the evolutionary origins of diversity. Reduced to its simplest form, this is the Darwinian question of how new species arise and multiply. This question is the main focus of this article, and we illustrate our points with Darwin's finches of the Galápagos Islands.

Some organisms are unusually suitable for answering particular questions. The squid, for example, has served neurobiology well because it has a giant axon; *Drosophila* species have contributed much to cytogenetics because of the giant chromosomes in their salivary glands; and *Arabidopsis*, *Caenorhabditis*, and a few other small organisms have been well chosen to investigate the construction of entire genomes. Darwin's finches are particularly suitable for asking evolutionary questions about adaptation and the multiplication of species: how these processes happen and how to interpret them.

All species of Darwin's finches are closely related, having derived recently (in geological terms) from a common

ancestor. They live in the largely undisturbed environment in which they evolved, and none has become extinct as a result of human activity. Consequently, whatever we can learn about their ecology and evolution gives us insights into the process of speciation under entirely natural conditions. Populations of the same species occur on different islands, and in some cases they have different ecologies. This allows us to investigate the reasons for their divergence. Closely related species occur together on the same island and differ. This allows us to investigate the nature of the reproductive barrier between them and the question of how and why species stay apart. Thus, considering populations across the entire archipelago, we can see all stages of the speciation process, from start to finish, at the same time.

In this article we survey the evidence from field studies of the ecological causes of diversification. The explanation for

B. Rosemary Grant (e-mail: rgrant@princeton.edu) is a senior research scholar and professor in the Department of Ecology and Evolutionary Biology, and Peter R. Grant is the Class of 1877 Professor of Zoology, at Princeton University, Princeton, NJ 085440. They have studied the ecology, behavior, biogeography, and genetics of Darwin's finches for the last 30 years. This article is an expanded version of a plenary address delivered at the 53rd annual meeting of the American Institute of Biological Sciences, held in Arlington, Virginia, 22–24 March 2002. The title of the symposium was "Evolution: Understanding Life on Earth." © 2003 American Institute of Biological Sciences.

diversification involves natural selection, genetic drift, introgressive hybridization, and genetic as well as cultural evolution. Linking all these factors are the frequent and strong fluctuations in climatic conditions, between droughts on the one hand and extremely wet (El Niño) conditions on the other. An important conclusion of this study is that environmental change is an observable driving force in the origin of new species. Using information from the study of contemporary finches, we then turn to questions of how and why their adaptive radiation unfolded in the way that it did. We focus on how environmental change in the past has guided the multiplication of finch species. Whereas the microevolutionary principles were probably the same throughout the finches' radiation, the circumstances differed in important ways at different times. General principles coupled with specific circumstances explain the particular features of the radiation.

The pattern of adaptation

At least 14 species of Darwin's finches were formed in the last 2 million to 3 million years in the Galápagos archipelago and on Cocos Island. They stand as a model of adaptive radiation, that is, the production in a short period of time of many species from one occupying different ecological niches (Schluter 2000). Figure 1 shows the four points of the Darwin's finch compass to illustrate the finches' diversity, and figure 2 shows three closely related species to illustrate how similar the intervening species are. That similarity makes it relatively easy to reconstruct the evolutionary transition from one species to another. Darwin (1842) wrote about this phenomenon 7 years after he, FitzRoy, and their assistants collected the first specimens: "The most curious fact is the perfect gradation in the size of the beaks of the different species of *Geospiza*.... Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might fancy that, from an original paucity of birds in this archipelago, one species has been taken and modified for different ends" (p. 458).

Translated into the modern language of evolutionary biology, "modified for different ends" means adapted by natural selection (figure 3). The modern evidence for this begins with an association between beak size and diet (Lack 1947, Bowman 1961). There is a strong relationship between the beak size of ground finch species and the maximum size and hardness of the seeds that the birds can crack (figure 4). The association between beak size and diet is most obvious when comparing the species that have contrasting morphology, such as the insectivorous small warbler finches (about 8 grams [g]) and the granivorous large ground finch (about 30 g). It is less obvious when comparing populations of the same species on different islands. Nevertheless, different populations of the sharp-beaked ground finch, *Geospiza difficilis*, feed in different ways on different foods with beaks of different size and shape. On the high islands of Santiago, Fernandina, and Pinta they have relatively blunt beaks and feed on arthropods and mollusks, as well as fruits and seeds in the dry

season. On the low island of Genovesa, where their beaks are much smaller, they are more dependent on small seeds, as well as on nectar and pollen from plants, including the *Opuntia* cactus. Apparently uniquely on the low island of Wolf, they exploit seabirds (boobies, *Sula* spp.) in two dramatic ways. First, they kick the booby eggs until the eggs fall or hit a rock and crack, enabling the finches to open them and consume the contents. They also inflict wounds at the base of the sitting boobies' wing feathers and consume the blood. On this island the finches' beaks are long.

In contrast to the sharp-beaked ground finches, birds with large robust beaks, such as the large tree finch, *Camarhynchus psittacula*, do not probe *Opuntia* flowers or poke at eggs. Instead, the beak of this finch is a tool for tearing bark and crushing twigs and small branches—a beak modified for a different end. These examples illustrate some of the ways that Darwin's finches vary in beak morphology and are versatile in their feeding habits. This versatility is fostered by ecological opportunity and impelled by food scarcity in the dry season and in dry years.

As evidence of adaptive diversification, associations like this do not satisfy everyone, because causality can be argued from beaks to diets as well as from diets to beaks. For example, it can be said that finches feed in different ways because they have different beak sizes and shapes (e.g., Newton 1967). They surely do, but this begs the question of why the species' beaks differ in the first place. Another objection has been raised on the grounds of insufficiency of evidence. When David Lack (1947) argued that evolution had caused the fit between birds' beaks and their food, an ecologist commented, "The problem, for instance, of whether certain specific characters (e.g. beaks of *Geospizinae*) are or are not adaptive (vague term) is one involving studies of field populations, genetics, and variation. It is a problem which might be largely solved by teams of workers dealing for a number of years with a particularly favourable example. It is not one, I think, which can be settled in a four months stay, even if supplemented by the examination of skins in museums" (Richards 1948, p. 84).

Without knowing about this critique at the time, we picked up the challenge 30 years ago. Over the years the team consisted of Ian Abbott, Peter Boag, Trevor Price, Lisle Gibbs, several assistants, and ourselves. Our study took place on the island of Daphne Major—a particularly favorable location, although one would not think so judging from its steep topography (see the photograph on p. 970).

Adaptation as a process

By virtue of its small size (0.34 square kilometers [km]), moderate degree of isolation (8 km from the nearest island), undisturbed habitat, and resident populations of finches, Daphne Major is a particularly favorable location for studying Darwin's three essential ingredients of adaptive evolution: variation, inheritance, and selection. We accomplished this by capturing and measuring many finches to determine phenotypic variation, comparing offspring with their parents to determine inheritance, and following their fates across years

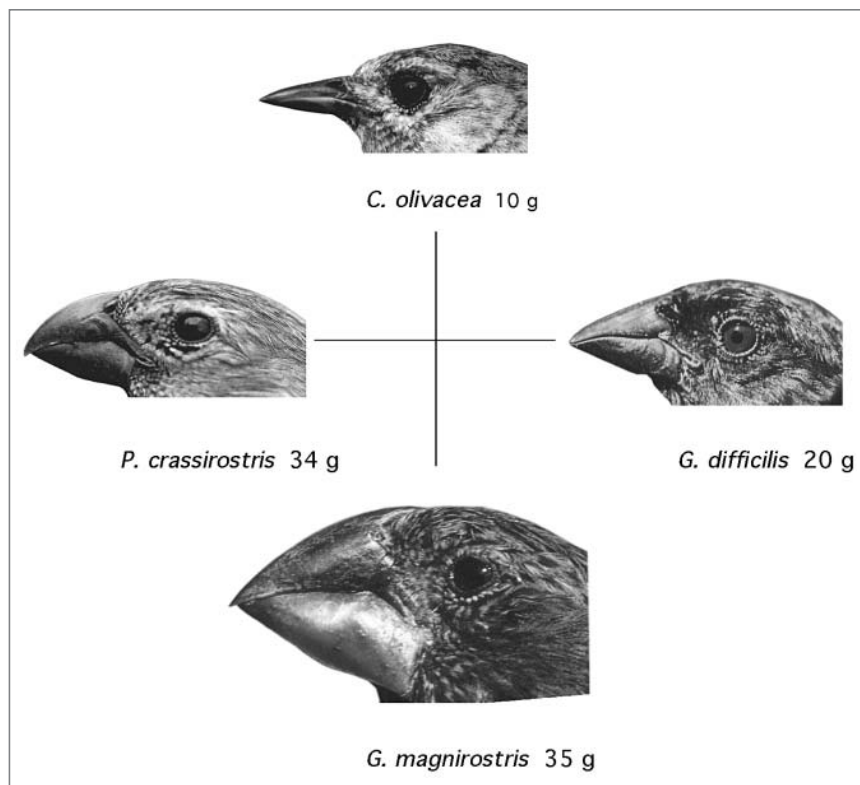


Figure 1. Four points of the Darwin's finch compass. Species with contrasting morphology (*Certhidea olivacea*, *Geospiza difficilis*, *Geospiza magnirostris*, and *Platyspiza crassirostris*) show the range of sizes and shapes in beaks, from small to large and from blunt to pointed. Photographs: B. Rosemary Grant and Peter R. Grant.

to detect selection. We found pronounced heritable variation in beak size and body size within populations of the medium ground finch (*Geospiza fortis*) and the cactus finch (*Geospiza scandens*). We also found that when the environment changes, some of the variants in each population survive while others die. This amounts to a vindication of David Lack's views on adaptation.

Birds with small beaks and small body size suffered selective mortality in 1977, during a severe drought (figure 5). The larger members of the medium ground finch population survived on a diet of large, hard seeds, which increasingly dominated the food supply as a result of an initial preferential consumption of small seeds. Smaller birds, lacking the mechanical power to crack the large seeds of *Tribulus cistoides* and *Opuntia echios*, died at a higher rate than large birds. An evolutionary response to directional natural selection followed in the next generation (figure 5), because beak size variation is highly heritable (Keller et al. 2001).

Natural selection in the opposite direction, with small birds surviving disproportionately, occurred 8 years later. The island experienced a major, prolonged El Niño event from November 1982 to August 1983. The abundant rain and high temperatures transformed the vegetation and food supply of the finches, and they bred for 8 months as opposed to the usual 1 or 2 months. Vines and other plants multiplied and

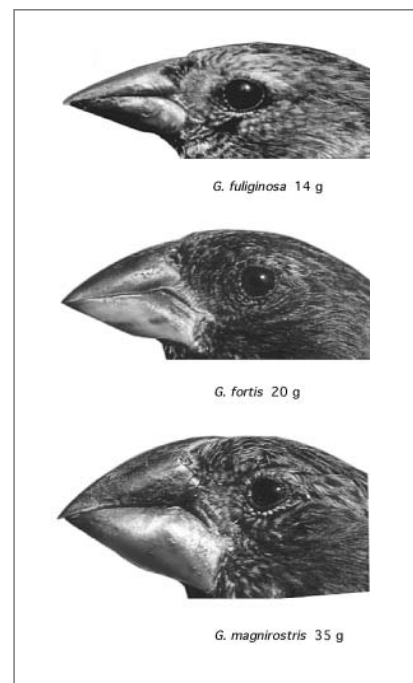


Figure 2. Three recently evolved species of Darwin's finches (*Geospiza fuliginosa*, *Geospiza fortis*, and *Geospiza magnirostris*) differ principally in size, but also in beak shape. Photographs: B. Rosemary Grant and Peter R. Grant.

spread, smothering the low-growing *Tribulus* plants and *Opuntia* cactus bushes. The seed supply became dominated by small seeds, and seeds of *Tribulus* and *Opuntia* became scarce. When the island entered the next drying-out episode during the drought of 1985, the supply of seeds fell, and so did the numbers of finches from high points in the productive years of 1983 and 1984. Large birds died at the highest rate; hence, the medium ground finches that were small, with relatively pointed beaks, were selectively favored.

Thus selection oscillates in direction. We have observed this repeatedly over the full 30-year period (Grant and Grant 2002a). As a consequence, neither the medium ground finch nor the cactus finch has remained morphologically constant or static. In fact, the mean body size and beak shape of the two species are not the same now as they were at the beginning of the study (figure 6). In an environment subject to climatic and floristic change, the finches have changed (evolved). We have directly observed the sort of adaptive change that is normally only inferred from a comparison of related populations differing in mean morphology.

Summarizing, this study has taught us four things about natural selection:

- It is an observable, interpretable, and repeatable process in a natural environment.

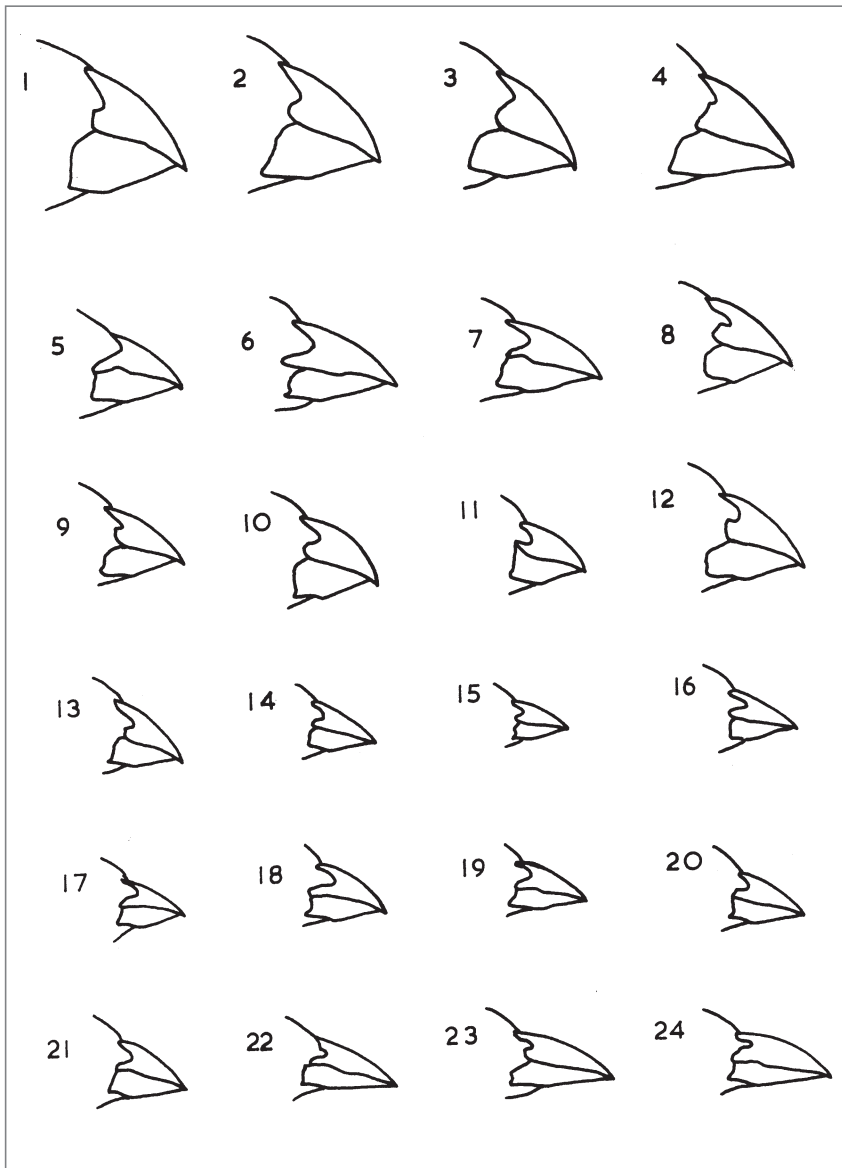


Figure 3. The intergradation of beak sizes and shapes, illustrated with outlines of the six species in the genus *Geospiza*. 1–3, *Geospiza magnirostris*; 4–7, *Geospiza conirostris*; 8–13, *Geospiza fortis*; 14–15, *Geospiza fuliginosa*; 16–21, *Geospiza difficilis*; 22–24, *Geospiza scandens*. Illustration by Swarth (1931), from Abbott and colleagues (1977).

- It oscillates in direction.
- It happens when the environment changes.
- It has evolutionary consequences (adaptive change).

Almost 100 years after Darwin's visit to the Galápagos, a systematist, Harry Swarth, came close to suggesting that evolution was not over and done with but could actually be witnessed when he wrote that "the extraordinary variants that crop up in a series [of museum specimens] give an impression of change and experiment going on" (Swarth 1934). Based on the evidence of Darwin's finches, evolutionary changes are indeed going on.

Speciation: The beginning

Speciation begins with the divergence of a population and is completed when two populations that have diverged on different islands establish coexistence with little or no interbreeding (Mayr 1942, Grant 2001). We obtained insight into the initial process of divergence on Daphne Major, thanks to a highly fortuitous circumstance: the founding of a new population.

The large ground finch (*Geospiza magnirostris*) became a breeding member of the community in late 1982, when two females and three males began to breed. In preceding years we had observed immigrant members of this species on the island in the dry season, but when the rains began they disappeared, presumably returning to their island of origin to breed. Not so in El Niño! The breeding birds produced 17 fledglings in 1982–1983, but only one of the breeding pairs produced the next generation. A daughter bred at different times with two brothers, one of which can be ignored because the offspring did not survive to breed. Thus, the population was effectively founded by a single pair, and the next generation comprised a sister–brother pair. We have followed the fate of this population ever since (Grant et al. 2001). There are now 30 to 40 breeding pairs on the island.

Observations of a newly founded population go to the heart of the question of how biodiversity generation begins. Environmental change appears to have been a key factor in facilitating population establishment and subsequent exponential growth. The *G. magnirostris* population experienced a genetic bottleneck (microsatellite allelic diversity fell), and inbreeding depression occurred, as shown by the relatively poor survival of the 1991 cohort. Small additional changes were caused by natural selection on beak morphology and probably by genetic drift. All of this is to be expected, but some other features were surprising. Immigration did not occur just once but repeatedly, especially in the 1990s. With one exception, immigrants that stayed to breed came not from the obvious and closest potential source (Santa Cruz Island) but mainly from one farther away (Santiago), as revealed by their microsatellite DNA. A major change took place in the frequency of song types in the population. This change was initiated by a single male that bred for the first time in 1991. In addition to this nongenetic, culturally transmitted contribution, he introduced a total of 11 new alleles at the 16 microsatellite loci surveyed.

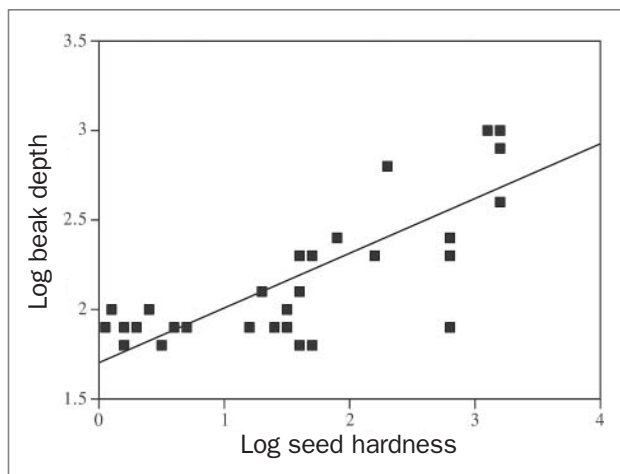


Figure 4. As the average beak depth of a population of granivorous *Geospiza* species increases, so does the maximum size and hardness of the seeds they can crack. Based on Schluter and Grant (1984).

Thus, while environmental change was the key factor that triggered the founding of a new population, some idiosyncratic genetic and nongenetic factors determined the fate, development, and composition of the population. Even though one individual made a large contribution to the population, overall changes were relatively small in magnitude, for three reasons: Selection pressures were weak, the population did not remain small enough for random genetic drift to be effective, and continuing immigration would have retarded divergence. If the case of *G. magnirostris* can be considered representative of how speciation begins, we would have to conclude that it starts slowly, with small steps.

Speciation: The end

Speciation is completed when two populations that have diverged in allopatry can coexist with little or no interbreeding. Medium ground finches and cactus finches occupy different ecological niches, although their diets overlap. The ecological differences presumably permit coexistence in sympatry, in an environment (e.g., Daphne Major) whose food supply fluctuates in abundance and composition. To paraphrase David Lack (1947), the species are ecologically isolated through niche differences that evolved by natural selection in allopatry. The differences may have been enhanced by selection in sympatry, thereby reducing interspecific competition for food. But how do the species maintain coexistence without interbreeding? What are the differences that keep them reproductively isolated, and how did the differences evolve?

Members of the group of closely related ground finch species do not differ in plumage or courtship behavior, but they do differ in beak morphology, and they differ conspicuously in song (Grant 1999). These two sets of cues, visual and vocal, have been shown in separate field experiments to be used by finches in discriminating between their own and

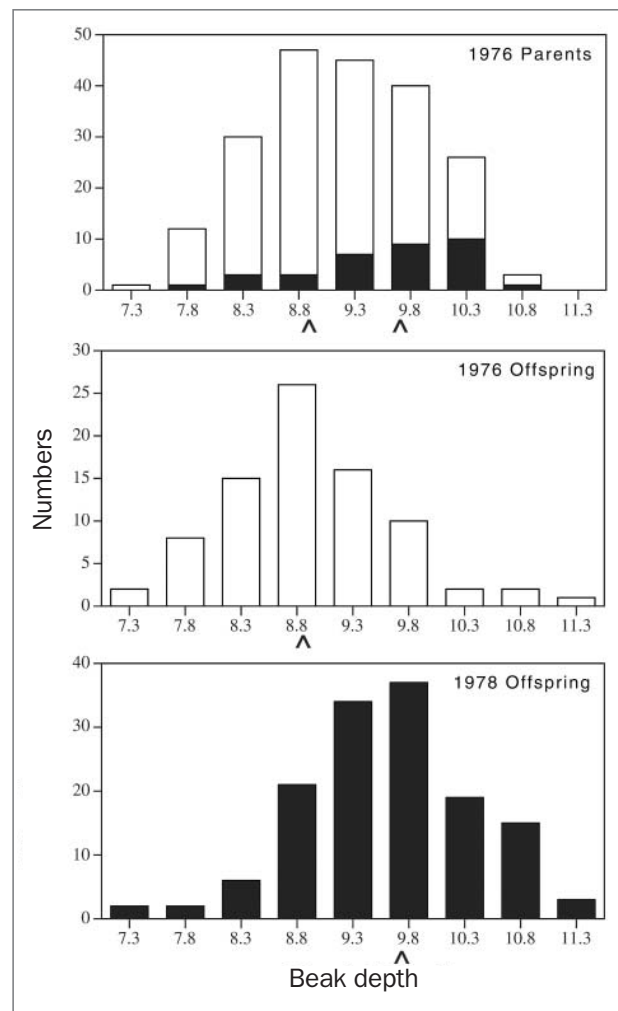


Figure 5. Evolutionary change in beak depth in the population of *Geospiza fortis* on the island of Daphne Major. The upper panel shows the distribution of beak depths in the breeding population in 1976, with the survivors of the 1977 drought that bred in 1978 indicated in black. The difference between the means, indicated by a caret, is a measure of the strength of natural selection. The middle and lower panels show the distributions of beak depths of fully grown offspring hatched in 1976 and 1978, respectively. Evolutionary change between generations is measured by the difference in mean between the 1976 population before selection and the birds hatched in 1978.

other species (Ratcliffe and Grant 1983a, 1983b, 1985). Thus, part of the answer to the question of reproductive isolation is that it evolves as a consequence of adaptive evolution of beak sizes and shapes in allopatry. The other part, centered on song, is more complex.

Song differences play a major role in keeping species apart. Like beak differences, song differences presumably arise through divergence in allopatry for reasons that are not entirely clear. Song is an interesting trait because it is culturally, and not genetically, inherited. We know this from a few



Daphne Major, a volcanic remnant in the Galápagos archipelago, is the site of the authors' long-term study of evolution in Darwin's finches. Photograph: David Parer.

experiments with captive birds (Bowman 1983), supplemented by field observations of songs of offspring, parents, and even grandparents (Grant and Grant 1989, 1996). Only males sing an advertising song; it is simple and is sung unaltered throughout life, which may be as long as 16 years. Most sons sing the same song subtype as their fathers, while a minority sing a different song subtype that is sung by other male members of the same population. Thus, song is acquired through learning early in life in a process that resembles imprinting; it is generally acquired from fathers during the period of parental dependence, in association with parental morphology. By their pairing patterns, females give evidence of learning song at the same time and from the same sources.

Rare exceptions to these rules provide additional valuable information on the role of learning and its bearing on the question of what keeps species apart. Once again, environmental change associated with an El Niño event has provided crucial information. Medium ground finches and cactus finches hybridize rarely. Before 1983 the hybrids died without breeding, at a time when most of the “pure” species produced in the same years also died without breeding. The El Niño event of 1983, resulting in an abundance of small seeds, altered the environment in a way that was favorable to the survival of the hybrids. The hybrids that were produced in 1983 backcrossed to medium ground finches in 1987, and others that were produced in 1987 backcrossed to cactus finches in 1991. The direction of backcrossing differed because in 1983 the hybridizing male was a cactus finch that sang a medium ground finch song, whereas in 1987 the hybridizing males were cactus finches that sang cactus finch songs. Sons of all families sang the same song as their fathers, and daughters in each case mated with males that sang the same song type as their fathers.

Hybridization is sometimes the result of heterospecific singing through apparent misimprinting. The causes of misimprinting and hybridization are idiosyncratic and difficult to determine. They include extra-pair mating, interspecific takeover of nests with eggs, and dominant singing of a close neighbor. Ecologically, the significant feature is a change in the environment that has facilitated the introgression of genes. F_1 hybrid and backcross survival is not intrinsically lower than the survival of the parental species, and there is no sign of diminished fitness when hybrids breed. In fact, in the 1990s and up to the present, the flow of genes from the medium ground finch to the cactus finch population has contributed to a decrease in mean body size and a blunter beak morphology of cactus

finches (Grant and Grant 2002a). The barrier to gene exchange erected by song differences has been breached, and environmental change appears to have been the most important factor.

To summarize, the coexistence of finch species is facilitated by divergence in beak morphology and song. Beaks diverge under natural selection, but why songs diverge is less clear. Cultural drift, a process of random change in culturally transmitted (learned) traits, is probably involved, and sexual selection may be involved as well. The end point of speciation is the complete absence of gene exchange. Many, if not all, coexisting populations of Darwin's finches have not quite reached that point, although they function as species by remaining distinct even in the face of occasional gene exchange. This offers two important lessons. First, species diverge in mate preferences before genetic incompatibilities evolve. Second, different populations can function as biological species before they would be recognized as species solely on the basis of genetic distinctness.

History: The initial colonization

The present is known; the past is inferred. To understand the past of Darwin's finches, the first question that needs to be addressed is when the radiation began, because the answer sets the boundary on relevant Galápagos history. In the absence of fossils, genes are our best source of information about this history (Price et al. 2000). The closest genetic relatives of Darwin's finches on the South American continent, in Central America, and in the Caribbean are a group of seed-eaters (*Tiaris* and relatives) allied to tanagers (Sato et al. 1999, Burns et al. 2002). Darwin's finches diverged from them in the last 2 million or possibly 3 million years, according to calculations based on an assumed molecular clock applied to mitochondrial DNA and allozyme data (Grant 1999). The

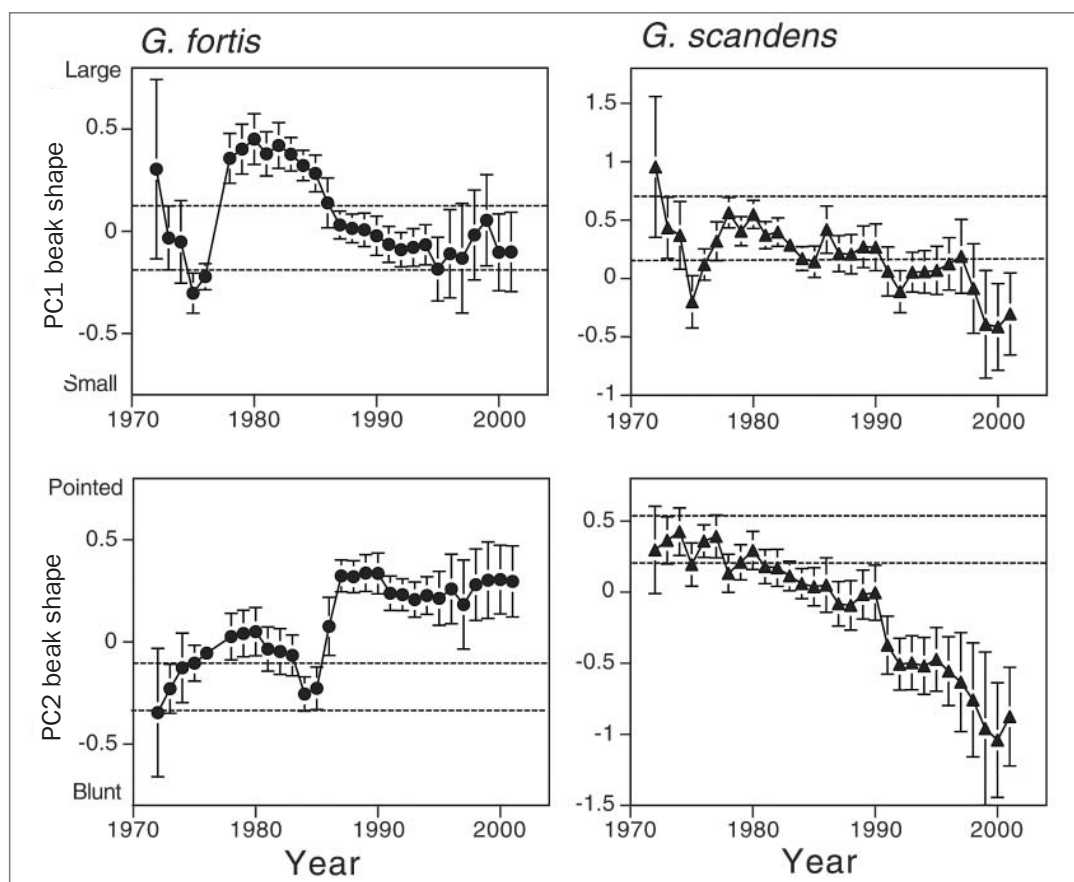


Figure 6. Changes in the beak size and shape of *Geospiza fortis* and *Geospiza scandens* on the island of *Daphne Major*. Mean trait values for each year are indicated by solid circles, and 95% confidence intervals are shown by vertical bars above and below the mean. In the absence of change, the means should remain within the 95% confidence intervals (horizontal broken lines) of the mean estimates from the 1973 samples. PC refers to principal component, obtained from a principal components analysis of size and shape variables. From Grant and Grant (2002a).

recent origin of Darwin's finches helps to explain why they are still capable of exchanging genes.

Divergence from their mainland relatives began when the finches colonized the Galápagos islands. Situated 900 km from continental Ecuador on the Nazca plate and moving imperceptibly toward the mainland, the archipelago is a remote place for birds to visit. Colonization is an improbable event. Nevertheless, according to one calculation, ancestral Darwin's finches arrived in a moderately large flock (or several small ones). Modern finches are genetically diverse at the major histocompatibility complex locus, and Vincek and colleagues (1996) used the allelic diversity of class II genes to calculate that the original colonists numbered at least 30 individuals.

Improbable events may arise in improbable and hence rare circumstances. What might those circumstances have been? Any answer must be speculative, even if rooted in current phenomena. The circumstances that promote dispersal of contemporary finches within the Galápagos archipelago are (a) high finch density following prolific breeding in El Niño years and (b) forest fires caused by volcanic eruptions. If the

unusual dispersal activity from the mainland followed similar patterns, it may have been induced by unusual volcanic activity in the Andes. Burning of the forests in one such episode would be followed by the establishment of large areas of shrub and secondary growth. With the buildup of finch populations in secondary forest, and another round of fires and burning, large numbers of finches and other birds in coastal regions would fly out to sea to escape the flames and smoke. The colonists would be helped if mats of vegetation were rafted out to sea by strong El Niño-associated flooding from the Guayas River. Global temperatures were warmer 2 million to 3 million years ago, and permanent El Niño conditions are thought to have occurred until about that time (Cane and Molnar 2001). The most marked shift in climate seems to have occurred at 2.4 million to 2.5 million years ago. This may be when the ancestral Darwin's finches arrived.

Relevant history of the Galápagos

To understand the past, the second question that needs to be addressed is how the islands have changed, if at all, since the first finches arrived. The simplest possible answer would be

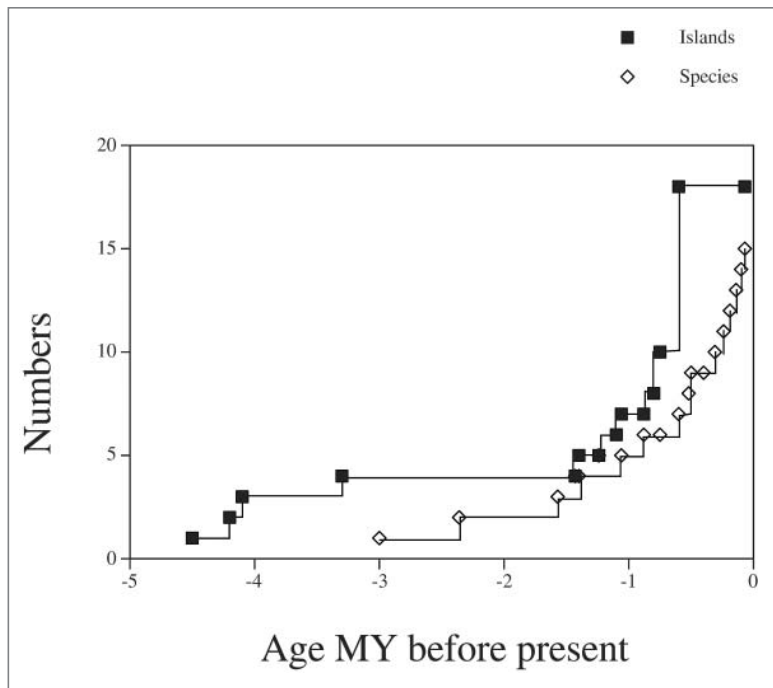


Figure 7. The accumulation of species of Darwin's finches with time, back-calculated from the estimated ages (in millions of years, or MY) of contemporary species in the absence of known extinctions. The accumulation of species parallels the accumulation of islands with time, as determined from estimations of island age and elevation in relation to sea level. More islands provide more conditions for speciation to occur and species to persist. From Grant (2001).

that the islands have always been much as they are today in terms of geography, climate, and vegetation. If this is correct, the finches' adaptive radiation can be viewed as a process of differentiation that results in the occupancy of all ecological niches present at the outset—rather like filling empty boxes, one species per box. Indeed, this is how early writers on the subject viewed the radiation of the finches, stressing the absence or scarcity of competitors in the boxes as a facilitating factor (Huxley 1942, Simpson 1944, Lack 1947, Grant 1999). In the modern version, the boxes are replaced by adaptive peaks in a more or less fixed landscape. This view implies that diversification is rapid early in the radiation and then slows down as ecological opportunities diminish. Some radiations of other organisms elsewhere conform to this pattern (Schluter 2000). However, taken at face value, the phylogeny of Darwin's finches shows exactly the opposite pattern: a slow start followed by recent, rapid diversification (figure 7). The species occupy adaptive peaks, but the fixity of the ecological landscape that allowed them to do so is questionable.

In fact, the islands and their inhabitants have changed radically. Three million years ago, there were far fewer islands than today, perhaps only five (Grant and Grant 1998). The number of islands increased as a result of volcanic activity centered on and near a hotspot beneath the western island of Fernandina. Climate changed as well. The average air

temperature declined but, more important than this, the world's climate underwent a sharp transition 2.75 million years ago with the abrupt onset of glaciation (Cane and Molnar 2001). In the last million years the climate has oscillated between glacial and interglacial conditions at about 100,000-year intervals. Global fluctuations in climate were experienced locally, in the Galápagos and elsewhere in tropical America. This has been revealed by the isotopic oxygen signatures of temperature in Andean ice cores (Seltzer et al. 2002), by coral cores in Galápagos (Dunbar et al. 1994), and by pollen cores in Galápagos (Colinvaux 1972, 1984) and in continental South and Central American lakes (Bush et al. 1992).

Most of the contemporary finches evolved in the last million years, so it is important to know what happened during these cycles. The two major effects of glacial–interglacial cycles were the depression of temperatures and of sea level relative to contemporary levels. The last Ice Age cooling resulted in a drop of 3°C to 4°C in the equatorial Pacific, reaching a minimum about 21,000 years ago (Kerr 2001). The previous deglaciation, about 130,000 years ago, was associated with a drop of 2°C to 6°C (Tudhope et al. 2001). Sea level fell with the temperature. The decline was gradual from the current level (about 120,000 years ago) to about 60 meters (m) lower (about 30,000 years ago); then an abrupt further decrease occurred to

about 125 m below the current level (Lambeck and Chappell 2001). As a consequence, islands were larger and distances between them were shorter. Thus, both temperature and sea level were usually lower and never much higher than they are today.

The food of finches—plants and arthropods, the latter feeding on the plants and on each other—must have been affected by these geophysical and climatic changes. First, new species of plants and arthropods would have arrived by immigration. We do not know when this happened or which species were involved. For Galápagos, unlike Hawaii (e.g., Givnish 1998, Wright et al. 2000), there are no molecular phylogenies of plants to help in reconstructing paleofloras, and the phylogenies of insects are too scarce to be useful (Finston and Peck 1997, Sequeira et al. 2000). That situation needs to be rectified. Second, other species, perhaps influenced by the immigrants, would have become extinct. Severe and extensive droughts would have been particularly crucial and cruel times for many organisms, including finches. Third, the temperature- and moisture-dependent altitudinal zonation of plants would have shifted upward and downward at different times; hence, the highest and lowest habitats would have been most vulnerable to elimination, as noted elsewhere (Prodon et al. 2002). Plant distributions would have changed across the archipelago.

The evidence of a change in the upland forests is the relative scarcity of endemic plants (Johnson and Raven 1973). The evidence of a change in the lowest zone is the anomalous occurrence of plants on some islands with apparently unsuitable climates and soil. For example, the tree *Erythrina velutina* occurs at mid elevations on the high islands of Santa Cruz, Santiago, and Isabela. A single tree of this species occurs on the low arid island of Genovesa, and fewer than a dozen occur on the low, arid, and even more remote island of Wolf. Similarly, a few *Zanthoxylum fagara* trees on Santa Cruz and San Cristóbal occur close to the coast. These may be the remnants of much larger populations on these islands under cooler, wetter, or less seasonally arid conditions than those that prevail today. Temperatures and precipitation changed markedly from one state to another long enough (> 1000 years; Colinvaux 1972, Riedinger et al. 2002) for vegetation zones to shift (Woodward 1987). On some occasions, however, significant changes in temperature occurred in as short a time as a hundred years, perhaps less (Bush et al. 1992). Large, abrupt, and widespread climate changes with major consequences for the biota have occurred repeatedly in the past, when the Earth system was forced across thresholds (Alley et al. 2003).

The macroevolutionary pattern and the buildup of complex communities from simple ones

In view of the strong environmental changes in the archipelago, it is scarcely likely that all current ecological niches were available when the finches' ancestors arrived. Rather, the numbers and types of opportunities for finch evolution increased as the number of islands increased and the climate and vegetation changed. According to this view, the adaptive radiation and the buildup of species-rich communities were largely molded by environmental change; the particular species originated when they did, and no earlier, in response to particular environments prevailing then.

When the first finches arrived on Galápagos, they may have encountered a climate and vegetation more like those of modern-day Cocos Island: warmer, wetter, and more humid conditions, fostering rain forest from the coast to the island peaks (Grant 1999, Grant and Grant 2002b). Cocos Island has temperatures similar to those of the coastal habitats in the Galápagos and rainfall equivalent to what the Galápagos now receives in an El Niño year at high elevations. Reasoning from the evidence of modern finches, we suggest the initial evolutionary pathway taken by the finches was toward the exploitation of small arthropods, and of nectar and pollen from small flowers, in a rain forest-like environment.

The radiation began when the initial species split into two lineages of *Certhidea* warbler finches (figure 8) after the initial pathway had been taken. One group of populations (*Certhidea olivacea*) inhabits moist upland forest, and the other group (*Certhidea fusca*) occupies lower habitats on other, mainly low, islands. Remarkably, despite their long separation, the two groups have retained similar mate recognition systems, and for that reason we refer to them as lineages

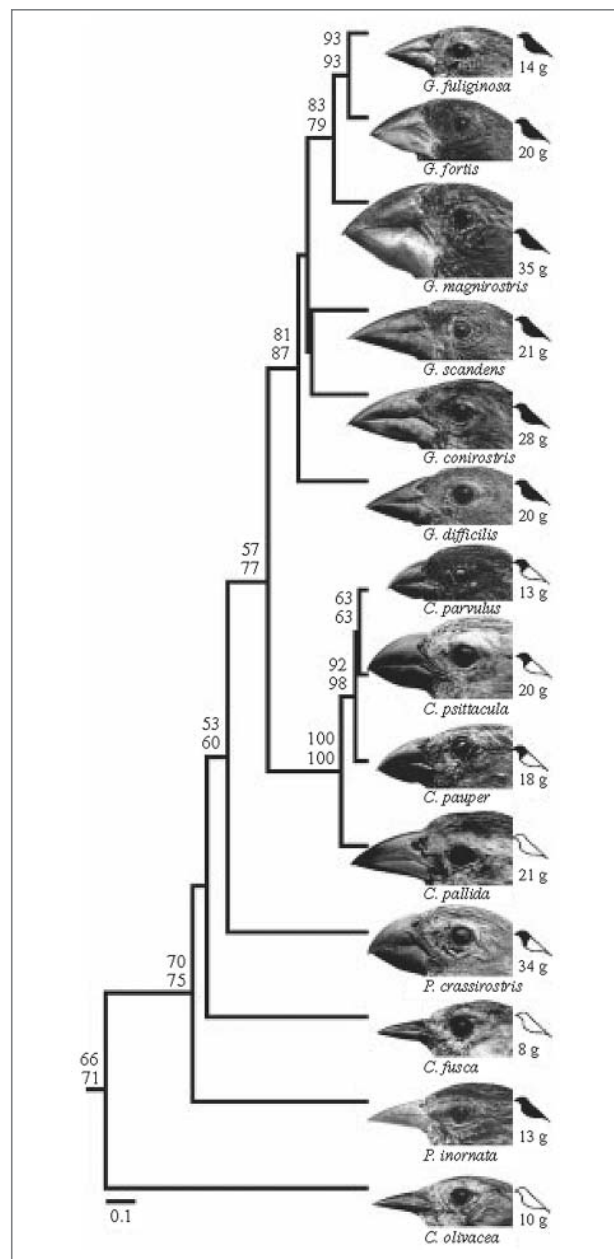


Figure 8. Reconstruction of finch phylogeny based on microsatellite DNA. Horizontal branch lengths are proportional to units of genetic distance (G_{ST}) as indicated by the scale. Numbers refer to percentage bootstrap support for the nodes by two methods. Mean weights are given on the right, together with symbols of male plumage: fully black, partially black, or brown or green. Alternative reconstructions that use morphology, allozymes, or mitochondrial DNA are similar, differing in relatively small details. Species, from top to bottom: *Geospiza fuliginosa*, *Geospiza fortis*, *Geospiza magnirostris*, *Geospiza scandens*, *Geospiza conirostris*, *Geospiza difficilis*, *Camarhynchus parvulus*, *Camarhynchus psittacula*, *Camarhynchus pauper*, *Camarhynchus pallida*, *Platyspiza crassirostris*, *Certhidea fusca*, *Pinaroloxias inornata*, and *Certhidea olivacea*. From Petren and colleagues (1999).

and not species (Grant and Grant 2002b). Another remarkable feature is that they have remained relatively undifferentiated in morphology, ecology, and behavior. This is not expected on the basis of the view that niches were varied, plentiful, and evolutionarily within reach at that time. However we must acknowledge the possibility, perhaps even the probability, that extinction has robbed us of other species that were formed then. The morphological similarity of these finches, contrasting with their distinctness from continental relatives, argues for an early adaptation to an unusual niche.

One of the warbler finch lineages gave rise to all other finch species. Early products of the diversification were the vegetarian finch (*Platyspiza crassirostris*), the Cocos finch (*Pinaroloxias inornata*) on either Galápagos or Cocos Island (Grant and Grant 2002b), and the sharp-beaked ground finch (*G. difficilis*). The most recent products were a group of ground finch species (*Geospiza*) and a group of tree finch species (*Camarhynchus* and *Cactospiza*) (figure 8).

Effects of environmental change have left a different historical imprint on the older species. Populations of *G. difficilis* differ strongly in morphology and ecology, to a degree unmatched by all other, and younger, species in the genus *Geospiza* and by the warbler finches that preceded them. Some *G. difficilis* have persisted in *Zanthoxylum* forest at mid and upper elevations, which we believe to be old, and others have entered arid lowland habitat, perhaps when the *Zanthoxylum* forest gradually disappeared from low islands as the climate changed. This may have been the first step of the radiation of ground finches. In contrast to the *G. difficilis* populations, populations of the vegetarian finch are morphologically and ecologically very similar. Limited genetic data (Petren et al. 1999) suggest that they separated from each other recently. This is surprising, as it is not expected from the age of the species or from the presumed stability of its mid-elevation transition zone habitat. The vegetarian finch may have become restricted to one or two islands, and other populations or even related species may have become extinct, in response to one of the recent extreme fluctuations in climate. Its vegetarian diet may have made it vulnerable in times of drought, and competition with other species may have been an additional factor.

The importance of environmental change in speciation is further suggested by the fact that in the last million years new species evolved in the habitats most vulnerable to change: *Geospiza* were added to lowland habitats, and *Camarhynchus* were added to the upland humid forest. The change in climate toward seasonal aridity and the development of arid lowland habitat provided the opportunity for a new, granivorous way of finch life, now adopted by *Geospiza* species. Some of these modern species may have contributed to the extinction of older ones through competitive superiority in a changing environment. This is one possible interpretation of the contrast between the morphological distinctness of the three older groups, *Certhidea*, *Platyspiza*, and *G. difficilis*, and the morphological similarity of species in the younger genera, *Camarhynchus*, *Cactospiza*, and *Geospiza*.

These ideas on speciation and extinction, together with observations of the colonization of Daphne Major by *G. magnirostris* (Grant et al. 2001), suggest that periods of expansion such as the one in progress are preceded and followed by periods of range contraction and extinction caused by environmental change. Distributions of habitats, sea level, island and population sizes, and degrees of isolation provide favorable conditions for divergence of small populations in isolation at some times and for dispersal, mixing, establishment of sympatry, and hybridization at others. The buildup of complex communities from simple ones is not smooth, continuous, and regular, but a process of gains and losses with a net accumulation of species over the long term.

Conclusions

According to the standard allopatric model, speciation begins with the establishment of a new population, continues with the divergence of that population from its parent population, and is completed when members of two diverged populations can coexist in sympatry without interbreeding. We stand a virtually negligible chance of observing the whole process under natural circumstances. Nevertheless, it is possible to make relevant observations in nature of all steps in the process. We have described the strong role played by environmental change at each of the three steps in the speciation of Darwin's finches. The full adaptive radiation was produced by a repetition of these steps, each with a different product under somewhat different circumstances. The challenge now is to account for the differences in terms of past environments, without the help of fossils of finches or of other members of the biota. We have sketched a framework for doing this by using molecular genetic information to estimate the finch phylogeny and using geological and climatic information to reconstruct Galápagos environments in the past 2 million to 3 million years. A better understanding of environmental change on this time scale will help to explain why 14 species were formed, what their sequence of origin was, and why they evolved their particular unique features. There may be more history to uncover in finch DNA, if only we can work out how to read it.

Acknowledgments

We thank Ken Petren for figure 8 and Phil Hedrick, Fritz Trillmich, and an anonymous reviewer for comments on the manuscript. We are grateful to the Galápagos National Park and the Charles Darwin Research Station for permission and logistical support for the fieldwork, and to the National Sciences and Engineering Research Council of Canada and the National Science Foundation for funding support.

References cited

- Abbott I, Abbott LK, Grant PR. 1977. Comparative ecology of Galápagos ground finches (*Geospiza* Gould): Evaluation of the importance of floristic diversity and interspecific competition. *Ecological Monographs* 47: 151–184.
- Alley RB, et al. 2003. Abrupt climate change. *Science* 299: 2005–2010.

- Bowman RI. 1961. Morphological Differentiation and Adaptation in the Galápagos Finches. University of California Publications in Zoology, Vol. 58. Berkeley: University of California Press.
- . 1983. The songs of Darwin's finches. Pages 237–537 in Bowman RI, Leviton AE, Berson M, eds. Galápagos Organisms. San Francisco: American Association for the Advancement of Science, Pacific Division.
- Burns KJ, Hackett SJ, Klein NK. 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution* 56: 1240–1252.
- Bush MB, Piperno DR, Colinvaux PA, DeOliveira PE, Krissek LA, Miller MC, Rowe WE. 1992. A 14,300-yr paleoecological profile of a lowland tropical lake in Panama. *Ecological Monographs* 62: 251–275.
- Cane MA, Molnar P. 2001. Closing of the Indonesian seaway as a precursor to east African aridification around 3–4 million years ago. *Nature* 411: 157–162.
- Colinvaux PA. 1972. Climate and the Galápagos Islands. *Nature* 240: 17–20.
- . 1984. The Galápagos climate: Present and past. Pages 55–69 in Perry R, ed. Galápagos. Oxford (United Kingdom): Pergamon Press.
- Darwin CR. 1842. Journal of Researches into the Geology and Natural History of the Various Countries Visited during the Voyage of H. M. S. *Beagle*, under the Command of Captain FitzRoy, R.N., from 1832 to 1836. London: Henry Colburn.
- Dunbar RB, Wellington GM, Colgan MW, Glynn PW. 1994. Eastern Pacific sea surface temperature since 1600 A.D.: The O¹⁸ record of climate variability in Galápagos corals. *Paleoceanography* 9: 291–315.
- Finston TL, Peck SB. 1997. Genetic differentiation and speciation in *Stomion* (Coleoptera: Tenebrionidae): Flightless beetles of the Galápagos Islands, Ecuador. *Biological Journal of the Linnean Society* 61: 243–266.
- Givnish TJ. 1998. Adaptive plant evolution on islands: Classical patterns, molecular data, new insights. Pages 281–304 in Grant PR, ed. *Evolution on Islands*. Oxford (United Kingdom): Oxford University Press.
- Grant BR, Grant PR. 1989. *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos*. Chicago: University of Chicago Press.
- . 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* 50: 2471–2487.
- Grant PR. 1999. *Ecology and Evolution of Darwin's Finches*. Princeton (NJ): Princeton University Press.
- . 2001. Reconstructing the evolution of birds on islands: 100 years of research. *Oikos* 92: 385–403.
- Grant PR, Grant BR. 1998. Speciation and hybridization in island birds. Pages 142–162 in Grant PR, ed. *Evolution on Islands*. Oxford (United Kingdom): Oxford University Press.
- . 2002a. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296: 707–711.
- . 2002b. Adaptive radiation of Darwin's finches. *American Scientist* 90: 131–139.
- Grant PR, Grant BR, Petren K. 2001. The founding of a new population by a single pair of individuals: Establishment, selection, and population expansion. *Genetica* 112/113: 359–382.
- Huxley JS. 1942. *Evolution: The Modern Synthesis*. London: Allen and Unwin.
- Johnson MP, Raven PH. 1973. Species number and endemism: The Galápagos archipelago revisited. *Science* 179: 893–895.
- Keller LF, Grant PR, Grant BR, Petren K. 2001. Heritability of morphological traits in Darwin's finches: Misidentified paternity and maternal effects. *Heredity* 87: 325–336.
- Kerr RA. 2001. The tropics return to the climate system. *Science* 292: 660–661.
- Lack D. 1947. *Darwin's finches*. Cambridge (United Kingdom): Cambridge University Press.
- Lambeck K, Chappell J. 2001. Sea level change through the last glacial cycle. *Science* 292: 679–686.
- Mayr E. 1942. *Systematics and the Origin of Species*. New York: Columbia University Press.
- Newton I. 1967. The adaptive variation and feeding ecology of some British finches. *Ibis* 109: 33–98.
- Petren K, Grant BR, Grant PR. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length variation. *Proceedings of the Royal Society of London, B* 266: 321–329.
- Price T, Lovette IJ, Bermingham E, Gibbs HL, Richman AD. 2000. The imprint of history on communities of North American and Asian warblers. *American Naturalist* 156: 354–367.
- Prodon R, Thibault J-C, DeJaive P-A. 2002. Expansion vs. compression of bird altitudinal ranges on a Mediterranean island. *Ecology* 83: 1294–1306.
- Ratcliffe LM, Grant PR. 1983a. Species recognition in Darwin's finches (*Geospiza*, Gould), I: Discrimination by morphological cues. *Animal Behaviour* 31: 1139–1153.
- . 1983b. Species recognition in Darwin's finches (*Geospiza*, Gould), II: Geographic variation in mate preference. *Animal Behaviour* 31: 1154–1165.
- . 1985. Species recognition in Darwin's finches (*Geospiza*, Gould), III: Male responses to playback of different song types, dialects and hetero-specific songs. *Animal Behaviour* 33: 290–307.
- Richards OW. 1948. Species formation in islands (review of Darwin's Finches, by Lack D). *Journal of Animal Ecology* 17: 83–84.
- Riedinger MA, Steinitz-Kannan M, Last WM, Brenner M. 2002. A ~6100 ¹⁴C yr record of El Niño activity from the Galápagos Islands. *Journal of Paleontology* 27: 1–7.
- Sato A, O'Huigin C, Figueroa F, Grant PR, Grant BR, Tichy H, Klein J. 1999. Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proceedings of the National Academy of Sciences* 96: 5101–5106.
- Schluter D. 2000. *The Ecology of Adaptive Radiations*. Oxford (United Kingdom): Oxford University Press.
- Schluter D, Grant PR. 1984. Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist* 123: 175–196.
- Seltzer GO, Rodbell DT, Baker PA, Fritz SC, Tapia PM, Rowe HD, Dunbar RB. 2002. Early warming of tropical South America at the last glacial–interglacial transition. *Science* 296: 1685–1686.
- Sequeira AS, Lanteri AA, Scatagliini MA, Confalonieri VA, Farrell BD. 2000. Are flightless *Galapaganus* weevils older than the Galápagos Islands they inhabit? *Heredity* 85: 20–29.
- Simpson GG. 1944. *Tempo and Mode in Evolution*. New York: Columbia University Press.
- Swarth HS. 1931. The avifauna of the Galápagos islands. *Occasional Papers of the California Academy of Sciences* 18: 1–299.
- . 1934. The bird fauna of the Galápagos islands in relation to species formation. *Biological Reviews* 9: 213–234.
- Tudhope AW, Chilcott CP, McCulloch MT, Cook ER, Chappell J, Ellam RM, Lea DW, Lough JM, Shimmiel GB. 2001. Variability in the El Niño–Southern Oscillation through a glacial–interglacial cycle. *Science* 291: 1511–1517.
- Vincek V, O'Huigin C, Satta Y, Takahata N, Boag PT, Grant PR, Grant BR, Klein J. 1996. How large was the founding population of Darwin's finches? *Proceedings of the Royal Society of London, B* 264: 111–118.
- Woodward FI. 1987. *Climate and Plant Distribution*. London: Cambridge University Press.
- Wright SD, Young CG, Dawson JW, Whittaker DJ, Gardner RC. 2000. Riding the ice age El Niño? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences* 97: 4110–4123.