Darwin's Finches

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Secondary article

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Darwin's finches are a prime example of adaptive radiation and of evolution in action. Beak size of these equatorial bird species repeatedly changed within two decades as a response to environmental changes during El Niño conditions.

Article Contents

The Species, Natural History

Darwin's finches are a unique group of birds from the isolated islands of the Galapagos archipelago, Ecuador, and Cocos island, Costa Rica. Together with Hawaiian honeycreepers, Darwin's finches are famous because they are a textbook example of adaptive radiation and impressively illustrate how a variety of different species of birds can evolve from a single lineage. Long-term morphological data on Darwin's finch beak sizes also provide one of the most convincing evidences for 'evolution in action'.

Popular and scientific interest in these birds has a long history and began with the historic voyage of Charles Darwin in 1835. About a century and more later, excellent studies have been conducted by David Lack (1947), Robert Bowman (1961), and especially Peter and Rosemary Grant (Grant, 1986; Grant and Grant, 1989). Unique data on evolution and ecology of natural populations have been accumulated owing to the special situation on the Galapagos islands – where population sizes and number of species are limited, birds are extremely tame and easy to observe, and there are many islands with different habitats, and predation pressure is low. Remarkably, most of the data on the biology of Darwin's finches have been obtained without experimentation. Instead, by observing characteristics of individual birds and making use of natural experiments that take place in years with extreme climatic conditions, scientists have successfully been able to infer processes underlying microevolution (evolutionary processes on the scale of years or decades).

The Galapagos islands lie in the Pacific ocean about 1000 km west off the coast of Ecuador, on the equator between 2°N and 2°S latitude. The archipelago consists of about 13 large and 6 smaller islands ranging in size between less than 1 ha and more than 450 000 ha and in altitude between sea level and 1700 m. All the islands are of volcanic origin, consisting of different kinds and forms of magma, lava and tuff that were produced by an ancient fixed hotspot (still active today). The oldest sunken island has been dated to at least 9 million years of age, whereas the oldest present island is about 3 million years old.

The climate in Galapagos is seasonal. A hot and wet period persists from about January to May, followed by a cooler and drier period for the rest of the year. Average air temperatures range from about 19°C to 30°C and mean yearly rainfall on the lowland coast of San Cristobal island is roughly 380 mm. However, air temperatures and amounts of rainfall can vary greatly between islands and depend strongly on the location of an island within the archipelago and also on its altitude. The hot and wet season is caused by warm waters flowing in from the northeast (Panama current) when the cold Humboldt Current loses its influence owing to a southward movement of the intertropical convergence zone. Additionally, the Cromwell countercurrent that brings cold, nutrient-rich bottom water from the west towards Galapagos decreases during the hot season. More than 90% of the annual rain falls during the hot and wet period. During the cool and dry season, precipitation comes mainly as a light, misty rain (called 'garúa'). While environmental conditions during the hot season are variable between years, dry-season conditions show remarkably low interannual variance. The beginning of the hot and wet season as well as the total amount of rainfall can vary strongly between years. The climatic variability is amplified by El Niño–Southern Oscillation (ENSO) events, which recur at irregular intervals of 2 to 11 years in differing strengths. During ENSO periods, rainfall is heavy and extensive in Galapagos (e.g., more than 3500 mm on San Cristóbal island in 1983). The years following an ENSO event, called 'La Niña', are often exceptionally dry (e.g. no rain on Daphne island in 1985).

Thirteen species of Darwin's finches inhabit the Galapagos archipelago; a fourteenth species, the Cocos Finch, can only be found on the isolated island of Cocos, Costa Rica (**Table 1**). Cocos island is located 630 km to the northeast of Galapagos and about 500 km southwest of the coast of Costa Rica. Most Darwin's finches belong to one of the two bigger ecological groups, the Ground finches and the Tree finches. The Warbler finch and the Cocos finch are viewed as separate ecotypes.

All species have a fairly dull plumage. In Ground finches the plumage colour ranges from light brown in females and young birds to completely black in adult males. Typically, males need at least four years to obtain a completely black

Table 1 Characteristics of all extant Darwin's finches

English name	Scientific name	Occurrence (islands) (breeding/extinct)	Body size (g)	Diet
Small ground finch	*Geospiza fuliginosa*	14/0	14	Mainly granivorous
Medium ground finch	*Geospiza fortis*	13/0	20	Mainly granivorous
Large ground finch	*Geospiza magnirostris*	12/2	35	Mainly granivorous
Cactus ground finch	*Geospiza scandens*	12/0	21	Mainly granivorous, flowers/nectar
Large cactus finch	*Geospiza conirostris*	2/0	28	Mainly granivorous
Sharp-beaked ground finch	*Geospiza difficilis*	6/4	20	Granivorous and insectivorous
Small tree finch	*Camarhynchus parvulus*	10/0	13	Mainly insectivorous
Medium tree finch	*Camarhynchus pauper*	1/0	16	Mainly insectivorous
Large tree finch	*Camarhynchus psittacula*	9/1	18	Mainly insectivorous
Vegetarian finch	*Platyspiza crassirostris*	8/2	34	Almost entirely herbivorous
Woodpecker finch	*Cactospiza pallida*	6/0	20	Mainly insectivorous
Mangrove finch	*Cactospiza heliobates*	2/0	18	Mainly insectivorous
Warbler finch	*Certhidea olivacea*	17/0	8	Insectivorous: small arthropods and nectar
Cocos finch	*Pinaroloxias inornata*	1/0	16	Omnivorous

plumage, but there is also a high variability in this trait due to both genetic and environmental factors. All other finch species either have a uniform light brown or olive plumage with black heads in males of some species. The morphological characteristics that differ most between species are beak size and shape and body size (**Figure 1**). However, there is also a large variation in these morphological traits within a single species, especially between populations from different islands. Therefore, sometimes species cannot safely be identified on morphological characters alone (see below for the occurrence of hybrids).

Most finches breed during the hot and wet season, when food is most abundant (Grant, 1986; Grant and Grant, 1989). In most species, breeding is closely tied to rainfall. In light of the close temporal correlation of rainfall and egg laying, Darwin's finches have been considered one of the classic examples for opportunistic breeding. Their breeding system can be described as permanently (socially) monogamous, but polygyny and mate changes can occasionally be observed. Pairs maintain small all-purpose territories. However, outside their breeding season, finches also forage off their territories in sometimes large mixed-species flocks of several hundred individuals. Nests are dome-shaped with a side entrance, usually built out of dry grass and placed in cacti or bushes. Males often build display nests before both partners jointly construct the actual nest. Average clutch size is three, but up to six eggs per clutch can be laid in good years. Eggs are incubated by the female for about 12 days, and nestlings leave the nest after about two weeks. The number of broods per year (1–9) varies according to environmental conditions. The main predator of Darwin's finches is the Short-eared owl (*Asio flammeus*), which preys mainly on nestlings and young birds. Occasionally, Galapagos hawks (*Buteo galapagoensis*) and Lava herons (*Butorides sundevalli*) also eat adult Darwin's finches. Potential egg predators are larger birds (Mockingbirds, *Nesomimus* spp.; Anis, *Crotophaga ani*) and snakes. Moult often starts after the breeding season, but moult–breeding overlap is commonly observed. Moult can also become interrupted, or 'arrested', when a new breeding attempt starts.

The song of the social father is imprinted on the offspring and many dialects exist on different islands or in different habitats. The role of female song is still largely unexplored. Females appear to actively select or choose their mate, and song, plumage types and physical characteristics of males play a critical role during male–female interactions. Most Ground finches feed on seeds, but all finches need at least some insect food to raise hatchlings. All Darwin's finches have only weak flight abilities, as they usually only make very short flights. Their wing geometry is rounded and thus suitable for short flights, hops and manoeuvres in dense vegetation. Similarly, their tails are very stumpy and short. Outside of the breeding season, competition between different species of finches is very low, especially in mixed-species flocks. However, during the breeding season, interspecific competition, e.g. between Cactus finches and Small ground finches for territories and associated resources may be very intense.

Figure 1 Darwin's finches show most extreme differences in beak size and shape. The Warbler finch (a) has the smallest, the Large ground finch (b) the largest beak. Medium ground finches (c, left) and Small ground finches (c, right) are typical seed eaters and have graded differences in beak size. Photographs © Martin Wikelski.

Classical Influence on Darwin

Charles Darwin, at age 24, visited the Galapagos islands together with Captain Robert FitzRoy in 1835 for a good two weeks, during their famous voyage on the HMS *Beagle*. Both men were impressed by the flora and fauna they encountered there. Darwin was not the first person to write about the finches, but he made detailed notes about them, and collected the first specimen. Upon realizing the large variation in beak sizes and shapes of these birds, Darwin thought that the different species had each warbler, finch and tanager ancestors. Only for the Ground finches with their astounding gradation in beak size did Darwin suspect evolution from one species. During his visit, however, he did not see all species of finches and collected only nine of them. Furthermore, in his collection he had difficulties in properly distinguishing the different species and also forgot to label them separately according to the island where he collected them. This would have been instrumental for the insight that birds can evolve different traits on closely located islands, simply in adaptation to local environmental conditions. Due to this oversight during his visit of the Galapagos archipelago, Darwin did not recognize the potential importance of the finches for the theory he developed later. However, while he was working on his Galapagos Mockingbird collection it struck him that some specimens were specific to their islands.

Darwin's collection of finches was later (1837) studied in detail by John Gould in England. Gould suggested that the finches are a completely new group of birds restricted to the Galapagos islands and that all species belong to the same group. Together with the evidence from the Mockingbirds, the tortoises and the plants, Darwin began to realize that species may evolve from ancestral forms into different new species. However, it took him many years of study (especially of pigeon breeds) before he finally published his famous book on the *Origin of Species*, in which he announced his theory about evolution and natural selection. Interestingly, Darwin never mentions the 'Darwin's finches' in his notebooks on transmutation of species or in the *Origin of Species*.

Several other subsequent expeditions were fascinated by the adaptive radiation of Darwin's finches. Most prominently, the year-long expedition of the Californian Academy of Sciences in 1905–1906 collected about 5000 specimen of finches in Galapagos. Most recently, work by Peter and Rosemary Grant and collaborators provides one of the brilliant demonstrations that evolution can be witnessed 'in action' within a short period of time (few years).

Beak Sizes and Ecology

One of the most distinguishing characteristics of the different finch species is their beak size and shape. The beak dimensions range from thin and long warbler-like beaks to enormous grosbeak-like or parrot-like beaks. Associated with the different beak sizes are skull and musculature specializations to support the mechanics of beak movements. There is large variation in beak sizes within populations of one island, as well as between the same species on different islands (Lack, 1947; Boag and Grant, 1984).

Beaks of Darwin's finches are highly specialized according to dietary needs (see also **Table 1**). Robert Bowman (1961) was struck by the different utilities of the beaks and compared them to different kinds of pliers (**Figure 2**). He classified the feeding function of the different beak types into three main categories: (1) long and pointed beaks are best for probing, e.g. in flowers, foliage or wood; (2) convex curved beaks can apply force especially at the tip of the mandibles and are useful for tip-biting; (3) deep-based beaks are useful for cracking open hard food (seeds) at their base.

In general, the seed-eating finches have thick and short beaks to crack open seeds. The bigger their beaks, the harder seeds they can eat. Most Ground finches (*Geospiza* spp.) are granivorous, although all of them feed their young on arthropods. Thus they are insectivorous at least during the reproductive season, which is typical for most granivorous species.

Some species can be described as food generalists such as the Medium ground finch, others are much more specialized on certain kinds of food. Several impressive feeding specializations evolved. There is the purely insectivorous Warbler finch, with a thin warbler-like beak. The famous Woodpecker finch can use tools (sticks, spines) to probe for insects in holes, under the bark of trees and in leaves. Woodpecker finches make their own tools by

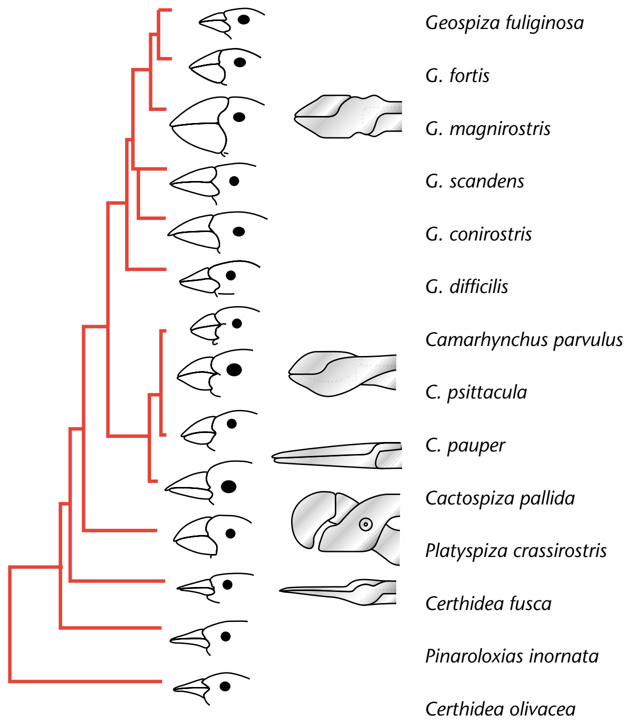

Figure 2 Phylogram of Darwin's finches based on microsatellite length variation. Birds are drawn at approximately actual size. Horizontal branch lengths represent genetic distance. Names are given in full in **Table 1**. The beak shapes of Darwin's finches are compared to different types of pliers. Redrawn from Petren *et al.* (1999) and Bowman (1961).

breaking small twigs or spines in the right length to be able to poke into tree holes. The Sharp-beaked ground finch pecks at the shafts of growing feathers of seabirds and drinks their blood. It also smashes booby eggs against rocks and drinks the contents. Such an adaptation is facilitated by the unique soil scratching behaviour of this group of finches. Darwin's finches scratch with both legs at the same time, thus they can produce a force strong enough to move large objects such as booby eggs. The Vegetarian finch feeds mainly on plant matter in the forests at higher elevation. The Cactus finch exploits *Opuntia* (prickly pear) flowers and pads. Some Ground finch species (*G. fortis*, *G. fuliginosa* and *G. difficilis*) remove ticks from iguanas and tortoises. During the dry season finches on Daphne island can obtain important protein and mineral supplements by scavenging on seabird offal, but also drink blood when it is available (Boag and Grant, 1984).

Beak size and shape are highly heritable, but also remarkably variable within and between populations of Darwin's finches. Within the Medium ground finches there is an intraspecific correlation between food size and beak morphology, suggesting a morphologic component to food selection. Thus, individuals with small beaks eat smaller seeds than individuals with larger beaks. Medium ground finches are also known for sex differences in diet, which may even lead to the differential mortality during ENSO events observed by Boag and Grant (1984). The availability of different seed classes is different between islands because of differences in vegetation. Moreover, in the wet seasons and during wet years the abundance of small, soft seeds increases, whereas during dry seasons and dry years hard seeds are proportionally more abundant.

Although diets will vary within a species and between islands, the species usually maintain separate food niches on each island. On Daphne island the highest diet overlap was observed between Medium ground finches and Cactus finches during peak plant and insect production. Diet overlap was lowest during severe drought seasons because the two species have different responses to food availability. Medium ground finches broaden their diet when food diversity declines, whereas Cactus finches become more selective and specific on various parts of *Opuntia* bushes.

A caveat in generalizing these results is that the Ground finches (in particular the Medium ground finch and Common and Large Cactus finches) have been studied best, while only very little information is available on the tree finches, with the possible exception of the Woodpecker finch. Thus, many of the data presently mainly pertain to Ground finches.

Adaptive Radiation and Character Displacement

Darwin's finches probably all stem from a single ancestral flock of birds that arrived in the Galapagos islands a few million years ago. How did so many different species evolve from this ancestor? Much of this speciation depends on the specialization on different food types. Beak dimensions contribute most to the separation between species, whereas wing length, tarsus length and mass contribute the least (Grant, 1993). The diversity of form and function in this single subfamily of passerines is remarkable, especially in beak structure and associated feeding habits. In short, food specialists with highly specialized beaks are better at exploiting specific food types than are generalists. Thus, food specialists are more likely to survive during the recurring drought conditions on the islands. As a consequence, one can observe adaptive changes in beak structure that facilitate feeding behaviour (Grant, 1986). The resulting adaptive radiation in beak (and body) size and beak shape is partly a response to ecological pressures imposed upon the birds by such severe environmental conditions. In addition, isolation of birds on different islands and from the mainland, empty niches at colonization, and initial small population sizes likely contributed to the observed adaptive radiation.

Over and above severe environmental circumstances, one can clearly see the action of competition between different species of finches. The most impressive manifestation is what is called 'character displacement'. This describes the fact that beak sizes of two species are very different when they co-occur on one island, whereas beak sizes are quite similar when both species occupy separate islands (**Figure 3**).

Competition between species living in the same habitat promotes evolutionary divergence. The reversal of this process, i.e. the lack of competition, promotes 'allopatric convergence': different species living on different islands converge towards each other, partly filling the other niche by using the same type of seeds as the other species.

In Darwin's finches, Boag and Grant (1984) found evidence for competition-mediated character displacement. Medium and Small ground finches have more similar bill depths in allopatry (when they inhabit different islands) as compared to sympatry (when they live together on one island; **Figure 3**). In sympatry, Medium ground finches have bigger and Small ground finches have smaller beaks.

The detailed study of Darwin's finches allowed researchers to reexamine the 'character release' hypothesis against three other hypotheses to explain the smaller (intermediary) beak size of Medium ground finches when occurring in allopatry on Daphne island. (1) Intermediate phenotypes

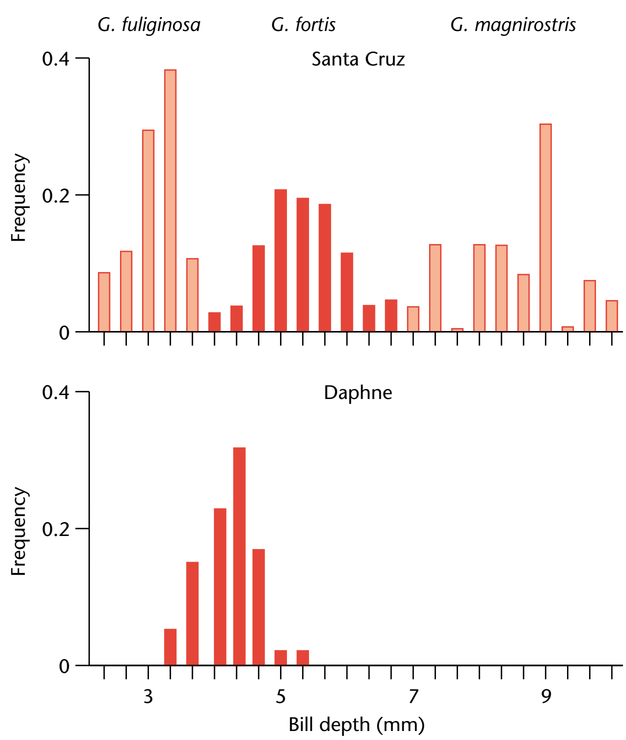

Figure 3 Frequency distributions of beak depths of three species of adult male Ground finches (*Geospiza*) on the two islands of Santa Cruz and Daphne. Note that beak sizes are different between the species on Santa Cruz and that *G. fortis* beaks on Daphne are smaller than on Santa Cruz. Redrawn from Grant (1986).

could arise from genetic drift/founder effects. Genetic drift could influence evolutionary processes particularly during times of extremely harsh environmental conditions when the population sizes are minimal. However, Daphne island is not isolated enough and immigration of finches occurs too frequently to cause strong effects of genetic drift. Moreover, there is strong natural selection happening during droughts, which should counteract effects of genetic drift. (2) Hybridization with small species could lead to intermediary morphologies. However, hybridization is not common enough in these finch populations to lead to such large-scale effects. On the other hand, hybridization can certainly accelerate evolution and help maintain genetic variance in a population. (3) A third way to explain intermediate beak morphologies of birds in allopatry is that they adapted to local food supplies. This would imply that food/seed size would need to be intermediate as well. Such an argument could apply to some islands, but does not predict the generality of intermediate beak sizes in allopatry. It was therefore concluded that competition between species was indeed the most important factor to accelerate the differences in beak sizes between finch species that live on the same island – and release of competition (in allopatry) would allow beak sizes to be more similar. It should be obvious that such a selective force has important consequences for the evolution of different finch species.

Natural Selection

Much of what is known about natural selection in Darwin's finches comes from studies of Ground finches on the small island of Daphne major (Grant, 1986; Grant and Grant, 1989). The Galapagos islands are usually very arid and rain falls only during a few months per year. Food abundance is strongly tied to the amount of rain. Therefore, many finches starve to death during dry years and consequently there are enormous fluctuations in finch numbers between years: population sizes can be only about a quarter during dry years compared to subsequent wet years. During such population bottlenecks, only individuals with certain traits will survive. Most important for survival is beak size, as it determines the efficiency of foraging on the available seed bank. As seeds are slowly depleted after an El Niño, only certain seed sizes will remain available to the finches, and only finches with certain beak sizes will exploit such seeds efficiently. The beak sizes are strongly heritable (heritability $> 75\%$) and thus there will only be certain genotypes of finches represented among the survivors of a dry period. It is presently unknown whether similar conditions apply to highland birds, where environmental changes are more buffered by the clouds that bring in at least some moisture from the sea during dry periods.

Survival of finches over dry seasons can vary strongly between years. Dry season survival may be as high as 90% or as low as 15%, and almost no young birds survive severe droughts. Similarly, reproductive output varies strongly between years, both in number of clutches (1–9 per year) and clutch size (2–6 eggs). Survival of adults during the (wet) breeding season is extremely high, owing to the general scarcity of predators. High population densities after successful breeding seasons contribute to low chance of survival because of high intraspecific competition for food. Ground finches can become very old and annual adult survival is relatively constant until age 7 years, whereafter it drops. Adult survival rates vary slightly among species and gender, and possibly with body size. For example, Medium ground finches survive better than Small ground finches, and often one sex survives better than the other in a given habitat. Similar environmental conditions may affect finch species differently. For example, natural selection on beak size fluctuated temporally in generalist Medium ground finches, favouring small beaks during some years but large beaks during others. During the same time, Cactus finches experienced stabilizing selection for specific beak dimensions.

Hybridization

Earlier research had speculated about the occurrence of hybridization in Darwin's finches, attributing some of the observed variance in morphological characters to this process. However, hybridization was only more recently demonstrated by the Grants and their coworkers. Hybridization is always rare but seems to occur between a variety of species (Grant, 1993). On Daphne island, about 1.8% of breeding Medium ground finch individuals and 0.8% of breeding Cactus finch individuals hybridized (Grant and Grant, 1989). However, many more Small ground finch individuals hybridized, possibly because of the scarcity of Small ground finch mates on this island. Hybrids are both viable and fertile. Most hybrids backcrossed, i.e. mated again with members of their parental species, but not with other hybrids. Thus, true hybrid grandchildren are rare, a fact that may also be explained by the overall scarcity of potential hybrid mates. Males and females hybridized at approximately equal frequencies and the reproductive success of hybrid pairs was usually similar to that of nonhybrid pairs. There is no evidence for an absolute genetic barrier between Darwin's finch species, thus many species can potentially hybridize. The reasons for hybridization include morphological similarity between individuals and biased sex ratios, that is the scarcity of conspecific mates (Grant, 1993). The relative fitness of hybrids depends on ecological conditions, thus ecological factors are at least as important as genetic factors in determining the relative fitness of hybrids. Hybridization has only a small directional effect on beak and body size within a population (Grant and Grant, 1995) because hybridization is rare and individuals may breed with species of both larger and smaller beak sizes. However, hybridization may increase the potential for evolutionary change as it increases the genetic variation upon which natural selection can draw. The latter explanation potentially accounts for the relatively rapid radiation process in Darwin's finches.

Hybridization can also be caused by occasional misimprinting of song characteristics. Sons learn their father's song, but in crowded populations where different species breed close together, some sons may learn songs from the nonparental species, or at least include some heterospecific song elements. Since females choose males that sing slightly differently from their own fathers, they may choose heterospecific rather than conspecific mating partners as a result of cultural learning errors. During some environmental conditions, hybrids do better than their parental species because their intermediate beak sizes may enable them to better exploit certain food sources.

Although hybridization and high survival and fecundity of hybrids may at first appear to challenge the biological species concept, hybridization may also be seen as a creative element in speciation: it could either directly produce a new species, or indirectly contribute to speciation by providing genetic variation for each of the interbreeding species, thereby facilitating further evolutionary change in each.

Speciation, Phylogeny and ' Evolution in Action'

The Galapagos archipelago (including now-sunken islands) is probably older than 10 million years, while present-day islands were formed between 0.5 and 5 million years ago. This geological dating sets the time frame for evolutionary processes. Genetic analysis of Mhc class II genes suggest that Darwin's finch ancestors colonized the Galapagos islands in a single event as a group of more than 30 individuals between 600 000 and 5 million years ago (Vincek *et al*., 1997).

Genetic results using microsatellite techniques support such a monophyletic origin of Darwin's finches (Petren *et al*., 1999). They also support the grouping into Ground and Tree finches (including the Woodpecker finch). A most fascinating result is that Warbler finches are basal to the phylogeny and occur in two genetically distinct populations within the archipelago despite little morphological variation. Even more exciting, the Cocos finches fall within this clade, indicating that Cocos island was colonized after Darwin's finches evolved on the Galapagos (**Figure 2**).

Speciation of Darwin's finches is probably based on the evolutionary divergence of populations. Speciation starts from a single population and results in the coexistence of reproductively isolated populations: two species from one. In most cases, one can only observe the end result of such processes. However, the Grants could directly observe an adaptive change in a trait (beak size) in response to environmental changes (Grant, 1986; Grant and Grant, 1989). Because this trait is highly heritable, not only the phenotypic but also the genetic composition of the entire finch population of one island had changed – a direct demonstration of evolution in action.

Interestingly, the above-mentioned information about sexual imprinting, hybridization and the fitness of hybrids led the researchers to suggest that premating isolation arises before postmating isolation. Thus, mate choice processes appear to be more important in speciation than the direct compatibility of the genetic information of two mating partners. In particular, the involvement of culturally inherited traits like song may be partly responsible for the relatively rapid rate of speciation in birds. The most likely model of speciation in Darwin's finches is 'allopatric', i.e. populations on different islands develop slightly different traits in isolation. If members of such populations come together again after some time, they are imprinted to the song and morphology of the home population, and are thus largely reproductively isolated from each other, fulfilling the general criterion distinguishing two species.

Conservation

The major threat to Darwin's finches is the introduction of new, alien parasites and pathogens to which they are not adapted. Such pathogens are known to wipe out, or seriously threaten, entire avian island biota as in Hawaii. Introductions can occur naturally with new immigrant bird species, but are much more likely caused by human introductions of new avian and other vertebrate species. Habitat destruction and alteration, especially in the humid highlands, may also seriously endanger many finch populations. However, little is known so far about either of these potential dangers. The conservation status of the Mangrove finch is unclear: presently perhaps only a few dozen to a few hundred individuals exist. It is unclear, however, whether scarce mangrove habitat always restricted the finch numbers or whether human alteration of habitat decreased population sizes. In any case, the Mangrove finch may be one of the rarest bird species worldwide.

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