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Speciation

Looked at in the broadest possible way the species problem thus becomes the problem of the establishment of group discontinuities in the evolutionary continuum.

(Huxley 1938, p. 254)

If one accepts some version of the biological species concept, then the central problem of speciation is understanding the origin of those isolating barriers that actually or potentially prevent gene flow in sympatry.

(Coyne and Orr 2004, p. 57)

Introduction

CHAPTER 1 INTRODUCED THE MAIN PROBLEM that has motivated research on *Daphne*: the problem of explaining how one species of Darwin's finch became many by repeated speciation through morphological and ecological diversification. Speciation occurs when one species splits into two populations or sets of populations (fig 1.2) that do not interbreed or interbreed rarely with little genetic consequence (Grant and Grant 2008a). We observe the products, species, and the challenge we face is to reconstruct the process by which they were formed. One purpose of this chapter is to use information from the study on *Daphne* to reconstruct and interpret the morphological transformation of species to answer the question of how speciation occurs.

A second purpose of the chapter is to discuss the interactions that take place when previously separated and divergent populations come into contact. According to the allopatric model of speciation, splitting of a species into two is initiated allopatrically, for example, when individuals disperse from one island to another and establish a new population (fig 1.1). They evolve by natural selection and genetic drift, and become adapted to each ecologically distinctive environment. A sympatric phase may then follow, as a result of dispersal of individuals from one island to another occupied by a related population. The outcome depends on the degree of prior divergence: reproductive isolation if divergence was large or interbreeding with residents if it was small. Theory is clear on the essential ingredients—natural selection, genetic variation, ecological divergence, and reproductive isolation (Coyne and Orr 2004)—but not on what tips the balance toward fission or fusion. This is where a study on a single island such as *Daphne* can help, by throwing light on interactions at the secondary contact stage and later.

Morphological Transformation in Speciation

The ground finches differ in size and shape. The three, coexisting, granivore species on *Daphne* differ by at least 15% in one beak dimension, which is equivalent to approximately two standard deviations either side of each mean value (Grant 1986). Beak dimensions change across decades as a result of fluctuating selection (chapter 11), but how much selection is required to transform one species into another by changing a mean by 15%? This question can be approached at two different but complementary life history stages: adults or embryos. The adult approach uses genetic variances and covariances for the species on *Daphne* and the phenotypic (morphological) differences between them (Price et al. 1984a) to estimate the minimum cumulative or net forces of selection required to effect the transformation of adults (Lande 1979, Price et al. 1984a, Schluter 1984). The other approach examines the underlying genetic developmental program leading to different beak sizes and shapes. We will discuss the two approaches in turn, and consider how together they reveal the way changes in size and shape can occur.

Size transformation occurs readily because there is a large amount of genetic variance for size. Genetic covariances and correlations between *fortis* traits are uniformly strong and positive (chapter 3). This implies (Grant 1981c, 1983), and analysis shows (Price et al. 1984a, Schluter 2000), that transformations involving primarily overall size

require less selection than those involving primarily shape; from the *fortis* starting point the *magnirostris* and *fuliginosa* morphologies can be reached more easily than can the *scandens* morphology. Simultaneous changes in shape tend to be opposed by the strong, positive genetic correlations between traits, and in this sense they encounter genetic resistance (Schluter 1984, 1996, 2000); changes in shape are constrained but not prevented (Connor 2012).

SPECIES THAT DIFFER IN SIZE

These points are illustrated with calculations of residual shape change that remains after size changes have been accomplished in the transformation of one species to another (box 12.1). A low value of residual shape change in standard deviation units implies that the transition from one species to another has been largely accomplished by selection on size alone. A high value implies that selection on shape itself is needed. In this exercise we are not attempting to reproduce the actual transitions in both size and shape, nor are we using a known, statistically well-supported phylogeny, which is still not available (Petren et al. 2005). Instead, we use the calculations to illustrate the fact that some morphological transformations are much more easily accomplished than others, perhaps more likely to have occurred than others (Schluter 1996), and possibly to have occurred in less time. In doing so we assume that the genetic covariance matrix changes relatively little during the transformations, which may not always be correct (Grant and Grant 2000a, Björklund et al. 2013). We also assume a continued and sufficient supply of genetic variation, which is supported by experience of long-term responses to selection in animal and plant breeding (Hill and Kirkpatrick 2010). Strong directional selection, continued for up to 50 or 100 generations, has produced continued evolutionary responses in flies (Weber 1996), mice (Keightley 1998), and corn (Walsh 2004). This has been interpreted as the result of new mutations arising continuously and supplementing standing genetic variation (Hill and Kirkpatrick 2010).

Selection on a size factor alone can easily transform species differing in size but scarcely in shape (fig. 12.1). The transformation from *fortis* to *fuliginosa* morphology is a clear example of this. The little variation in shape that is left after selection on size is actually less than the observed change in beak shape from selection in 1985 and 1986 (fig. 11.12). The *fortis* to *magnirostris* transition differs in that the correlated effect on shape of selection on size has been too strong. Genetic facilitation rather than genetic resistance has caused an overshoot of the shape target.

Box 12.1. Species Transitions in Morphology

The core species with genetic and phenotypic data are *fortis* and *scandens* from Daphne (chapter 3). We lack quantitative genetic data from *fuliginosa* and *magnirostris*, and therefore used *fortis*, the most similar species, as the starting point for reconstructing the transitions to *fuliginosa* and *magnirostris* morphologies. We used equal numbers of families for a correlation-based principal components analysis to characterize structural size variation among pairs of these species as the first component. Between 63.0% and 84.9% of the total variation is accounted for in each analysis by PC1, and in all analyses the six morphological traits have approximately equal loadings, which justifies using it as a measure of overall size. The second principal component accounts for most of the remaining variation, 7.8%–25.7%. In each analysis, loadings on PC2 for beak depth and beak width are large and positive, whereas the loading for beak length is negative, and loadings for the other traits are generally small. Therefore, PC2 is mainly a beak-shape factor, varying from pointed to blunt (also Boag 1983, Grant and Grant 1989; chapter 4).

Next we calculated heritabilities for PC1 and PC2 scores for *fortis* and *scandens* and genetic correlations between them. Even though the two axes of variation are uncorrelated in the combined data, the individual species do sometimes display positive correlations. Heritable variation for the size and shape factors and the additive genetic correlation between them vary strongly among the species (table 1.10 in Grant and Grant 2000a). Third, we calculated the net forces of selection on the size factor (alone) involved in each of the four possible (reciprocal) species transformations using these genetic parameters and the phenotypic distances in standard deviation units of principal components scores. Shape changes arising from selection solely on size were calculated from these measures of selection and genetic variation and covariation; they are the product of the net forces of selection on size, the square root of the heritability of size, and the genetic correlation between size and shape (Lande 1979, Price et al. 1984b, Schluter 1984). What remains is residual shape differences between species.

SPECIES THAT DIFFER IN SHAPE

Among the four species on Daphne those that differ most in shape, *fortis* and *scandens*, are the least interconvertible by selection. Asterisks in the lower part of figure 12.1 show that selection on size of either

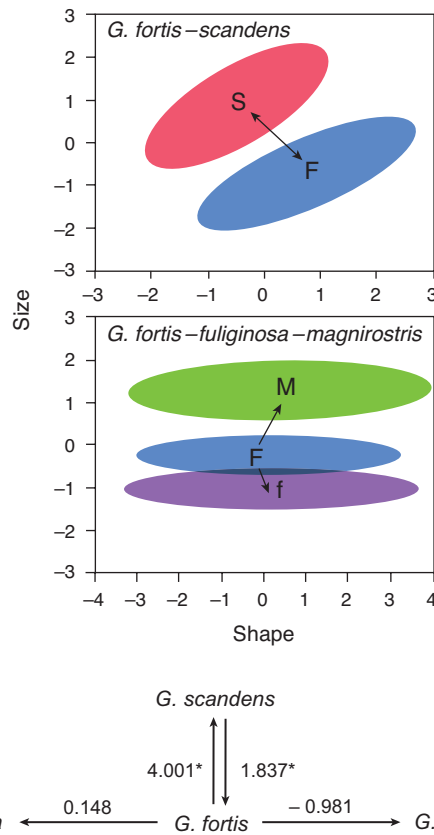


Fig. 12.1 Evolutionary transitions along body size (PC1) and beak shape (PC2) axes (upper), and residual shape changes in standard deviation units after the size changes alone have been effected (lower). A negative sign indicates that change in shape associated with a change in size has gone too far, and residual shape change must be in the reverse direction. An asterisk shows that the difference in shape between two species has increased as a result of a change in size. From Grant and Grant 2000a.

species results in a correlated shape change in the opposite direction, so that the difference between species in shape becomes magnified as selection decreases the difference in size, and vice versa. We reason from this conflict that the ancestor was possibly smaller than both of the extant species and possessed a pointed beak, for then each transformation would have proceeded with little genetic resistance. This reasoning is consistent with the molecular phylogeny (Petren et al. 1999b, 2005, Sato et al. 1999) that shows pointed-beaked species, and

specifically *Geospiza difficilis* (Sharp-beaked Ground Finch), to be basal to cactus and granivorous ground finches.

Despite strong positive correlations between the primary traits of beak length, depth, and width, changes in shape do occur, as shown by both *fortis* and *scandens* but in different ways (fig. 11.12). Changes in beak proportions of *fortis* were produced by natural selection (chapter 4), which shows that heritable beak proportions and not just individual beak dimensions are sometimes the target of selection. Changes in beak proportions of *scandens* were produced by introgressive hybridization with *fortis* in the absence of selection. Therefore genetic constraints on changes in shape are not absolute in these species; they can be circumvented. Furthermore the genetic constraints themselves change when the genes governing development of different beak dimensions undergo change.

Genetic Transformation in Speciation

In the absence of genetic incompatibilities, the genetics of speciation is the genetics of beak divergence. What are the genetic changes involved in the morphological changes taking place during speciation? The place to look for them is in development (Price and Grant 1985, Björklund 1993, Grant et al. 2006). The four species differ in beak proportions at the time of hatching, which implies differences in embryonic growth, and they also differ in relative growth rates of different dimensions after hatching (Grant 1981c). Hence the genetic divergence that accompanied species formation involved evolution of developmental differences. Recent discoveries in developmental genetics have identified genes affecting embryonic beak development in the finches, and have characterized differences in expression patterns among closely related species (fig. 12.2). These are parallel to discoveries in plants and animals in other systems, in both plants and animals, of key regulatory genes that have undergone change by mutation (Shapiro et al. 2004), introgression (Kim et al. 2008), or polyploidization (Barrier et al. 2001), and been subject to selection.

G. magnirostris, *fortis*, and *fuliginosa* differ in the size and robustness of their beaks. This variation in adult beak morphology is paralleled by variation in the expression of a gene responsible for producing a signaling molecule, *Bmp4*, in the prenasal cartilage (*pnc*) in all three species at days 5 to 6 during 12 days of embryonic development—earlier and more intensely in the development of *magnirostris* than in the other species (Abzhanov et al. 2004; also Wu et al. 2004, Campàs et al. 2010). The association is more than just a correlation: experiments

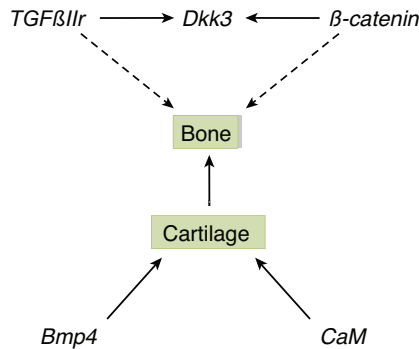


Fig. 12.2 Growth of beak dimensions is affected by the expression of different genes at different times during development. Bone morphogenetic protein 4 (*Bmp4*) affects beak depth and width, and Calmodulin (*CaM*) affects beak length in the developing prenasal cartilage. At the later premaxillary bone stage a pathway involving different signaling molecules affects development of beak length and depth only. Based on Mallarino et al. 2011.

have demonstrated a causal role of the molecule (Abzhanov et al. 2004). Thus agents that govern the timing and intensity of expression of the gene, such as other gene products and feedback loops, modulate the development of these beaks differently in the three species. Later in embryonic development the premaxillary bone (*pmx*) is laid down, and another interacting set of genes—*TGFβIIr*, *β-catenin* and *Dickkopf-3*—have similar differential effects on beak development of the three species (Mallarino et al. 2011). Relatively simple changes in gene regulation and the timing of gene expression must have occurred along the *fuliginosa-fortis-magnirostris* axis of the Darwin's finch radiation.

Development of *scandens* is different in two respects: the nature of the molecule and where it is expressed. At the prenasal cartilage stage another signaling molecule involved in a different pathway, calmodulin (*CaM*), is expressed in the growing tip of the embryonic *scandens* beak, but weakly if at all in the other three species (Abzhanov et al. 2006). The longer beak of adult *scandens* is the product of this influence, together with the later-acting set of three molecules at the premaxillary bone stage (Mallarino et al. 2011). The *pmx* trio of genes is expressed dorsally in the granivores and distally in *scandens*. A significant consequence of the combined differences in gene expression is that adult beak length in *scandens* is less strongly correlated genetically with depth and width than are depth and width with each other (chapter 10), and has more freedom to evolve independently (Grant and Grant 1994).

From the static comparison of species differences a picture is beginning to emerge of the evolutionary changes in developmental genetics that accompany speciation. Beak depth, width, and length can be altered one at a time by differential expression of the five identified molecules in three different biochemical pathways, either singly or in combination (Mallarino et al. 2011): length alone by calmodulin (*CaM*), depth and width (but not length) by bone morphogenetic protein 4 (*Bmp4*), and, a little later in development, depth and length (but not width) by *Dickkopf-3*, *TGF β IIr*, or β -*catenin*. Undoubtedly there are many more important molecules yet to be discovered: some candidates, in addition to *Bmp4*, have been discovered in the North American House Finch *Carpodacus mexicanus* (Badyaev et al. 2008, Badyaev 2010, 2011) and Caribbean tanagers related to Darwin's finches (Mallarino et al. 2012).

We would like to know how genes such as *Bmp4* are regulated because changes in regulatory networks are the causes of evolution in the size and shapes of beaks: the *Bmp4* gene itself varies very little among Darwin's finch species (A. Abzhanov pers. comm.). For example, a change in the timing of activation of *Bmp4* in *fortis*, resulting in an earlier onset of tissue-specific expression, potentially results in a deeper and wider adult beak, which is a shift in the direction of *mag-nirostris*. A question for future research is whether such change requires a new mutation, or whether a shuffling of existing variation is all that is necessary to produce just the right combination of genes in the formation of a new species. The next advance in our understanding will come with the identification of genetic differences in development among individuals within a population. Then it will be possible to discover the genetic consequences of selection on adults, because directional selection on adults is indirect selection on developmental programs (Price and Grant 1985). Equally valuable will be determining the genetic and developmental consequences of combining the genomes of species as different as *fortis* and *scandens* through introgressive hybridization.

Growth after Hatching

Nothing is known about gene function after hatching, but there are hints of interspecific differences in expression patterns from differences in growth trajectories, first as nestlings and then as fledglings (Grant 1981c, Boag 1984, Price and Grant 1985, Grant et al. 2006). As adults the three granivore species differ conspicuously in size and to a lesser extent in proportions (chapter 11), so we might expect that they

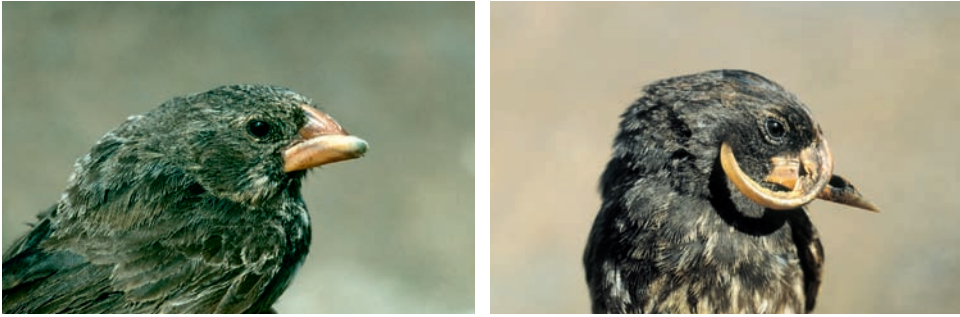


Fig. 12.3 Deformed beaks: disturbance to the normal process of growth cessation. **Left:** Mild hypertrophy of a side of the lower mandible. **Right:** Extreme hypertrophy. This bird picked up small seeds at the base of its beak on the left side. It was able to live for two to three months at the end of the wet season in the presence of plentiful food but failed to survive the following dry season of declining food supply. Birds elsewhere develop similar abnormalities. These include, for example, cardueline finches (Badyaev 2010) and titmice (parids; Handel et al. 2010) in North America.

grow along the same growth trajectory but achieve different adult proportions by stopping at different points along their trajectory (e.g., Badyaev et al. 2001). This turns out to be wrong; each species has a unique trajectory. A significantly faster proportional elongation of the beak occurs in *fuliginosa* than in the other two species. Growth of beak length relative to depth is slowest in *fortis*. Compared with *magnirostris*, the *fortis* trajectory is displaced in the direction of a greater beak length for a given beak depth. Perhaps this reflects a past history of introgression of genes from *scandens*. On Santa Cruz island, where hybridization appears to be much rarer, there is no such displacement (Boag 1984).

G. magnirostris (on Genovesa, and presumably Daphne) is unique in that beak depth initially increases at a faster rate than the other beak dimensions, and then there is a switch, and beak length increases at the faster rate during terminal growth (Grant 1981c). Two associated features of *magnirostris* imply a profound reorganization of timing and amount of resource allocation to the development of these dimensions: reversal of the relative sizes of adult beak lengths and depths, and the unique pattern of static allometry in which beak depth, but not length, varies in proportion to body size among years (fig. 11.11). The lack of scaling, and the same for *scandens* beak depth, is unexpected. It will remain a puzzle until more is known about gene expression in late development, the possible influence of fledgling diets (Genbrugge et al. 2011), and the factors that normally bring growth to an end (fig. 12.3).

Thus expression of developmental genes is likely to vary throughout the growth period in both scale-dependent and scale-independent ways, and not just in early embryonic growth. Although we know that species differ in gene expression and regulation, we are not yet in a position to quantify the differences that accompany speciation.

Rapid Tempo of Speciation

The four finch species on Daphne originally formed and diverged in less than a million years (Petren et al. 2005, Grant and Grant 2008a). Hypothetically the morphological transition from one species to another differing mainly in size, e.g., *fuliginosa* to *fortis*, could take place very rapidly, perhaps in a few hundred years, according to some simple arithmetic. For species of similar beak shape the difference between them in one dimension is about 2 standard deviations of each species' distribution, or 4 standard deviations in total. An evolutionary response of approximately 0.5 standard deviations followed selection events in *fortis* in 1977 and 2004 (table 7.2, fig. 7.5); therefore eight such events could effect a transition from one species to another.

The same conclusion of potentially rapid speciation has been reached in a study of three species of crossbills (*Loxia*) in Europe. They differ in body size and beak size in a manner parallel to the *fuliginosa-fortis-magnirostris* sequence, and differ ecologically too (Marquiss and Rae 2002), yet no difference in mitochondrial and microsatellite DNA has been found, a failure that cannot be attributed to introgressive hybridization (Piertney et al. 2001). Reproductively and ecologically they are three species, whereas genetically, at the studied loci, they are one (Piertney et al. 2001). These examples share with each other and with several other closely related species of birds (e.g., Lack 1944, Schoener 1984) the characteristic of feeding on foods of different size. As more examples of rapid speciation come to light (Milá et al. 2007, Moyle et al. 2009, Kirchman 2012), more will be sought and more will be found.

The two favorable conditions for the Darwin's finch radiation were ecological opportunity and genetic responsiveness. Like archipelagos elsewhere (Hawaii, Caribbean), Galápagos are unusually suitable for rapid diversification because they comprise many islands, well isolated from numerous competitors and predators on continents, and supporting populations in diverse habitats (Ricklefs and Bermingham 2007). Moreover the Galápagos environment changed over the last two million years, with a trend toward aridification in the last million years and presumably colonization of new plant species adapted to those condi-

tions (Grant and Grant 2008a), which permitted exploitation of new food resources in new ways, especially by the granivores. Being phylogenetically young under favorable environmental conditions for diversification, finch populations evolved rapidly owing partly to elevated levels of genetic variation from introgressive hybridization. Rapid evolution of Darwin's finches (fig. 12.4) stands in contrast to slower patterns of diversification elsewhere on continents (Price 2010, Weir and Price 2011). Slower diversification has been characterized by Uyeda et al. (2011) as evolutionary fluctuations apparently bounded within a stable adaptive zone for one million years, and interpreted as local variations in niche optima due to restricted environmental variation. Causes and characteristics of the contrasting finch radiation are discussed further in chapter 15.

Interactions in Sympatry

A critical stage in the evolution of beak differences between species is the encounter of two populations derived from a common ancestor. There must have been countless dispersal and colonization events throughout the archipelago in the course of the Darwin's finch radiation. We witnessed one in 40 years. It gave us insights into both ecological and reproductive interactions between colonists and residents at this critical stage of the speciation cycle when divergence can be enhanced or reversed. Such interactions, occurring frequently, may have contributed to the rapid diversification of the ground finches.

Colonization by *magnirostris* led to ecological character displacement of *fortis* (chapter 7). This demonstrates an evolutionary adjustment of competitors to a limited resource. The two species did not interbreed either at initial contact or any time in the following 30 years, and therefore they are not strictly an example of secondary contact of differentiated populations as in figure 1.1. A hypothetical example of this process would be colonization of Daphne by unusually large *fortis* from another island such as San Cristóbal. They are 20% larger in average beak depth on this island than on Daphne, and with such large beaks they would be, like *magnirostris*, superior exploiters of *Tribulus* fruits.

Lack of interbreeding between *fortis* and *magnirostris* on Daphne shows that they were sufficiently different in beak morphology and song. Both cues are important in mate recognition and choice, but one piece of evidence suggests morphology can be the more important. A minimum of nine *fortis* males sang *magnirostris* song, presumably

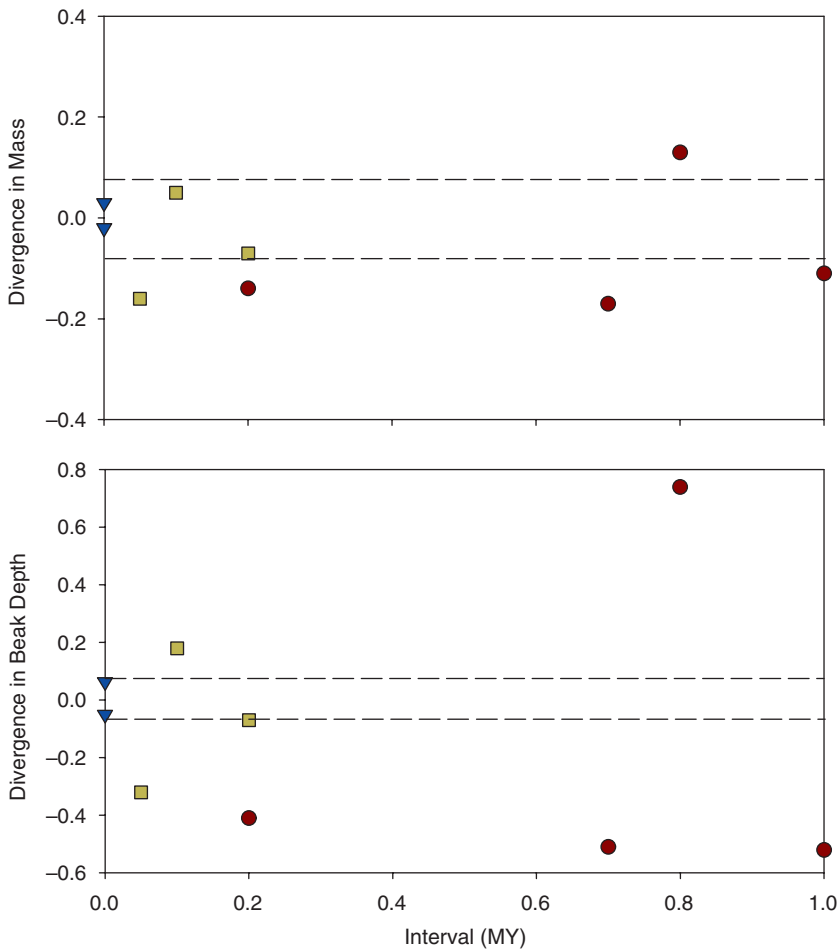


Fig. 12.4 Finches in the genus *Geospiza* have diverged relatively rapidly in beak depth, less so in body size. Divergence is measured as the difference between the means of log-transformed size in pairs of species, and, in the case of mass, weight is divided by 3 to correct for dimensionality. The broken lines show the maximum divergence up to one million years in a large data set of birds in Uyeda et al. 2011: after one million years of independent evolution divergence increases in this set. Squares identify pairs of tree finch species (*Camarhynchus* species), and circles identify pairs of *Geospiza* species. Morphological data are from Grant et al. 1985, and phylogenetic data are from Petren et al. (2005). The two strongest observed selection events in *fortis* are shown by solid triangles: before and after selection means are contrasted.

through learning the song during their sensitive period (figs. 8.6 and 8.9), yet none of them bred with *magnirostris* females. *G. magnirostris* males recognized their songs and responded by chasing the *fortis*. We interpret these observations to signify that the beak and body size differences between the species were large enough to prevent interbreeding, regardless of their song.

Nevertheless interactions involving song differences are also important at this stage of secondary contact. The songs of both *fortis* and *scandens* underwent a change after *magnirostris* numbers had increased, starting in the 1990s (Grant and Grant 2010c). Songs of both species became faster in rate of note repetition or trill rate, and in doing so they diverged from the songs of *magnirostris* but not from each other (fig. 12.5). Divergence began well before the character displacement shift in *fortis*, and therefore cannot be simply accounted for as a correlated effect of a change in beak morphology that affects song characteristics (Podos 1997, 2001, Huber and Podos 2006). It happened without a change in the structural habitat more than one meter above ground where birds sing, therefore it cannot be explained as a change in the sound transmission properties of the environment (Wiley 1991, Luther and Wiley 2009). Since songs of two species, *fortis* and *scandens*, changed in the same direction and at the same time, divergence is unlikely to have been caused by random changes (cultural drift). The most likely explanation is acoustic interference between species (Nelson and Marler 1990, Luther 2009). *G. magnirostris* are large and aggressive, frequently interfering with and attempting to take over the nests of *fortis* and *scandens*. Their songs are louder and are in the same frequency bandwidth as the songs of *fortis* and *scandens*. According to this explanation, divergence reduces acoustic and physical interference (Grether et al. 2009), as well as improving communication through learning (Peters et al. 2012, Ríos-Chelén et al. 2012) and transmission (Luther and Wiley 2009, Nemeth et al. 2013) in a noisy environment.

A MECHANISM PRODUCING SONG DIVERGENCE

Divergence from *magnirostris* songs appears to be an example of the phenomenon known as a peak shift (ten Cate et al. 2006, ten Cate and Rowe 2007). During the process of discriminatory learning and production, an individual learns to respond to an exaggerated form of the desired signal or part of the signal in a direction away from a negative stimulus. This happens if there is a penalty to interactions with a heterospecific individual, such as the larger, socially dominant *magnirostris*. For example, a son, surrounded by singing heterospecifics during

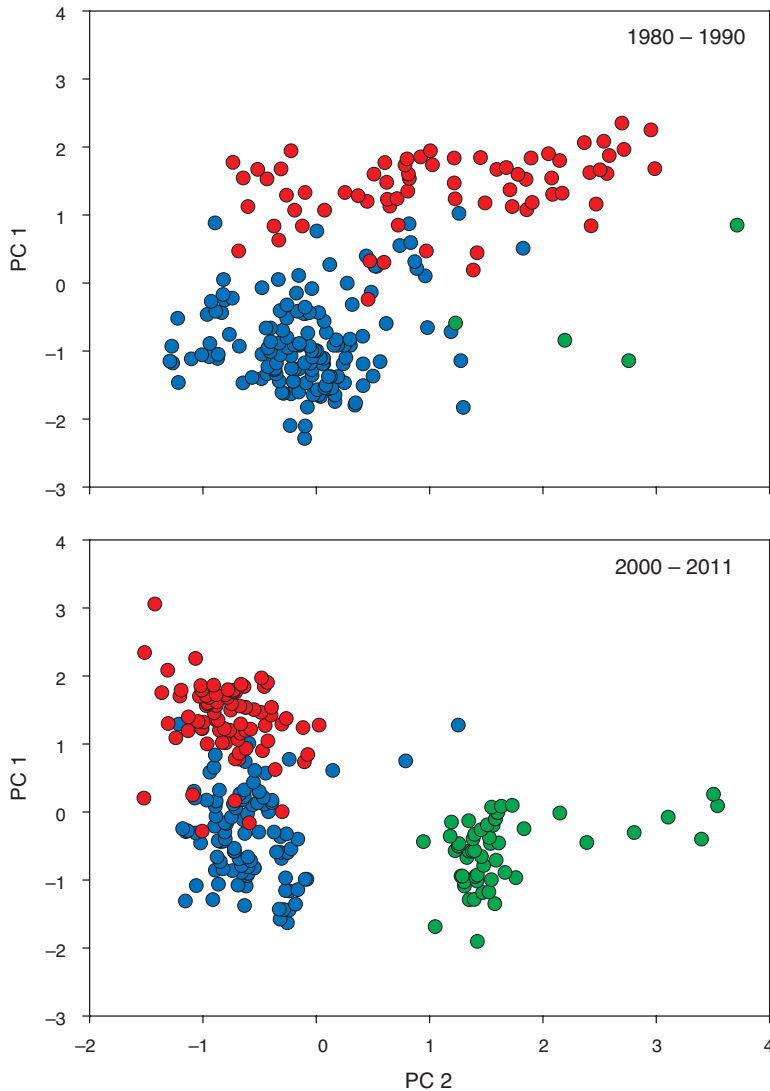


Fig. 12.5 Songs of *fortis* (blue), *scandens* (red), and *magnirostris* (green). Songs were recorded from 1980 to 1990, when there were few or no singing *magnirostris* present, and again from 2000 to 2011, when *magnirostris* were common. All individuals were recorded once only. Comparison of the two time periods shows the extent of divergence of *fortis* and *scandens* songs away from *magnirostris* songs. Variables used in the analysis were trill rate, song duration, and frequency bandwidth. Both *fortis* and *scandens* songs became shorter and trill rate (notes/sec) became faster (PC2), whereas frequency bandwidth (PC1) did not change. The songs of two *scandens* recorded in 2011, 19527 and 19518, were outliers and were removed from the analysis. Both had very fast songs of 35 and 36 notes per second respectively, and were furthest removed from *magnirostris*. Adapted from Grant and Grant 2010c.

his sensitive period of learning or production of song, would be expected to learn and produce elements of conspecific song that were clearly distinct and not blocked by sympatric heterospecific song.

We investigated the mechanism of change and found the origin was in the song learning process (Grant and Grant 2010c). Although sons copy songs of their father quite faithfully, we discovered they produced slightly faster songs than their fathers during this period of change. For those individuals of each species tested in adulthood twice, trill rate was faster at the second time in the 1990s than at the first time in the 1980s. This trend occurred in all of 10 *fortis* individuals and in 8 of 9 *scandens* individuals. Other characteristics of the song, such as song length and number of notes, did not change.

We found no evidence of a female mating preference for males that sang an exaggerated form of conspecific song that is clearly distinct from *magnirostris* song, even though one might be expected. Thus the song shift was restricted to males, a form of agonistic reproductive character displacement (Grether et al. 2009).

Summary

Speciation occurs when one species splits into two populations or sets of populations that do not interbreed or interbreed rarely with little genetic exchange. We observe the products, species, and attempt to reconstruct the process by which they were formed. In this chapter we use information from adult morphology of Daphne finches and genes expressed in the development of beaks to reconstruct and interpret the transformation of species. The three granivore species, *fuliginosa*, *fortis*, and *magnirostris*, constitute an allometric series of large differences in size accompanied by small changes in beak shape. Transformation of these morphologies in either direction can be effected mostly by selection on highly heritable size variation alone; beaks change in shape as a correlated effect. *G. scandens* differs from the granivorous species in beak proportions, and correspondingly the change from one adult morphology to another is less easily effected by selection on size variation alone. A different transformation is suggested by the genetic factors in beak development of *scandens*: they differ in kind and in location of expression from those governing beak shape development of the granivores. The three granivore species differ primarily in timing and intensity of expression of a few developmental genes.

Other species are part of the selective environment of each species. When previously separate populations encounter each other, they may

diverge as a result of selection, which promotes speciation, or converge through introgressive hybridization, causing speciation to collapse. Separate populations encountered each other when Daphne was colonized by *magnirostris*. In addition to causing ecological character displacement in *fortis*, *magnirostris* affected the songs of *fortis* and *scandens*. Their songs diverged from the songs of *magnirostris*, which we interpret as a learning response that resulted in a reduction of both acoustic and physical interference from a socially dominant species.