Beaks, Adaptation, and Vocal Evolution in Darwin's Finches

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Darwin's finches are well known for their remarkable diversity in beak form and function. Field studies have shown that beaks evolve by natural selection in response to variation in local ecological conditions. We posit a new hypothesis: As a consequence of beak evolution, there have been changes in the structure of finch vocal signals. We base this hypothesis on the discovery that beaks play a functional role in song production in songbirds. Recent field studies provide support for a link between beak morphology and song structure in Darwin's finches, although much remains to be learned. Because song plays a significant role in finch mating dynamics, we suggest that the functional link between beaks and song may have contributed to the process of speciation and adaptive radiation in these birds.

Keywords: adaptive radiation, birdsong, speciation, vocal production, animal behavior

Darwin's finches of the Galápagos Islands, Ecuador, are one of the most celebrated illustrations of adaptive radiation (Schluter 2000, Grant PR and Grant BR 2002a). These birds have evolved an impressive array of specializations in beak form and function, in accordance with the diverse feeding niches they have come to occupy (Lack 1947, Bowman 1961, Grant PR 1999). The evolutionary processes that drive beak diversification in Darwin's finches are particularly well documented, largely because of the long-term field studies of Peter Grant and Rosemary Grant and their colleagues. One major finding of the Grants' research program is that beaks evolve, by means of natural selection, in precise correspondence to changing ecological conditions, including food availability and interspecific competition (Schluter et al. 1985, Grant PR and Grant BR 1995, 2002b). A well-known study on medium ground finches (*Geospiza fortis*) of Daphne Major Island illustrates this process. During drought conditions, birds with relatively deep beaks were shown to enjoy a disproportionate likelihood of survival because of their superior ability to husk the hard seeds that were available (Boag and Grant 1981, Price et al. 1984). Because beak morphology is highly heritable (Boag 1983), subsequent generations expressed deeper beaks, on average, following drought years. Studies of Darwin's finches have provided some of science's most compelling examples of how natural selection can drive phenotypic change (Endler 1986, Weiner 1994, Schluter 2000) and have played an important role in the dissemination of core concepts in evolution to the broader public (Weiner 1994).

Here we describe a new avenue of research with Darwin's finches, which posits that the adaptive evolution of beaks for feeding has influenced, as an incidental consequence, the acoustic structure of the songs these birds sing. This possibility was first suggested by studies of vocal mechanics in other songbird species, which demonstrated the essential contribution of beak movements to sound production. One finding in particular—that songbirds must actively adjust the extent to which their beaks are open and closed while singing to maintain the musical quality of their songs (a mechanism described in more detail below)—implies that divergence in beak form and function may drive divergence in vocal performance abilities and, ultimately, in the acoustic structure of song features. Darwin's finches are a promising group for exploring the evolutionary relationship between beaks and song, not only because of the wide diversity of their beaks but also because of the rich evolutionary and ecological context provided by prior research on these birds (Grant PR 1999). Our goal is to show how research on the relationship between beaks and song is providing novel insights into the interplay of morphological adaptation and the evolution of communication signals. Furthermore, because song is an important mating signal in these birds, this research program ultimately may provide insights into fundamental questions about

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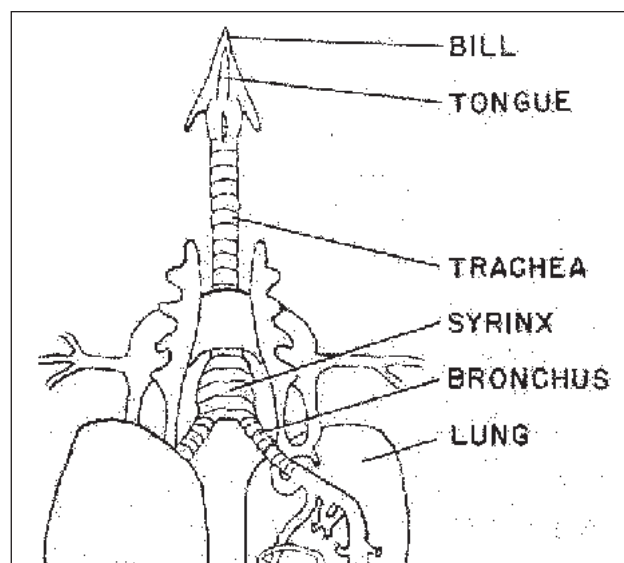
Figure 1. Schematic of the avian vocal apparatus. Modified from Welty (1982).

speciation and adaptive radiation in these birds. To begin, we outline recent advances in the study of vocal mechanics in songbirds, with emphasis on the role of the beak in sound production.

Beaks and sound production

Research on vocal mechanics in birds has a long and rich history, driven in part by curiosity about the distinctive vocal abilities of birds as compared with other vertebrates (Nowicki and Marler 1988). It has long been known that the sound source in birds is the syrinx, an organ found only in this class of animals (Greenewalt 1968). The syrinx, located near the base of the trachea (figure 1), produces sound in a manner analogous to the way the human larynx works during speech production: Air flow from the lungs causes tissues to vibrate in a periodic fashion, thus generating sound (Greenewalt 1968). In songbirds, a pair of thin membranes, the medial tympaniform membranes, are thought to act as dual sound sources (Greenewalt 1968, Ames 1971), although it now appears that additional syringeal tissues also contribute to sound production (Goller and Larsen 1997).

Recent studies have demonstrated that sound production depends not just on the syrinx but also on the activity of other musculoskeletal systems upstream and downstream of this organ. Movements of respiratory muscles, for example, are finely coordinated with syringeal activity and appear to be essential for controlling the timing of vocalizations (Suthers et al. 1999). Elements of the vocal tract anterior to the syrinx, including the trachea, larynx, and beak, also play a key role in sound production by modifying the spectral structure of sounds produced by the syrinx (Nowicki 1987). The syrinx itself is thought to generate a signal with acoustic energy at a wide range of frequencies representing harmonic overtones of a fundamental frequency, not unlike a voiced speech sound (albeit at a much higher frequency). As sounds pass

through the vocal tract, harmonic overtones are selectively dampened while the fundamental frequency tends to pass without attenuation (Nowicki 1987, Westneat et al. 1993, Beckers et al. 2003). The vocal tract thus acts as a resonance filter, enabling birds to produce highly pure tonal, whistlelike sounds in which acoustic energy is concentrated at a single frequency. The resonance function of the songbird vocal tract is roughly analogous to that of the horns of brass and woodwind instruments and contributes to the musical quality of birdsongs. (The avian vocal tract is like the tube of a woodwind or brass instrument primarily in the sense that it is an acoustic resonator. It is unlike a musical instrument, however, in that instruments tend to have their resonances tightly coupled [by impedance matching] to the sound source, so that the source is constrained to vibrate only at allowed frequencies. The avian vocal tract acts more as an uncoupled passive acoustic filter [Nowicki and Marler 1988, Rossing 1990].)

The demonstration that the avian vocal tract acts as a resonance filter raises an interesting question about song production. Songbird vocalizations are characterized by extensive and rapid changes in acoustic frequency. A typical sparrow or warbler, for example, may produce songs that sweep across thousands of hertz (cycles per second) in the course of only a few milliseconds. However, a vocal tract of a given physical configuration should be effective as a resonance filter over only a narrow range of source frequencies. How, then, do songbirds manage to produce pure tonal sounds across a wide range of frequencies? The answer is that singing birds actively adjust their vocal tract configurations, and thus vocal tract resonance properties, in a way that precisely tracks changes in frequencies produced by the syringeal source. A bird may change the configuration of its vocal tract in a variety of ways, the most obvious and best studied of which involves changes in beak gape. As a songbird opens or closes its beak, it effectively shortens or lengthens its vocal tract, respectively, with the acoustic result being a shift of vocal tract resonance properties (Nowicki 1987, Westneat et al. 1993). This relationship leads to the prediction, now supported by data from a variety of species, that birds open their beaks more widely when singing higher-pitched sounds than lower-pitched ones; moreover, they open and close their beaks in precise register with frequency changes at the syrinx (Hausberger et al. 1991, Westneat et al. 1993, Podos et al. 1995, Fletcher and Tarnopolsky 1999, Williams 2001, Podos et al. 2004). An analogy can again be drawn to brass and woodwind instruments. As musicians sweep through a range of frequencies, they adjust the resonance properties of their instruments using mechanisms such as valves, slides, or holes that can be opened or closed. These adjustments add to or subtract from the effective length of the tube, thus shifting its resonances to lower or higher frequencies. The importance of beak movements in song production has been supported by experiments in which the perturbation of normal beak movements leads to predicted changes in the tonal quality of songs (Hoese et al. 2000).

How then might natural variation in beak form and function, such as that expressed so prominently in Darwin's

finches, influence song production and evolution? Perhaps the most straightforward prediction is that species with large beaks, and therefore larger vocal tracts, should evolve songs with lower vocal frequencies. This is because longer tubes have lower frequency resonances. Maria Palacios and Pablo Tubaro (2000) conducted a test of this prediction in a group of Neotropical woodcreepers, the Dendrocolaptinae. These birds show unusually pronounced variation in bill length, and species with longer bills indeed produce calls with lower frequencies. These authors recognized, however, like others before them (Ryan and Brenowitz 1985), that call frequencies may also be influenced by variation in body size and phylogenetic history. Birds with larger body sizes, for example, tend to have larger syringes, and larger syrinx tissues are expected to vibrate more slowly and thus produce vocalizations at lower frequencies. To account for this possibility, Palacios and Tubaro controlled for body size and phylogeny by analyzing the residuals (that is, deviations from a linear regression) of beak length over body size within a comparative context. With these factors controlled, beak length and emphasized vocal frequencies retained their significant negative relationship, thus supporting the original prediction.

The preceding example shows how aspects of beak form can influence vocal evolution. Patterns of vocal evolution may also be shaped by variation in beak function, given the active role of beak movements in sound production. This idea was first suggested by Nowicki and colleagues (1992), who hypothesized that the diversification of beaks could bias the evolution of song parameters that depend on dynamic changes in vocal tract configuration. If, for example, selection drives a species to specialize on hard seeds, then corresponding changes in the biomechanics and neural control of jaw function may limit those birds' abilities to conduct rapid changes in beak gape. Such constraints, maintained over evolutionary time, may set limits on the evolution of particular song parameters (Nowicki et al. 1992, Podos and Nowicki forthcoming). For bird groups such as Darwin's finches, in which beaks have undergone broad changes in the context of selection for feeding, corresponding changes to vocal performance may lead to particularly pronounced variations in song structure.

In the next sections, we ask whether and how divergence in beak form and function in Darwin's finches might have influenced the evolution of their songs. To this end, we first provide a brief overview entitled "The Squeak of the Finch" (a title adapted shamelessly from Jonathan Weiner's acclaimed book [1994]), in which we summarize what is known about song structure and function in this group of birds.

The squeak of the finch

The first detailed descriptions of Darwin's finch songs were published a century ago, in Robert Snodgrass and Edmund Heller's (1904) field account of the Hopkins–Stanford expedition to the Galápagos Islands. (More rudimentary song descriptions had been provided by Rothschild and Hartert 2 years earlier, in their 1902 account of the Webster–Harris

expedition. See Larson [2001] for an engaging account of these and other Galápagos expeditions.) Snodgrass and Heller described finch songs using written annotations, as illustrated in the following example of a medium ground finch song type on Isabela Island: "One song consisted of two syllables of which the first had an ê sound (thêre)...while the second had a long e sound and carried the accent. The song may be represented thus: têr-r-r-wee', têr-r-r-wee'" (p. 322). Annotations were recorded for populations of 9 of the 15 presently recognized Darwin's finch species, and together they suggest three broad patterns characterizing songs in this group of birds. First, Darwin's finch songs were recognized as being simple in structure, often composed of two or three repetitions of the same syllable (as in the example above). Second, these authors observed substantial within-species variation in song structure. In their account of the small ground finch (*Geospiza fuliginosa*), for example, Snodgrass and Heller identified by ear over two dozen song types from five populations. The third broad pattern was that populations of different species sometimes produce similar songs. For example, Snodgrass and Heller (1904, p. 325) observed that a *G. fortis* song type from Floreana Island "almost exactly resembled" a *G. fuliginosa* song type from Isabela Island.

These three generalizations about Darwin's finch songs—simplicity, variability, and cross-species overlap—were consistent with subsequent observations made by David Lack (1945, 1947) and then confirmed through quantitative analyses by Laurene Ratcliffe (1981) and Robert Bowman (1983). Bowman's song sample was particularly impressive in its scope, including hundreds of sound recordings of all 15 finch species across 13 islands. A main thesis of Bowman's (1983) survey is that Darwin's finch songs are all variants of several simple structural patterns. Although this thesis is debatable, it seems clear from his account that finch songs are structurally simple, particularly in that they are often composed of several repetitions of the same syllable. Bowman's account also provides ample illustrations of within-species variation (e.g., Bowman 1983, figure 31) and of similarity in song patterns across different species (e.g., Bowman 1983, figure 33). Ratcliffe (1981) provided a more quantitative demonstration of song variation and overlap in her studies of the six *Geospiza* species. Analyses of variance on seven song features quantified by Ratcliffe illustrated significant within-species heterogeneity, thus indicating wide within-species variation in song. Moreover, over half of her song sample could not be accurately categorized to species using stepwise discriminant function analysis, which indicated that there was substantial overlap among species in the acoustic features of their songs.

These descriptive analyses of song structure in Darwin's finches raise important questions about their potential efficacy as communication signals. As is the case for many songbirds, the songs of Darwin's finches are produced exclusively by males and are used primarily in two contexts, territory defense and mate attraction (Lack 1947, Bowman 1983, Grant PR 1999). The effectiveness of songs in both of these contexts depends in part on how well they provide listeners

with accurate information about species identity (Catchpole and Slater 1995). In a number of songbirds, the functional effectiveness of songs has been shown to depend on the presence of both characteristic song features within species and distinctive song features among species (Emlen 1972, Nelson 1989). Both patterns make it easier for birds to identify members of their own species. The finding that Darwin's finch songs are highly variable and overlapping across species thus suggests that songs may not be reliable indicators of species identity in these birds (Lack 1947). A partial solution to this problem was offered by Ratcliffe (1981), who pointed out that song overlap is problematic only for populations that overlap geographically. Using a multivariate analysis of measured song parameters, she demonstrated that the songs of most sympatric *Geospiza* populations are indeed distinctive (Ratcliffe 1981). More significantly, song playback studies with territorial males confirmed that the birds themselves can discriminate between conspecific and sympatric heterospecific songs in the context of territorial defense (Ratcliffe and Grant 1985).

A significant role for song in the context of mate attraction and mate recognition has been confirmed through observations of finch mating patterns (Grant BR and Grant PR 1998). The Grants have found that nestlings of the two most abundant species (*G. fortis* and *Geospiza scandens*) on Daphne Major Island are reared on occasion by parents of the other species, as a result of nest takeovers. When this happens, the young males learn the song patterns of their adoptive, or "social," fathers and thus send mixed messages upon maturation; visual cues, including beak shape, indicate they belong to one species, whereas acoustic signals suggest they belong to the other. These misimprinted birds are observed to attract, in the vast majority of instances, heterospecific rather than conspecific mates (Grant BR and Grant PR 1998). Thus, vocal cues trump visual cues, at least when the two present conflicting information.

Growing evidence in Darwin's finches of a key role for song in species recognition and mate choice highlights the need to better understand the causes of song diversification, because patterns of song diversity have a direct influence on interspecies mating dynamics, probabilities of hybridization, and ultimately the process of speciation (e.g., Grant PR and Grant BR 1997). We argue that the mechanical relationship between beak function and vocal performance may contribute to the divergence in song parameters in a way that has interesting evolutionary consequences.

In the next section, we present our argument in more specific terms. We outline the biomechanical basis for the predicted link between adaptations for feeding and the divergence of vocal performance abilities, then describe recent tests of these hypotheses.

Darwin's finches: An avian symphony orchestra?

The diversity of Darwin's finch beaks has been famously described by an analogy to different types of pliers. Present-day species express a full toolbox: large and powerful lineman's pliers for *Geospiza* ground finches that must crack large, hard seeds; small and versatile needle-nose pliers for *Certhidea* warbler finches that glean insects from vegetation; and many models in between (Bowman 1963). The central implication of this analogy is that different beak forms are specialized for different feeding functions, such as crushing or manipulating food items. (The specialization of beak form and function for particular food items does not necessarily exclude finches from eating other foods, however. In fact, Darwin's finches appear to have fairly broad diets in comparison with their mainland emberizine relatives [Schluter 2000].)

We suggest a parallel analogy, relating beak form to the mechanisms of song production: Diversity in beak form and function influences the vocal capabilities of Darwin's finches, much as variation in the structure of musical instruments dictates the kinds of sounds they are best suited to produce. In other words, we expect birds with beaks adapted for particular dietary challenges to experience specific constraints and opportunities in their vocal abilities. In species with large, strong beaks adapted for crushing hard seeds, constraints may arise in the speed and complexity of the musical pieces that may be played, because of the burden of a cumbersome vocal instrument (Podos and Nowicki forthcoming). At the other end of the spectrum, birds with slender beaks evolved for probing or grasping should face less severe mechanical constraints on song dynamics.

The biomechanical basis for this analogy has been addressed in two recent field studies of beak function. The first study described patterns of beak gape in relation to the production of song features across a broad sample of Darwin's finch species (Podos et al. 2004). Previous studies of beak movements during song production had been conducted in laboratory settings (Westneat et al. 1993, Podos et al. 1995, Williams 2001), but such an approach is not possible with Darwin's finches because of their protected status. Fortunately, these birds are unusually tame, and singing birds can be videotaped at close range, often within several meters. Beak gape measures during song production were calculated from a sample of video clips, with song frequencies calculated from synchronized audio recordings (Podos et al. 2004).

The main finding of this study is that beak gape correlates positively and significantly with frequency for all seven species studied, as has been shown in other songbirds (figure 2). Furthermore, patterns of beak use during song were found to be mostly conserved across the Darwin's finches. (Patterns of beak use were quantified as the slopes of gape by frequency regressions. Slopes were statistically equivalent among the seven Darwin's finch species and distinct from slopes of white-throated and swamp sparrows [Podos et al. 2004].) These findings suggest that the tendency to match beak gape to source frequencies was present in the common ancestor of the finches, and the correlation was conserved during the finch radiation despite the evolution of substantial variation in beak morphology and body size. This conclusion suggests in turn that adaptations for feeding, and their resulting effects on beak versatility, are likely to have influenced the evolution
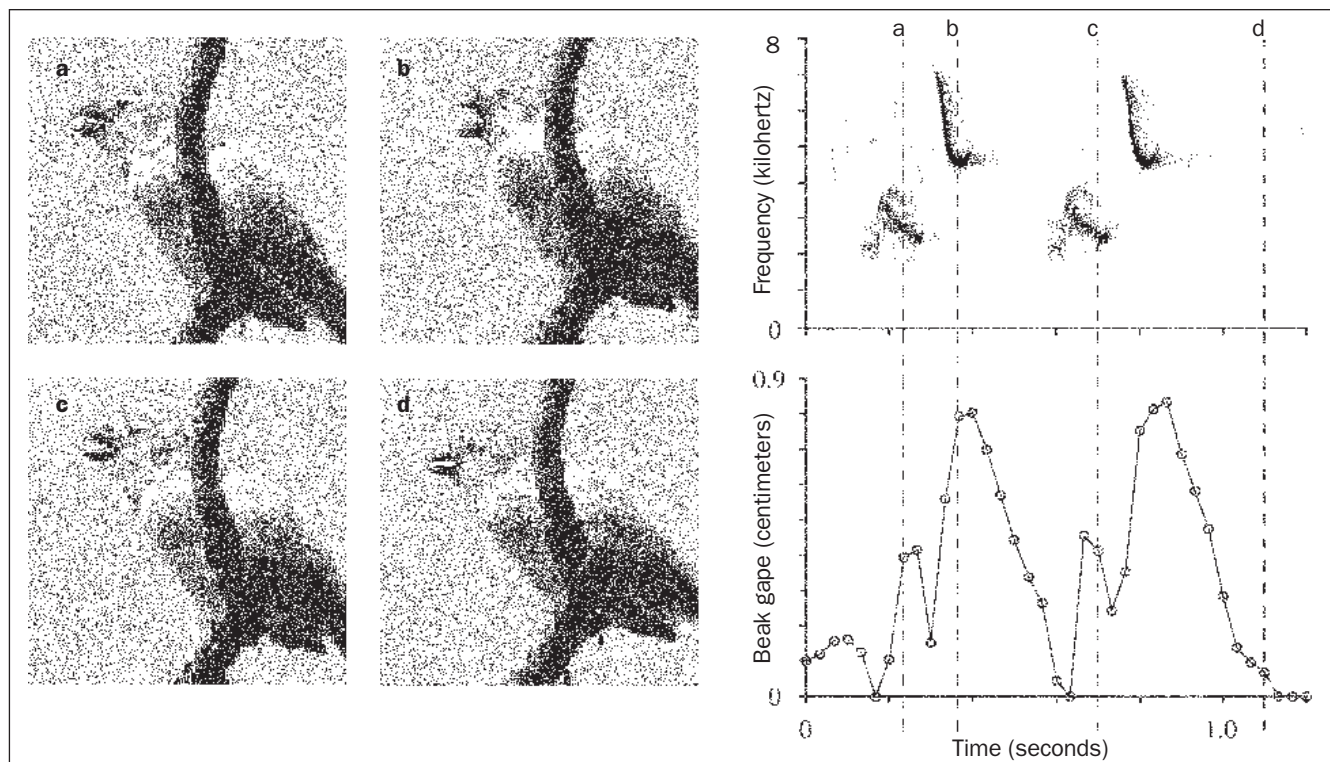
Figure 2. Video sequence of song production by a large tree finch (Camarhynchus psittacula). Left panels are video frames of the singing bird, with gape changes evident during the course of song production. The upper right panel illustrates the sound spectrogram of this song, and the lower right panel illustrates the gape profile for this song. Changes in beak gape map with precision onto changes in song requency. Modified from Podos and colleagues (2004).

of song structure as a secondary consequence. To return to the point first raised by Nowicki and colleagues (1992), consider species that have experienced an overall increase in beak size and strength during the finch radiation, such as the large ground finch *Geospiza magnirostris.* Along with an increase in beak strength, one would predict a reduction in the maximum speeds at which gape changes can occur, because of trade-offs between force and speed in musculoskeletal systems (Podos 2001). The only way for birds to retain the necessary functional relationship between gape and frequency, in the face of a loss in the versatility of vocal tract movements, is to modify patterns of syrinx activity over the course of song evolution.

The second recent study addresses more directly the biomechanical expectation that evolutionary changes in beak morphology and bite force will lead to a reduction in the maximum speed a beak can move (Anthony Herrel, Department of Biology, University of Antwerp, Antwerp, Belgium, personal communication, May 2004). In vertebrate motor systems, evolutionary increases in force can be accomplished through modification of either biomechanical structure or muscle architecture (Herrel et al. 2002). Biomechanical adaptations for force application often involve shifts in lever arm position, which enhance mechanical advantage but also diminish the potential for rapid movement. Adaptations of muscle architecture for enhanced force application, such as through in-

creased muscle size, necessarily reduce the speed of muscle activation. For these reasons we expect that bite-force capacities in Darwin's finches will correspond inversely to their maximum rates of beak movement (Podos 2001). To test this expectation, it is first necessary to quantify maximum bite-force capacities of the finches. Prior studies of bite-force capacities have been based on natural observations of feeding and on measures of the mechanical properties of the foods eaten (Bowman 1961, Abbott et al. 1977, Grant PR 1981). Herrel (personal communication, May 2004) measured maximum bite forces more directly, using custom-built force transducers placed in birds' beaks. This study demonstrated, in a large sample of medium ground finches (*G. fortis*), that two linear dimensions—beak depth and width—are strong predictors of bite force, as is the ratio of depth to width, an aspect of beak shape. These findings support the observation that beak measures are accurate determinants of feeding performance in ground finches (Boag and Grant 1981). The next step will be to quantify speeds of beak gape during song production for birds of known bite force and morphology, to test for the predicted inverse relationship. The recent development of portable video recording technology at higher sampling rates (up to 1000 frames per second) may make such measures possible (Bostwick and Prum 2003).

Insofar as the potential for beak movements is constrained by adaptations for feeding, particularly by adaptations for force

production, we expect to observe correlations between beak morphology and the evolution of song features that depend on the vocal tract matching mechanism described above (Nowicki et al. 1992, Podos and Nowicki forthcoming). Several prior studies identified broad associations between beak morphology and song features in Darwin's finches, although without reference to the possible mechanical influence of beaks on song production. These studies focused on the production of different song types within populations. Ratcliffe (1981) found that medium ground finches (*G. fortis*) on Daphne Major Island that produced different song types differed also in beak lengths and foraging patterns. Rosemary Grant and Peter Grant (1979) observed a similar pattern for large cactus finches (*Geospiza conirostris*) on Genovesa Island during the initial years of a long-term study, although the correlation between song type and beak shape was not maintained in subsequent years (Grant BR and Grant PR 1989). Bowman (1983) noted that the unusually high morphological variation expressed in one particular
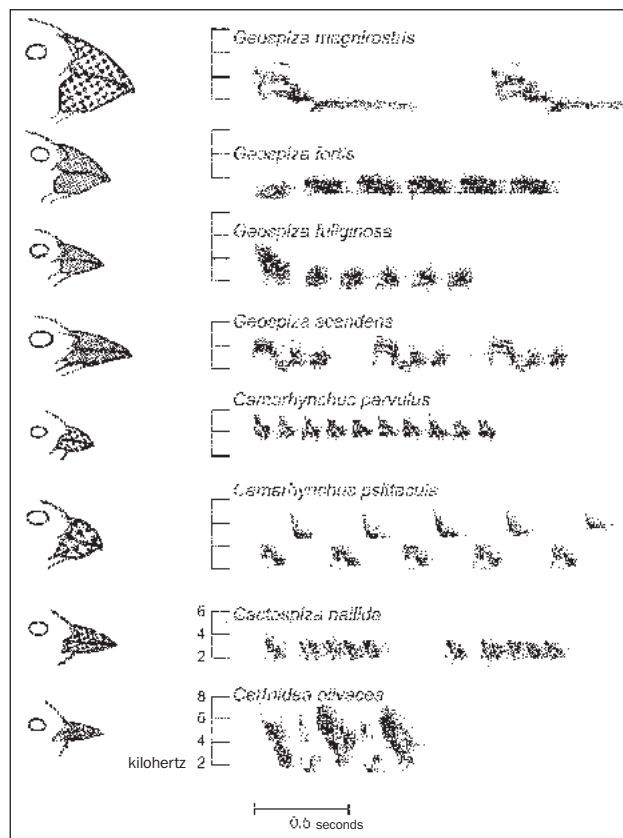

Figure 3. Beak morphology and representative song spectrograms from eight species of Darwin's finches. Interspecific variation is evident in both morphology and song structure. Each of these songs includes trilled segments, which we define as song segments composed of two or more repeated acoustic units. Birds with larger, more cumbersome beaks tend to produce trills with lower rates of syllable repetition and with more narrow frequency ranges. Modified from Podos (2001).

ground finch population—*G. fortis* of Santa Cruz Island (Grant PR 1999)—is matched by an unusually wide diversity of song types. These associations between morphology and song types all appear to be consistent with the hypothesis that the acoustic properties of vocal tracts constrain song production in some way, although this conclusion needs to be confirmed statistically.

A stronger case for an evolutionary relationship between beaks and song can be made if we relate continuous variation in specific song features to patterns of morphological variation. There are a number of song features that we predict are influenced by vocal tract constraints (Podos and Nowicki forthcoming). Two such features are trill rate and frequency bandwidth. Trill rate refers to the number of syllables produced per unit of time, and frequency bandwidth refers to the range of frequencies expressed within the repeating unit of a trill. Increases in both acoustic dimensions require increasingly pronounced or rapid vocal tract movements, if the vocal tract is to retain its function as a resonance filter (Westneat et al. 1993, Podos 1997). To test the potential influence of morphology on the evolution of trill rate and frequency bandwidth, Podos (2001) examined the songs and morphology of individually marked birds from eight Darwin's finch species on Santa Cruz Island. Trill rate and frequency bandwidth were found to correlate with measures of beak morphology in the predicted direction: Larger-beaked birds produced less-"challenging" songs (in terms of motor constraints on vocal production), whereas smaller-beaked birds apparently did not suffer the same severity of constraint (figure 3). There are additional features of Darwin's finch songs that we predict are influenced by mechanical constraints on song production, such as trill syntax and frequency modulation rate, which will be worth examining in future work.

The preceding results are based on interspecific comparisons. Other recent studies have tested for beak–song correlations within species. Within-species studies have the advantage of high comparability among songs (i.e., a clearer identification of homology) but the disadvantage of encompassing narrower ranges of morphological variation. The results of these studies have been mixed. Podos (2001) found that in *G. fortis* on Santa Cruz Island, birds with large beaks produce songs with lower trill rates and more narrow frequency bandwidth, a result that supports the vocal constraint hypothesis. However, in *Geospiza difficilis,* birds from Genovesa Island appear to produce trills with slower rates than their larger-beaked Wolf Island counterparts (Grant BR and Grant PR 2002a). This pattern opposes the predictions of the vocal constraint hypothesis, but it awaits confirmation through formal statistical testing as well as through inclusion of frequency bandwidth as a covariate. A third study examined song variation between the two warbler finch species (*Certhidea*) and showed that the longer-beaked species produces songs with more rapid trill rates and more narrow frequency bandwidths. But these populations showed no significant difference in beak depth, a variable that significantly outweighs beak

length as a determinant of bite force (Grant PR and Grant BR 1995) and thus, presumably, of vocal tract versatility.

We do not mean to imply that evolutionary changes in beak form will necessarily drive changes in song structure. This point is well illustrated in Slabbekoorn and Smith's study (2000) of the songs of large- and small-billed forms of the black-bellied seed-cracker, *Pyrenestes ostrinus.* Large-billed forms are specialized to eat comparatively hard seeds and are thus expected to face comparatively severe constraints on vocal performance. However, the songs of large- and small-billed birds were found to be statistically indistinguishable and overlapping in a wide diversity of song features (Slabbekoorn and Smith 2000). Thus songs were conserved in their structure even as beaks diverged. A possible explanation for this finding is that the songs of this species may not be particularly challenging to produce. Performance limits are expected to be expressed only in songs that require high levels of proficiency, for example, songs in which birds need to repeat quickly the same set of sounds (Podos 1996). Another possible (and complementary) explanation for this pattern is that sexual selection in *Pyrenestes* may be relatively weak, with little or no selective pressure on vocal performance (Podos and Nowicki forthcoming).

We also do not mean to imply that beak divergence is always a central agent of song evolution. Many other factors besides beak divergence have been shown to influence songbird song evolution, including adaptation to local acoustic environments, copy imprecisions during song learning, and patterns of female preference (reviewed by Catchpole and Slater 1995). In Darwin's finches, the most readily detected cause of song evolution appears to be copy error. For instance, in a longitudinal study of *G. fortis,* Grant and Grant documented substantial changes in song structure across generations as a result of errors in cultural transmission (Grant BR and Grant PR 1996). The influence of the other factors is more likely to be detected across broader temporal or comparative scales (Bowman 1979, Podos 2001).

A hypothesis about song and speciation
In this section we explore a new hypothesis about Darwin's finch evolution, which posits that the functional linkage between beaks and songs may have contributed to speciation and adaptive radiation in these birds (Podos 2001). Speciation often begins when ancestral populations separate into multiple daughter populations (Mayr 1963). For example, the rise of a mountain barrier may divide a previously continuous population of riverine fishes into distinct subpopulations. In Darwin's finches, ancestral populations separated into multiple daughter populations through systematic colonization of the Galápagos archipelago. Daughter populations invariably evolve genetic differences, through a combination of genetic drift and adaptation to distinct ecological environments. These genetic differences may accumulate if gene flow among daughter populations is minimal, leading to speciation. By contrast, substantial gene flow counteracts genetic divergence and thus reduces the likelihood

of speciation, unless divergent selection is particularly strong. An understanding of speciation thus requires attention to the nature and strength of barriers to gene flow and to the strength of selection (Dobzhansky 1951, Endler 1977). In many animal groups, including Darwin's finches, the principal barrier to gene flow among incipient species is premating reproductive isolation. Premating isolation refers to the tendency for individuals in descendant lineages to preferentially select mates from their own populations. The dominant role of premating isolation in Darwin's finches is supported by the observation that finch species retain the ability to interbreed and produce viable, fertile hybrids, even though they do so rarely (Grant BR and Grant PR 1998).

The evolution of premating reproductive isolation, in turn, is often contingent on the divergence of mating signals (displays and ornaments) and mate recognition systems (West-Eberhard 1983, Ryan 1986, Butlin and Ritchie 1994). Divergent evolution of mating signals increases the ability of animals to successfully identify conspecific mates and to successfully reject heterospecific mates (Ptacek 2000). Recent studies of speciation have emphasized the role of sexual selection as an agent of mating signal divergence. Sexual selection often drives signals to evolve towards increasingly elaborate and distinct forms (Ryan et al. 1990, Endler 1992, Panhuis et al. 2001).

Natural selection also can influence the evolutionary divergence of mating signals. In a comprehensive review of laboratory studies of speciation, Rice and Hostert (1993) argued that speciation events in animal groups are often catalyzed by the fortuitous pleiotropy (multiple effects of single genes) or close genetic linkage of adaptive loci and traits that mediate reproductive isolation. Under these conditions, selection on one trait may lead to evolutionary changes in the other, nonselected trait. To illustrate, divergent natural selection on the timing of breeding as an adaptive response may have the secondary effect of reducing gene flow among diverging lineages because of the importance of the timing of breeding in mate selection (Rice and Hostert 1993). This mechanism, referred to as "by-product speciation" (Schluter 2000), was first discussed by Dobzhansky (1951) and Mayr (1963) but has gained empirical support only recently (Schluter 1996, 2001, Foster 1999, Via 1999, Filchak et al. 2000, Grant PR et al. 2000, Jiggins et al. 2001). For example, Schluter (1996, 2001) argues that sticklebacks in North American lakes have diverged through by-product speciation. In hundreds of postglacial lakes, these fishes have evolved distinct morphs, benthic and limnetic, as a result of divergent natural selection for different ecological niches. It now appears that ecological divergence is also responsible for restricting gene flow among morphs. The best evidence for this conclusion is the demonstration that similar morphs from different lakes mate readily in experimental tanks because of convergent mating signals and mate recognition systems (Nagel and Schluter 1998, Rundle et al. 2000, Schluter 2000).

In Darwin's finches, feeding and singing behavior both depend on beak form and function, suggesting an opportunity

for by-product speciation. As finch beak morphology evolves by natural selection (Boag and Grant 1981, Price et al. 1984), songs are expected to diverge along predictable axes as a byproduct of selection on beak size and shape. The broad range of ecological opportunities on the Galápagos Islands, and the resulting large-scale divergence in beak morphology, enhances the potential relevance of this mechanism of signal divergence (Podos 2001). As songs evolve, we expect female preferences to evolve in tandem, not so much through genetic changes but because of plasticity in female preferences enabled by learning (Irwin and Price 1999, Sorenson et al. 2003).

Two lines of research will determine the degree to which this by-product speciation model applies to Darwin's finches. First, much remains to be learned about the influence of beak divergence on song evolution. The biomechanical hypotheses are clear but require additional empirical support. Of particular value will be a more complete understanding of how the vocal tract functions in song production. For example, measurements of tracheal and beak volumes will help specify the potential contribution of beak gape to vocal tract resonances (Fletcher and Tarnopolsky 1999). A better understanding of sound production mechanisms will help specify the kinds of vocal parameters that are influenced by variation in beak form and function. Available data are comparative in nature (Podos et al. 2004). It also will be useful to track changes in song structure within populations over time (Grant BR and Grant PR 1996) in tandem with observations of natural selection on beak morphology. Furthermore, studies of misimprinting (Grant BR and Grant PR 1998) can provide insight into the opportunities and constraints associated with different species' vocal mechanisms.

Second, we need to characterize the influence of evolutionary changes in performance-related song features on song function (Podos 2001, Ryan 2001). The extent of evolutionary changes in different song parameters that are required to impede normal species recognition is not known. Furthermore, there are no data addressing the relative importance in species recognition of song parameters linked to performance (e.g., trill rate) versus song parameters driven by other evolutionary factors (e.g., note phonology). These questions ultimately need to be posed to the birds themselves. Simulated territorial intrusions using playback of song have been used successfully to test the responses of male Darwin's finches to conspecific versus heterospecific songs (Ratcliffe and Grant 1985) and to test the functional consequences of within-species variation in song structure (Grant BR and Grant PR 2002a, 2002b). This method might also help quantify the relative salience of specific song parameters linked to vocal performance.

Of greater relevance for testing the by-product mechanism of speciation will be studies of female response to song playback. This is because females ultimately decide which potential mates are acceptable and thus more directly determine patterns of reproductive isolation (Slabbekoorn and Smith 2002). The study of female response is particularly challenging, however. For example, female Darwin's finches rarely respond to song playback in the field, and when they do, they tend to respond aggressively rather than with sexual displays (Ratcliffe and Grant 1985). Two recent studies examined responses of males to song playback in order to infer patterns of reproductive isolation (Grant BR and Grant PR 2002a, 2002b). Such inferences must be viewed with caution, however, because female songbirds tend to be more discriminating than males, given their greater investment in reproduction (Ratcliffe and Otter 1996, Searcy and Yasukawa 1996). An alternative approach that holds particular promise is the study of female Darwin's finches in captivity, using copulation solicitation displays as an assay of female preferences (Searcy 1992, Nowicki et al. 2001).

Conclusions

We have outlined a hypothesis positing that the divergence of beaks in Darwin's finches influences not only their feeding but also their singing behavior. Available data generally support this argument, although additional functional data are needed. It will be interesting to learn whether this kind of correlation also occurs in other songbird groups with specialized beak morphology, such as crossbills or Hawaiian honeycreepers. Darwin's finches exhibit a particularly high level of diversity in beak structure, which makes them more likely candidates for detecting correlated evolution between beaks and song (Podos 2001). Broader taxonomic groups may also include species that vary widely in bill morphology, but comparative studies in such groups would be more difficult, given their deeper phylogenetic separation. The fact that most Darwin's finch songs include trilled sequences provides a convenient way to measure vocal performance (Podos 1997). It may be more difficult to measure vocal performance in groups that produce different kinds of sounds.

We have also speculated on the possible influence of the mechanical link between beaks, song, and the process of speciation. This link is predicated on the hypothesis that performance-related vocal features are used in species recognition. It will be interesting to learn more about the mechanisms that drive evolutionary changes in female preferences. Do evolutionary changes in vocal performance abilities initiate corresponding changes in female preferences? If so, are evolutionary changes in female preferences more a product of imprinting experience than of genetic modification? It is also interesting to consider the possibility that females use performance-related song features in mate choice. Do female ground finches use song features as indicators of beak size, and does this information guide conspecific mate choice? For example, during dry years, might females attend to song features to help them choose large-beaked males? Do preferences for song features change as ecological conditions change? Answers to these and other questions await further field efforts.

Acknowledgments

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