

# Beak morphology and song features covary in a population of Darwin's finches (*Geospiza fortis*)

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Animal mating signals evolve in part through indirect natural selection on anatomical traits that influence signal expression. In songbirds, for example, natural selection on beak form and function can influence the evolution of song features, because of the role of the beak in song production. In this study we characterize the relationship between beak morphology and song features within a bimodal population of *Geospiza fortis* on Santa Cruz Island, Galápagos. This is the only extant population of Darwin's finches that is known to possess a bimodal distribution in beak size. We test the hypothesis that birds with larger beaks are constrained to produce songs with lower frequencies and decreased vocal performance. We find that birds with longer, deeper, and wider beaks produce songs with significantly lower minimum frequencies, maximum frequencies and frequency bandwidths. Results from the analysis of the relationship between beak morphology and trill rate are mixed. Measures of beak morphology correlated positively with 'vocal deviation', a composite index of vocal performance. Overall these results support a resonance model of vocal tract function, and suggest that beak morphology, a primary target of ecological selection in Darwin's finches, affects the evolution of mating signals. We suggest that differences in song between the two modes of the distribution may influence mate recognition and perhaps facilitate assortative mating by beak size and population divergence. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 88, 489–498.

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## INTRODUCTION

The songs of songbirds, produced primarily by males in the contexts of territorial defence and mate attraction, are remarkably diverse in their acoustic structure (e.g. Kroodsma & Byers, 1991; Catchpole & Slater, 1995). Songs of any given species are normally acoustically distinct from those of other sympatric or closely related species. Explaining the evolutionary causes of divergence in song features is a major challenge in the study of bird song.

Studies of song evolution tend to focus on the role of sexual selection in generating vocal diversity (Searcy & Andersson, 1986). However, natural selection can also influence song evolution (Irwin & Price, 1999; De Kort & ten Cate, 2001), and several recent studies

have examined how song features may evolve as a secondary consequence of selection on non-vocal traits (Podos, Huber & Taft, 2004a). Selection on body size, for example, may drive, as a secondary consequence, changes in syrinx size and thus influence the range of vocal frequencies a bird can sing (Ryan & Brenowitz, 1985). Recent evidence for a role of the vocal tract in song production similarly suggests that the evolution of beak form and function, a common axis of evolutionary divergence in birds, may influence song evolution (reviewed by Podos & Nowicki, 2004a, b). In brief, the vocal tract (i.e. trachea, larynx, and beak) acts as a resonance filter during sound production, suppressing the production of harmonic overtones relative to fundamental frequencies produced by the syrinx. The vocal tract, thus, enables birds to produce 'whistle-like' pure-tonal sounds (Nowicki, 1987; Nowicki & Marler, 1988; Beckers, Suthers & ten Cate, 2003). The volume of a bird's vocal tract correlates positively with

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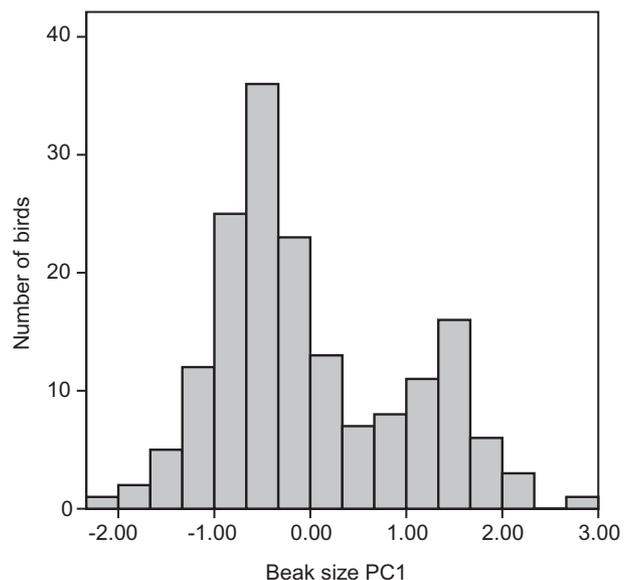
the range of frequencies over which it is best suited to act as a resonance filter. Therefore, birds with larger beaks are expected to produce songs that emphasize lower fundamental frequencies, relative to their body sizes (Palacios & Tubaro, 2000).

Another way that beaks can influence song evolution has been revealed in empirical studies of singing birds, which have shown that birds adjust vocal tract volume in precise register with changes in the fundamental frequencies of their songs (Westneat *et al.*, 1993; Goller, Mallinckrodt & Torti, 2004; Podos, Southall & Rossi-Santos, 2004b). These adjustments enable birds to rapidly alter vocal tract resonance properties and thus maintain the pure-tonal nature of their songs across different fundamental frequencies (Hoese *et al.*, 2000; Beckers *et al.*, 2003). Adjustments to vocal tract volume may be achieved in a number of ways, including through changes in beak gape. Given the observation that beak gape is often tightly correlated with acoustic features such as song frequency (Westneat *et al.*, 1993; Podos *et al.*, 2004b), it follows that limits on beak gape dynamics might impose constraints on song production and evolution (Nowicki, Westneat & Hoese, 1992; Podos, 1997). Constraints on vocal production are particularly evident in vocalizations that consist of repeated notes, known as 'trills'. (Podos, 1996, 1997). Trills require rapid and precisely coordinated modulations of syringeal, respiratory, and vocal tract motor systems. Fast or broad-frequency trills require particularly rapid adjustments in beak gape, which are expected to be challenging for birds with particularly deep or wide beaks, because of trade-offs between force and velocity (Nowicki *et al.*, 1992; Podos, 1997, 2001; see also Herrel, O'Reilly & Richmond, 2002 for an analogous situation in turtles).

The expectation of a functional relationship between beak morphology and trill features was tested by Podos (2001) for Darwin's finches of the Galápagos Islands. Podos (2001) quantified variation in two trill features related to vocal performance: 'trill rate' and 'frequency bandwidth'. Trill rate refers to the number of syllables produced per unit time and frequency bandwidth refers to the range of frequencies expressed within the repeated unit of a trill (Podos, 1997). Across seven species of Darwin's finches, vocal performance was found to correlate with beak morphology as expected; species with larger beaks were shown to produce songs with lower trill rates and narrower frequency bandwidths. An analysis within one species, *Geospiza fortis*, showed a similar result; larger-beaked birds were found to produce songs that require lower levels of vocal performance (Podos, 2001). These analyses, however, did not take into account variation in body size among finch species or individuals. Song frequency in Darwin's finches is correlated with body mass (Bowman, 1983), presumably

because syrinx size scales positively with body size (Cutler, 1970; Bowman, 1983). Moreover, body size has been shown to correlate closely with beak size (Grant *et al.*, 1985). Standardizing beak measures for the influence of body size may thus provide more direct insight into the influence of beak size on song production and evolution (as in Palacios & Tubaro, 2000).

In this study we characterize the relationship between beak morphology and song features within a bimodal population of *G. fortis* (Hendry *et al.*, 2006; Fig. 1). We test the hypothesis that birds with larger beaks produce songs with lower frequencies, as has been shown for dendrocolaptinid woodcreepers (Palacios & Tubaro, 2000). In addition, we characterize the relationship between beak morphology and trill production, as in Podos (2001), but here statistically controlling for the influence of body size. This study also differs from that of Podos (2001) because the focal population here features a bimodal distribution of beak dimensions. This allows us to test the impacts of categorical, as well as continuous, variation in beak morphology on song variation. Predicted outcomes of these tests are guided by the vocal tract constraint hypothesis (Podos & Nowicki, 2004a, b), which posits that birds with larger beaks are able to achieve only comparatively low levels of realized vocal performance.



**Figure 1.** Histogram of beak size in adult male and female *Geospiza fortis* at El Garrapatero, Santa Cruz Island, Galápagos. Beak size PC1 is the first principle component of an analysis that included beak length, beak depth, and beak width as variables. PC1 accounts for 86.30% of the total variation explained.

## METHODS

### STUDY POPULATION

We studied birds at El Garrapatero, Santa Cruz Island, Galápagos, Ecuador (00°40'20"–00°41'20"S, 90°13'10"–90°14'40"W) between January and March in 2003 and 2004. *Geospiza fortis* individuals were captured in mist nets, banded with unique combinations of colour bands, measured, and released. Morphological measurements include beak length, beak depth, beak width, tarsus, wing chord, and mass (as in Grant, 1999). We measured each beak dimension three times and used the median value of each for analyses described below.

We recorded the songs of 37 of our banded males using Sony TC-D5M stereo recorders and Sennheiser K6/ME62 or MKH20 omni-directional microphones, mounted on 22' Telinga parabolas, or K6/ME66 or MKH70 directional microphones. For all song analyses, we digitized songs at a 25 000 Hz sampling rate using SIGNAL sound analysis software (Beeman, 2002).

### SONG AND BEAK MORPHS

A study of morphological variation in this population (Hendry *et al.*, 2006) indicates that the distribution of beak dimensions is bimodal, meaning that individuals fall into two general morphological types, referred to as large and small 'morphs' (Fig. 1). Here we classified males into morphs based on an hierarchical cluster analysis of the first axis of a principle component analysis (PC1). The principle component analysis included beak length, beak depth, beak width, tarsus, wing chord, and mass as variables. PC1 accounts for 80.81% of variation in these variables. The cluster analysis classified 19 birds as large morphs and 18 birds as small morphs.

We then tested whether song types were more similar within morphs than between morphs. Our tests here are based on the expectation that birds with similar-sized beaks experience similar constraints on song production and are thus more likely to sing similar songs. Toward this end, we assessed degrees of song sharing within morphs and between morphs, in pair-wise comparisons of individuals, in both qualitative and quantitative analyses.

For qualitative analyses, printouts of sonograms (fast Fourier transformation (FFT) = 256, frequency resolution = 97.7 Hz, time resolution = 10.2 ms, transform interval = 2 ms, 80.5% overlap of frames in transformations) were sorted into song 'types' by two independent observers who were unaware of the morph designation of the singers. Because each male in our study only sang a single song type, one representative song for each individual was used for sorting ( $N = 37$ ; number of pair-wise comparisons = 666). Sort-

ers were directed to compare all possible pairs of songs and first sort them into 'exact' song type matches, defined as songs with nearly identical note phonology and timing, and then again into 'general' song types, a less stringent criterion, defined as songs that possess similar note phonology and timing. A strict consensus of the results of both sorters was used for further analyses. The strict consensus of exact song type matches resulted in the elimination of 7 pair-wise comparisons (number of pair-wise comparisons = 659). The strict consensus of general song type matches resulted in the elimination of 71 pair-wise comparisons (number of pair-wise comparisons = 595). We compared the number of pair-wise comparisons that resulted in a song type match within morphs and between morphs, with the expectation that more matches would occur within morphs than expected by chance.

For quantitative analyses, digitized song files corresponding to the sonograms used above ( $N = 37$ ) were compared, in a pair-wise fashion, using the cross-correlation function in SIGNAL (Beeman, 2002). This method calculates the similarity of pairs of songs in spectrogram structure (song duration, absolute frequency, and changes in frequency and amplitude). Low similarity, revealed by a correlation value near 0, indicates that the song pair differs greatly in acoustic structure. Correlation values near 1 indicate that the song pair is highly similar in acoustic structure. We compared the mean values of cross-correlation scores from within morph pair-wise comparisons to between morph pair-wise comparisons, to test the expectation that similarity scores would be higher within morphs than between morphs.

### SONG AND CONTINUOUS VARIATION IN BEAK DIMENSIONS

We next examined the relationship between features of song and continuous variation in beak dimensions. For the songs of each individual, we measured minimum and maximum frequencies of each note using power spectra (32 kilopoints, smoothed to a frequency resolution of 300 Hz, amplitude cut-off of -24 dB), calculated frequency bandwidth (maximum–minimum frequency), and measured trill rate from oscillograms (Podos, 1997: fig. 2).

To test the relationship between song features and continuous variation in beak dimensions, we performed a series of simple linear regressions. We used a standard method for removing the influence of body size from beak size. Each beak measure was regressed against the first axis of a principal component analysis that included tarsus, wing chord, and mass (PC1 accounts for 60.0% of the variation in these three measures). The regressions of beak size on body size were conducted for all *G. fortis* banded at El Garrapatero

and Academy Bay on Santa Cruz Island in 2003 and 2004 and included the 37 males used in this analysis ( $N = 591$ ; Beak Length vs. PC1:  $F = 327.93$ ,  $P < 0.0001$ ; Beak Depth vs. PC1:  $F = 517.09$ ,  $P < 0.0001$ ; Beak Width vs. PC1:  $F = 519.57$ ,  $P < 0.0001$ ). We then regressed each song feature on the beak-body size residuals. Simple linear regression analysis was used to quantify the relationship between song features and morphology. In addition, to control for correlations between the three beak measures, we performed stepwise multiple regressions, with all three residual beak measures as independent variables and each song feature as the dependent variable.

We then assessed the relationship between beak morphology and vocal performance. We plotted frequency bandwidth as a function of trill rate for each song and calculated the vocal deviation of each individual's song as an index of vocal performance. Higher vocal deviations indicate lower performance (for methods see Podos, 2001). We then performed a simple linear regression of vocal deviation on the residual beak measures determined above. We also performed a stepwise multiple regression, with all three residual beak measures as independent variables and vocal deviation as the dependent variable.

## RESULTS

### SONG AND BEAK MORPHS

Representative song types from large and small morphs are illustrated in Fig. 2. Song types were found to be more similar within morphs than between morphs. 'Exact' song type matches were identified for six within-morph pair-wise comparisons, but not for any between-morph pair-wise comparisons (Binomial test:  $\chi^2 = 6.00$ ,  $P < 0.05$ ). 'General' song type matches were identified for 223 pair-wise comparisons within morph, but for only 36 pair-wise comparisons between morphs (Binomial test:  $\chi^2 = 135.02$ ,  $P < 0.0001$ ). Cross-correlation similarity scores were higher for within-morph comparisons (mean  $\pm$  SE =  $0.43 \pm 0.006$ ) than for between-morph comparisons (mean  $\pm$  SE =  $0.39 \pm$

$0.004$ ;  $t = -6.49$ , d.f. = 664,  $P < 0.0001$ ). In addition, all song features were significantly different between morphs (Table 1). When frequency bandwidth is plotted as a function of trill rate, we find that small morphs tend to sing at slower trill rates and with wider frequency bandwidths (Fig. 3; see also Table 1).

### SONG AND CONTINUOUS VARIATION IN BEAK DIMENSIONS

In our analysis of the relationship between song features and continuous variation in beak morphology, we find that minimum frequency, maximum frequency, and frequency bandwidth of notes are all significantly negatively correlated with all three size-standardized beak dimensions (Fig. 4A, B, C). By contrast, trill rate was not significantly correlated with any of the size-standardized beak measurements (Fig. 4D). Regressions of vocal deviation on size-standardized measures of beak dimensions yielded significant positive correlations for all three beak measures (Fig. 4E). All stepwise multiple linear regressions retained a significant model with all three residual beak measures (minimum frequency:  $F = 2.81$ ,  $P = 0.05$ ; maximum frequency:  $F = 5.16$ ,  $P = 0.005$ ; frequency bandwidth:  $F = 3.15$ ,  $P = 0.04$ ; vocal deviation:  $F = 3.10$ ,  $P = 0.04$ ).

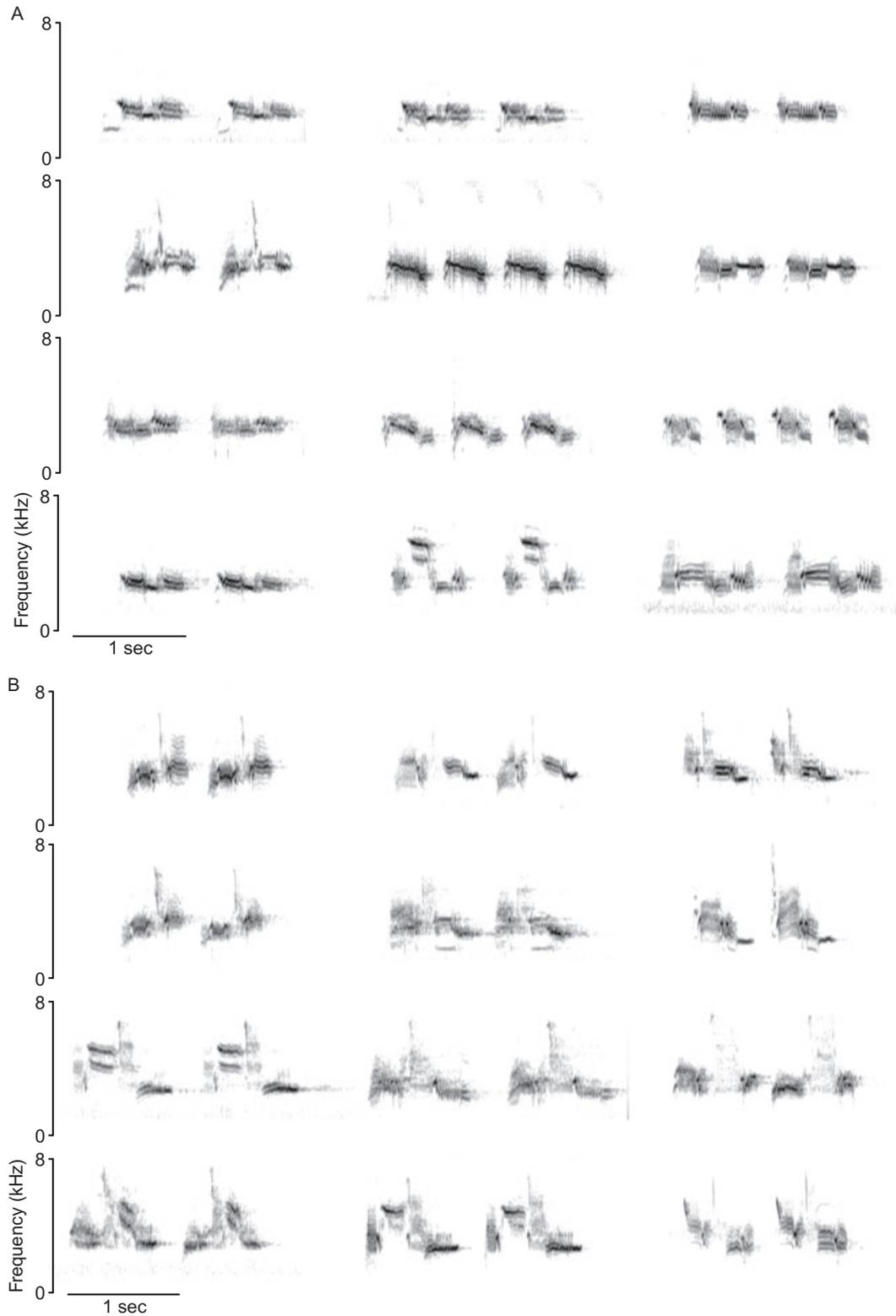
## DISCUSSION

### BEAK MORPHOLOGY AND SONG

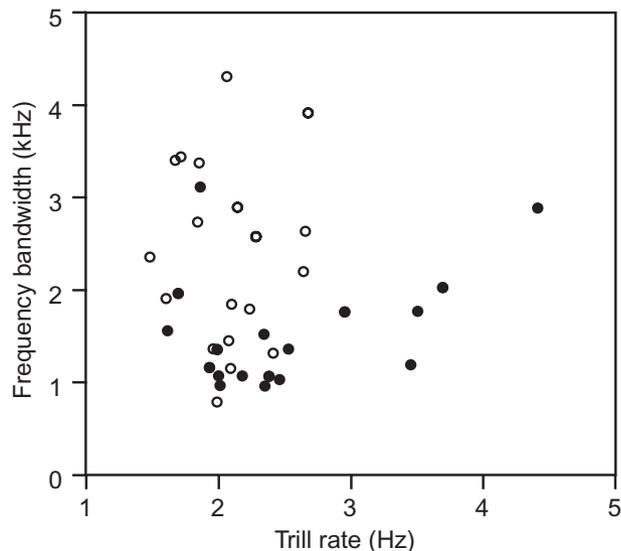
In prior studies, variation in beak morphology has been found to correlate with acoustic features of songs, presumably due to the role of beak morphology and function in song production (Palacios & Tubaro, 2000; Podos, 2001). Larger beaks increase the volume of the vocal tract, making it more suitable for the production of low frequency songs. Here we find, in *G. fortis* on Santa Cruz Island, that beak morphology is correlated with frequency components of songs, in a pattern that is consistent with vocal tract function: birds with longer, deeper, and wider beaks produce songs with

**Table 1.** Mean and standard error of song features for each *Geospiza fortis* morph (large morph:  $N = 19$ ; small morph:  $N = 18$ )

	Mean $\pm$ SE of song features			<i>t</i> -test (d.f. = 35)	<i>P</i>
	Large morph	Small morph			
Minimum frequency (kHz)	2.10 $\pm$ 0.05	2.34 $\pm$ 0.05		3.49	0.001
Maximum frequency (kHz)	3.71 $\pm$ 0.15	4.71 $\pm$ 0.23		3.63	0.001
Frequency bandwidth (kHz)	1.62 $\pm$ 0.16	2.37 $\pm$ 0.24		2.64	0.012
Trill rate (Hz)	2.50 $\pm$ 0.17	2.07 $\pm$ 0.08		-2.16	0.038
Vocal deviation	5.58 $\pm$ 0.16	4.89 $\pm$ 0.24		-2.41	0.021



**Figure 2.** Representative sonograms from 24 individual *Geospiza fortis*. A, sonograms from 12 different large morph males. B, sonograms from 12 different small morph males. Songs were digitized at 25 000 Hz sampling rate using SIGNAL sound analysis software (Beeman, 2002), and sonograms were produced with FFT = 256, frequency resolution = 97.7 Hz, time resolution = 10.2 ms, transform interval = 2 ms, and 80.5% overlap of frames in transformations.



**Figure 3.** The relationship between trill rate and frequency bandwidth for our study population of *Geospiza fortis*. Large morph songs are indicated by filled circles and small morph songs by open circles.

significantly lower minimum and maximum frequencies (Fig. 4A, B). These results are based on size-standardized measures of beak morphology, which thus isolates the influence of beak size alone on the evolution of song frequencies.

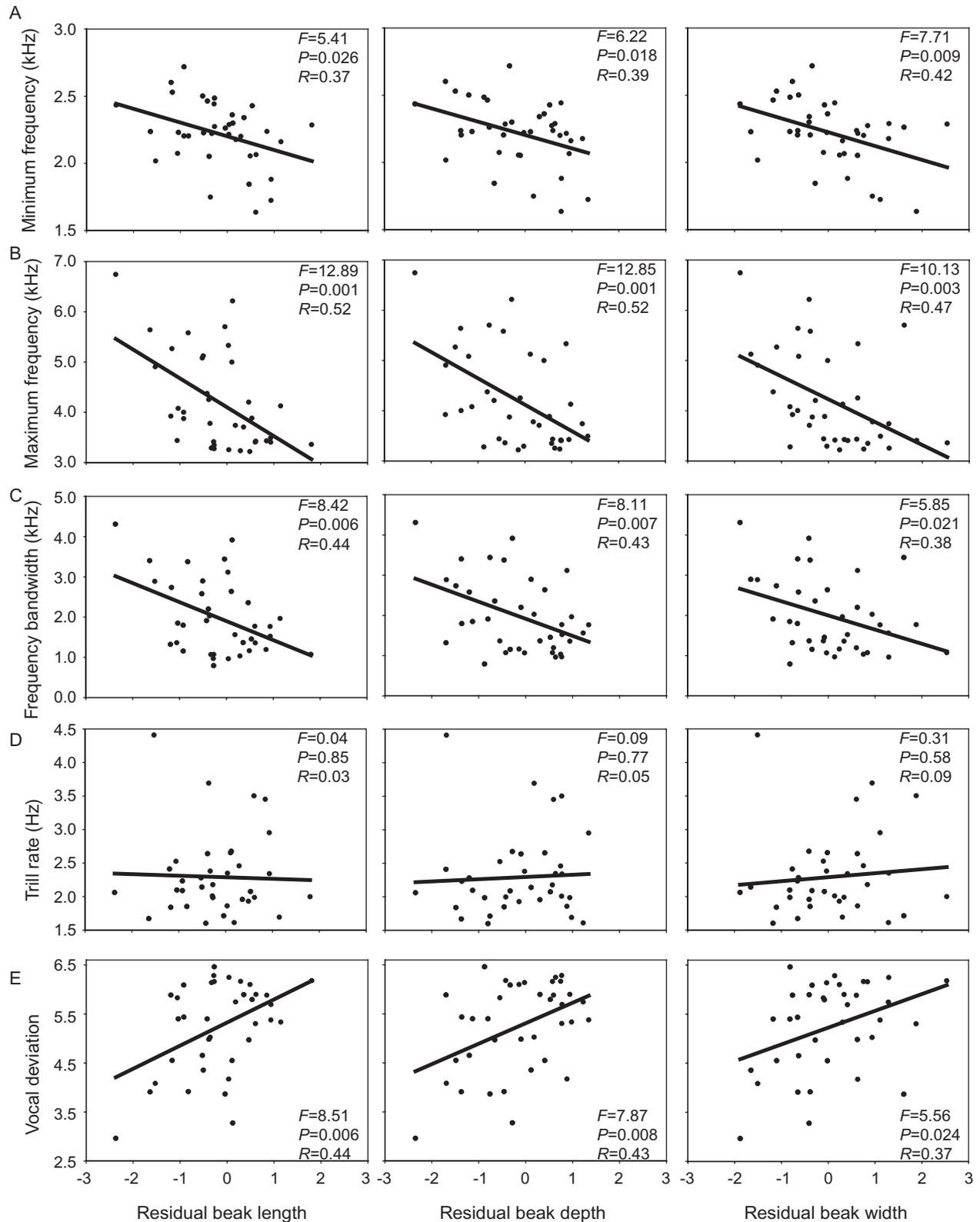
As birds sing, beak gape changes in a correlated fashion with the frequency of notes produced (Westneat *et al.*, 1993; Goller *et al.*, 2004; Podos *et al.*, 2004b). Birds with larger beaks and robust jaw muscles are expected to face greater constraints on the proficiency with which they can adjust beak gape (Herrel *et al.*, 2005a, b). This, in turn, may limit trill performance. Trill performance can be measured in both the frequency bandwidth and trill rate of songs. In this study we find a significant negative relationship between beak morphology and frequency bandwidth, both in our comparison of morphs (Table 1; Fig. 3) and in our analysis of continuous beak variation (Fig. 4C). By contrast, we see a positive relationship between beak morphology and trill rate in our comparison of beak morphs (Table 1), although the relationship between trill rate and beak morphology is non-significant in our analysis of continuous variation (Fig. 4D). Frequency bandwidth and trill rate are interrelated components of vocal performance, however, and when we examine these features in reference to an upper performance limit, we find a positive correlation between morphology and vocal deviation in the predicted direction; birds with longer, deeper, and wider beaks sing with decreased vocal performance, as indicated by higher vocal deviation from an upper-performance limit (Fig. 4E). This result is consistent

with findings of Podos (2001) for another population *G. fortis* on Santa Cruz Island.

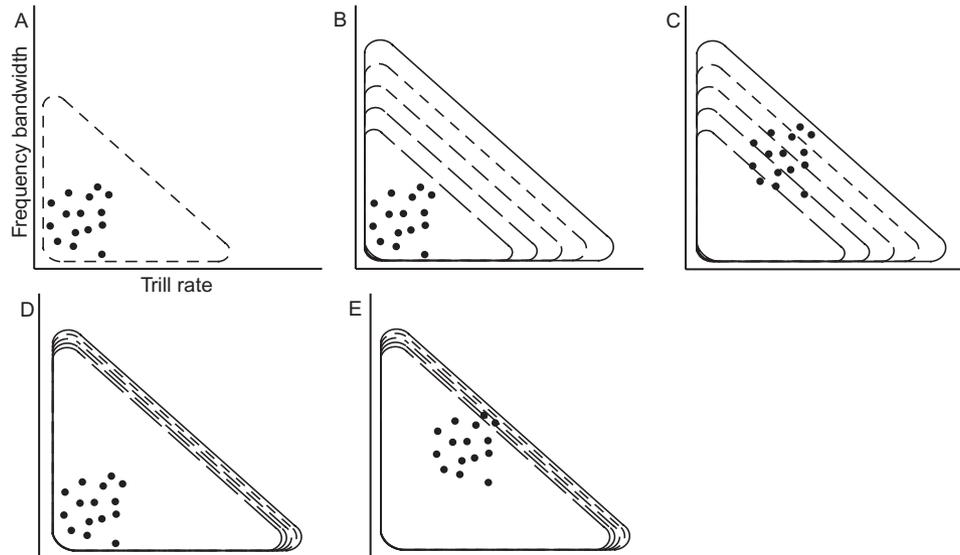
#### MODELS OF VOCAL POTENTIAL AND PERFORMANCE

In a number of comparative analyses, beak morphology has been shown to correlate with song features. Within woodcreepers (subfamily Dendrocolaptinae), Palacios & Tubaro (2000) found a significant negative relationship between beak size and the emphasized frequency of songs, but not with minimum frequency, maximum frequency or frequency bandwidth. In seven species of Darwin's finches, vocal deviation was found to correlate with beak and body size measures (Podos, 2001). Across different populations of the reed bunting, *Emberiza schoeniclus*, Matessi, Pilastro & Marin (2000) found that beak morphology correlates positively with the number and diversity of syllable types, although a mechanical link between syllable diversity and beak morphology has not been established for this species. On a within-population scale, *G. fortis* of Santa Cruz Island is the only species, of four examined to date, for which song features are correlated with beak morphology. Slabbekoorn & Smith (2000) did not identify any song differences between two morphs of the African finch, *Pyrenestes ostrinus*, and no relationship between beak morphology and vocal deviation has been found in Western Pennsylvanian populations of either the swamp sparrow, *Melospiza georgiana* (Ballentine, Hyman & Nowicki, 2004), or the yellow warbler, *Dendroica petechia* (Beebee, 2004a; M. D. Beebee, unpubl. data). These findings call into question the circumstances in which beak morphology will correlate with song features related to vocal performance.

According to the vocal tract model, constraints on vocal production should occur only when songs are produced at their maximum performance levels (Podos *et al.*, 2004a). This may help to explain inconsistencies of results across different species. Consider, for example, a bird that produces a broad range of song types (Fig. 5A). This bird might find some song types, such as those with wide frequency bandwidths and fast trill rates, more challenging to produce than others (Podos, 1997). When we consider multiple birds (Fig. 5B–E), different individuals may express different potentials in vocal performance, due in part to differences in aspects of the vocal apparatus. For species or populations with high variation in beak morphology, for instance, the vocal potentials of different individual members may be highly variable (Fig. 5B, C). If song types in a population are 'easy' to produce for all individuals, then we might not see an influence of beak morphology on song production (Fig. 5B), as may be the case for *P. ostrinus* (Slabbekoorn & Smith, 2000). However, if song types tend to be more challenging from a performance perspective, then beak morphol-



**Figure 4.** Relationship between three residual beak measures and (A) minimum frequency, (B) maximum frequency, (C) frequency bandwidth, (D) trill rate, and (E) vocal deviation. Residual beak measures were extracted from beak on body size regressions. The results of simple linear regressions are reported on each graph.



**Figure 5.** Model of how differences in vocal potential (indicated by triangles) will influence which song types (indicated by filled circles) a male can sing. A male can only sing those songs within the boundary of the triangle representing its vocal potential. Song types at wider frequency bandwidths and faster trill rates (i.e. songs closer to the hypotenuse of the triangles delimiting vocal potential) are more challenging to produce and thus require higher levels of vocal performance. A, males may sing a range of song types in a population. B, the vocal potentials of five different males vary greatly, but each male is able to produce all song types present. C, the vocal potentials of five different males vary greatly, but with some males unable to sing a subset of song types. D, the vocal potentials of five different males vary little, with all males being able to sing song types that are either low performance or (E) high performance.

**Table 2.** Coefficients of variation for beak morphology of three species of birds

	Coefficients of variation for beak measures		
	<i>Geospiza fortis</i> ( $N = 37$ )	<i>Melospiza georgiana</i> * ( $N = 103$ )	<i>Dendroica petechia</i> † ( $N = 28$ )
Beak length	0.10	0.06	0.05
Beak depth	0.13	0.04	0.04
Beak width	0.14	0.06	0.05

\*Ballentine *et al.*, 2004; B. Ballentine, unpubl. data.

†Beebee, 2004a; M. D. Beebee, unpubl. data.

ogy might influence which song types a bird can readily sing (Fig. 5C). We suspect this is the case in *G. fortis* at El Garrapatero. Other populations might still show low variation in beak morphology, resulting in individuals with more similar vocal potentials (Fig. 5D, E). In this scenario, beak morphology is expected to exert only minimal influence on song features, regardless of whether songs tend to be easy (Fig. 5D) or challenging (Fig. 5E) to produce.

We compared variation in beak morphology and song from two prior studies that failed to identify correlations between these two variables, *M. georgiana* (Ballentine *et al.*, 2004; B. Ballentine, unpubl. data) and *D. petechia* (Beebee, 2004a; M. D. Beebee, unpubl. data). We find that *G. fortis* has substantially higher

coefficients of variation for beak measures than either *M. georgiana* or *D. petechia* (Table 2). Thus, *G. fortis* fits more closely the scenario described in Figure 5C, whereas *M. georgiana* and *D. petechia* tend to fit the scenario described in Figures 5D or 5E. Hence, we suggest that variation in vocal potential, represented here as variation in beak morphology, can act together with song features to influence the likelihood of correlations between morphology and song features.

#### SELECTION ON VOCAL POTENTIAL

Overall, our data support the hypothesis that natural selection on aspects of the vocal apparatus influences the vocal potential of *G. fortis* individuals. Selection on

the vocal apparatus may be due to direct selection on songs (see next section), or as a by-product of selection on aspects of the vocal tract that serve dual functions. Bird beaks provide a clear, empirically supported example of a dual function structure. Beaks are used in the crushing and manipulation of food items. In Darwin's finches beak size is related to bite force (Herrel *et al.*, 2005a; b), and individuals with different beak sizes preferentially feed on food items of different hardness (Abbott, Abbott & Grant, 1977). As the availability of food items changes with differing environmental conditions, such as drought, selection favours individuals with the appropriate beak size and shape for the food items that are present (Boag & Grant, 1981). Our data further suggest that beak size evolution will have secondary consequences on song production, by altering the vocal potential of an individual and thus adjusting the range of song types that individual is able to produce. While our results and those of Podos (2001) do not directly test vocal potential, they do assess the outcomes of song production and present a pattern consistent with the scenario presented in Figure 5C. The protected status of Darwin's finches precludes our use of them for experiments that would directly test vocal potential; a test of this nature would require laboratory studies of song learning in young birds (as in Podos, 1996).

#### SELECTION ON SONGS

Multiple factors interact during song evolution, and it is unlikely that all songs in a population will be mechanically challenging from a performance perspective. Selection may favour songs that are mechanically easy to produce (Figs 5A, B, D) if, for example, these songs are distinct from sympatric heterospecific songs (Nelson & Marler, 1990), transmit more effectively through the environment (Richards & Wiley, 1980), or are favoured by sexual selection. Alternatively, each of these factors could result in the evolution of high performance songs (Figs 5C, E). There is evidence in two species that sexual selection may drive the evolution of high performance songs (Ballentine *et al.*, 2004; Beebee, 2004a; b). We currently do not know if selection is driving the evolution of high performance songs in Darwin's finches.

#### SONG AND POPULATION DIVERGENCE IN DARWIN'S FINCHES

Darwin's finches allow us to examine the impact of beak morphology on song production, because of their wide range of beak variation. The evolutionary response of beak morphology to ecological variation is very well characterized (for a review see Grant, 1999), and we are now beginning to understand how beak evolution may have secondary consequences on song production. As our data suggest, variation in beak

morphology affects song features related to vocal performance, with larger beaked birds producing lower performance songs. In addition, the songs between two morphological classes of *G. fortis* at El Garrapatero differ both in the overall amount of song type sharing and in song features related to vocal performance (Figs 2, 3; Table 1).

These results have potentially interesting implications for processes of population level divergence, given that the target of ecological selection also affects the production of mating signals. Darwin's finches recognize conspecific mates based in part on song features (Ratcliffe & Grant, 1985; Grant & Grant, 1998). We currently know that song features differ between *G. fortis* morphs at El Garrapatero. We do not know, however, if these differences can be detected by males or females. Nor do we know if barriers to gene flow, such as assortative mating, are present in this population. Answers to these questions would help us understand the possible evolutionary consequences of song differences that occur as a secondary by-product of ecological selection (Schluter, 2001).

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