

Vocal mechanics in Darwin's finches: correlation of beak gape and song frequency

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Summary

Recent studies of vocal mechanics in songbirds have identified a functional role for the beak in sound production. The vocal tract (trachea and beak) filters harmonic overtones from sounds produced by the syrinx, and birds can fine-tune vocal tract resonance properties through changes in beak gape. In this study, we examine patterns of beak gape during song production in seven species of Darwin's finches of the Galápagos Islands. Our principal goals were to characterize the relationship between beak gape and vocal frequency during song production and to explore the possible influence therein of diversity in beak morphology and body size. Birds were audio and video recorded (at 30 frames s⁻¹) as they sang in the field, and 164 song sequences were analyzed. We found that song frequency regressed significantly and positively on beak gape for 38 of 56 individuals and for all seven species examined. This finding provides broad support for a resonance model of vocal tract function in Darwin's finches. Comparison among species revealed significant

variation in regression y-intercept values. Body size correlated negatively with y-intercept values, although not at a statistically significant level. We failed to detect variation in regression slopes among finch species, although the regression slopes of Darwin's finch and two North American sparrow species were found to differ. Analysis within one species (*Geospiza fortis*) revealed significant inter-individual variation in regression parameters; these parameters did not correlate with song frequency features or plumage scores. Our results suggest that patterns of beak use during song production were conserved during the Darwin's finch adaptive radiation, despite the evolution of substantial variation in beak morphology and body size.

Movies available on-line.

Key words: vocal mechanics, song production, beak gape, vocal frequency, song evolution, Darwin's finch, songbird.

Introduction

The songs of many songbirds are characterized by a musical, whistle-like quality that can be attributed in part to the distinctive anatomy of the songbird vocal apparatus (Marler, 1969; Nowicki, 1987). The source of sound production, the syrinx, is located deep within the thoracic cavity at the base of the trachea. Sounds produced by the syrinx travel a considerable distance through the vocal tract (trachea and associated structures) before exiting the bird. Nowicki (1987) demonstrated that the songbird vocal tract significantly modifies the spectral properties of song by selectively dampening harmonic overtones relative to fundamental frequencies (see also Beckers et al., 2003). Acoustic energy is thus concentrated at narrow ranges of frequencies, and resulting songs are 'pure-tonal' in nature (Nowicki and Marler, 1988).

Songbird song often includes rapid changes in source frequencies. According to the resonance model of vocal tract function, birds should track changes in source frequencies with adjustments in the physical configuration of their vocal tracts

if songs are to retain their pure-tonal quality (Nowicki and Marler, 1988; Fletcher and Tarnopolsky, 1999; Hoese et al., 2000). This is because a vocal tract of given volume is effective as a resonance filter for only a narrow range of source frequencies. One way that birds can adjust vocal tract volume is through changes in beak gape. The beak extends the volume of the vocal tract, contributing to vocal tract resonances (Fletcher and Tarnopolsky, 1999), and adjustments in beak gape can be used to fine-tune the strength of this contribution (Nowicki, 1987; Westneat et al., 1993). Recent studies of beak gape during song production are consistent with the vocal tract resonance model: birds have been shown to gape widely during the production of high source frequencies and to reduce gape during the production of low source frequencies (Westneat et al., 1993; Podos et al., 1995; Moriyama and Okanoya, 1996; Gaunt and Nowicki, 1998; Fletcher and Tarnopolsky, 1999; Williams, 2001). The importance of beak movements in song production is supported by a study in which the experimental obstruction of normal beak movements caused significant

degradation in the tonal quality of songs at predicted frequencies (Hoese et al., 2000).

Evidence that the beak contributes to songbird song production suggests the possibility of correlated evolution among beaks and song. Beaks are a primary axis of avian diversification, as exemplified within adaptive radiations such as the Hawaiian honeycreepers and Galápagos finches (Freed et al., 1987; Grant, 1999). Might the evolutionary diversification of beaks influence, as an incidental consequence, the evolution of song structure? Perhaps the most straightforward prediction here is that species with long bills, and thus larger-volume vocal tracts, should evolve songs with low vocal frequencies. This is because large-volume vocal tracts are appropriate resonance filters for comparatively low source frequencies. Palacios and Tubaro (2000) tested this hypothesis in the dendrocolaptid woodcreepers, a group of birds with unusually pronounced variation in bill length. After controlling for phylogeny and body size, these authors identified a negative correlation between beak length and emphasized vocal frequencies, as predicted. Laiolo and Rolando's study of corvids (Laiolo and Rolando, 2003) identified the opposite relationship – higher emphasized frequencies for larger-billed birds – although the 'rattle calls' of this study were non-tonal and thus may not be expected to fit the vocal tract resonance model.

Patterns of song evolution might also be shaped by variation in beak function. Nowicki et al. (1992) hypothesized that diversification of beak function could bias the evolution of song parameters that make use of vocal tract reconfigurations (see also Podos and Nowicki, in press). Two such song parameters are trill rate and frequency bandwidth, both of which require increasingly rapid and/or pronounced beak movements at higher values (Podos, 1997). In a test of this hypothesis, Podos (2001) examined the songs and morphology of individually marked birds from eight species of Darwin's finches. Beak morphology and song features were found to evolve in correlated fashion, both across species and within the medium ground finch *Geospiza fortis*. Birds with large beaks were found to produce songs with comparatively low trill rates and narrow frequency bandwidths, whereas birds with small beaks were shown to produce songs with fast trill rates and wide frequency bandwidths. These patterns fit the expectation that beak size should covary negatively with vocal performance capacities, because of force–speed tradeoffs in jaw mechanics (Podos, 2001).

In the present study, we describe and analyze patterns of beak gape during song production in seven species of Darwin's finch. Our first goal is to determine whether these species modify beak gape in correspondence with changing vocal frequencies, as has been demonstrated in other songbirds in laboratory settings. We predict a positive relationship between beak gape and song frequencies for two reasons. First, patterns of beak–song co-evolution in Darwin's finches are consistent with the vocal tract resonance model of song production, which includes as a baseline prediction the matching of vocal tract and sound source activity (Podos, 2001). Second, all songbird

species formally examined to date show evidence of a positive relationship between beak gape and vocal frequency, which supports the provisional hypothesis that this matching is a basal, conserved trait across the songbirds (Podos, 1997). We also document relationships between beak gape and song amplitude, as in Westneat et al. (1993). The influence of gape on song amplitude might provide additional insights into vocal tract function.

Our second goal is to compare patterns of beak use during song production among and within species. Wide variation in beak form and function, such as that expressed in Darwin's finches, is likely to influence the potential contributions of the beak to song production. However, we predict that beak variation in Darwin's finches will exert only minimal influences on gape–song relationships. This is because Darwin's finches appear to have accommodated the evolutionary divergence of beaks, and resulting divergence in vocal proficiency, with adjustments to song structure that preserve vocal tract function (Podos, 2001). Darwin's finches also vary widely in body size (Grant et al., 1985). Species with larger bodies have correspondingly large syringes (Cutler, 1970) and, as a general rule, produce lower-pitched vocalizations (Bowman, 1983). We therefore hypothesize that y-intercepts of gape by frequency regressions will correlate negatively with body size. Slopes of gape by frequency regressions might also be influenced by species differences in body size, although we find it difficult to make specific predictions. On the one hand, we might predict steep regressions for small birds, because gape changes of a given magnitude should impose relatively pronounced changes in vocal tract volume and resonance properties (i.e. the volume and impedance of smaller vocal tracts should be disproportionately affected by any given gape change). However, small birds generally produce higher source frequencies, and the effects of gape changes on vocal tract resonances are disproportionately strong at higher frequencies (fig. 17 in Fletcher and Tarnopolsky, 1999). This suggests that small birds could track given frequency changes *via* smaller gape changes. Because of these conflicting predictions, we view our analysis of diversity in regression slopes as exploratory.

Materials and methods

During February and March of 2001 and 2002, seven species of Darwin's finches were videotaped and audio recorded as they sang at three field sites on Santa Cruz Island, Galápagos, Ecuador (Table 1). Darwin's finches on Santa Cruz Island generally breed during February and March, and many of the individuals filmed in this study were seen constructing nests and defending territories. Video recordings were made using a Canon XL1 digital video camera (miniDV format) with a 5.5–88 mm zoom lens, a 1.6× optical extender and a shoulder mount. The temporal resolution of this video recording system is 30 frames s⁻¹, equivalent to that used for prior laboratory studies on beak movements during song production in

Table 1. *Species, field sites and sample sizes*

Species	Common name	Field site*	<i>N</i> individuals	<i>n</i> song sequences analyzed
<i>Camarhynchus parvulus</i>	Small tree finch	LG	9	24
<i>Camarhynchus psittacula</i>	Large tree finch	LG	2	3
<i>Certhidea olivacea</i>	Warbler finch	LG	2	5
<i>Geospiza fuliginosa</i>	Small ground finch	LG, BA, EG	5	12
<i>Geospiza fortis</i>	Medium ground finch	BA, EG	34	110
<i>Geospiza magnirostris</i>	Large ground finch	EG	3	7
<i>Platyspiza crassirostris</i>	Vegetarian finch	LG	1	3

*LG: Los Gemelos, GPS coordinates S 00°37'20"–45", W 90°23'00"–15"; BA: Bahia Academia, GPS coordinates S 00°44'15"–30"; W 90°18'05"–09"; EG: El Garrapatero, GPS coordinates S 00°40'20"–41'20"; W 90°13'10"–14'40".

songbirds (Westneat et al., 1993; Podos et al., 1995). This frame speed is generally sufficient to avoid aliasing, because Darwin's finches cycle their beak gapes in accordance with syllable production (one cycle per syllable) and because Darwin's finch trills are almost always produced at rates of <10 syllables s⁻¹. Thus, each syllable is represented by at least three video frames. Iris and shutter speed settings ranged from F4 to F16 and 0.010–0.017 s, respectively. Audio recordings were made using a Canon electret condenser microphone mounted on the video camera, with the audio signal (16-bit) recorded directly onto miniDV cassette tapes.

In the field, we were able to approach and videotape singing birds at close range, often within 10 m and on occasion as close as 2 m. This was made possible by the unusual tameness of these birds in the field (e.g. Grant, 1999). Our sampling efforts were opportunistic – our aim was to secure as many high-quality recordings as possible – although we focused in particular on two species, *Geospiza fortis* and *Camarhynchus parvulus*, for which additional behavioral studies were being conducted. We obtained approximately 8 h of raw video footage.

Upon return to the laboratory, we selected a subset of song sequences for analysis following four criteria. First, the singing bird's head and beak had to be visible, in focus and discernible from the visual background during the entire sequence. Many sequences failed to meet this criterion because of a lack of contrast between the dark heads and beaks of these birds and the shadows cast by foliage, especially on bright, sunny days. Second, the bird's head and beak needed to appear in approximate profile, such that dynamic changes in both upper and lower beak tip position could be tracked during song production. Third, we discounted sequences that included head roll within the song sequence. Head pitch and yaw movements were acceptable for our analysis because such movements do not significantly affect calculations of beak gape. Our fourth criterion was that the audio signal from vocal sequences needed to be clearly discernible from background noise, to ensure meaningful acoustic frequency analyses. 164 vocal sequences from 56 individuals met these criteria (Table 1).

Beak gape: calculation and calibration

Sequences of video frames were transferred from the video camera to an Apple iMac computer using iMovie 2.0 (Figs 1i, 2i). iMovie files (.mpg) were converted to Quicktime files (.mov) and then imported into NIH Image 1.62 (.tiff) in order to measure beak gape. Beak gape was calculated as the distance between the tips of the upper and lower mandibles as it varied during song sequences. Beak gape was measured in pixels and then converted into cm distances using a calibration macro in NIH Image. For video frames in which the bird was not directly lateral to the camera, for example if the camera was pointing up towards the bird, we estimated the angle of filming ($\pm 15^\circ$) by comparing video frames to taxidermic mounts and adjusted our gape calculations accordingly.

Calibration of image data requires inclusion of standards of known dimensions within video fields. We were unable to include external standards in our film sequences because of difficulty in identifying and accessing the perches from which birds sang. We instead relied on either beak length (the distance between the anterior end of the nares and the tip of the upper mandible) or, for sequences in which the nares were not discernible, 'exposed culmen' (the linear distance, in profile, from the tip of the upper mandible to the dorsal juncture of the culmen and the forehead; Pyle, 1997).

Actual beak length measurements were taken either from caliper data for banded individuals or as mean values from our own measurements in these populations. The latter approach is compromised by variation among individuals in beak size, which is generally low in most species examined here (Grant et al., 1985) but unusually pronounced in one of the species, *Geospiza fortis*. Calibration errors due to the imprecise assignment of beak lengths should have little effect on the calculation of beak gape by acoustic frequency regressions within individual birds but more substantial effects on regressions pooled by species.

Direct field measurements of exposed culmen were unavailable. We thus calculated values of exposed culmen for each population using NIH Image 1.62 and a series of close-up photographs (Nikon Coolpix 995 digital camera) we had made of birds of known measurements. For each photograph,

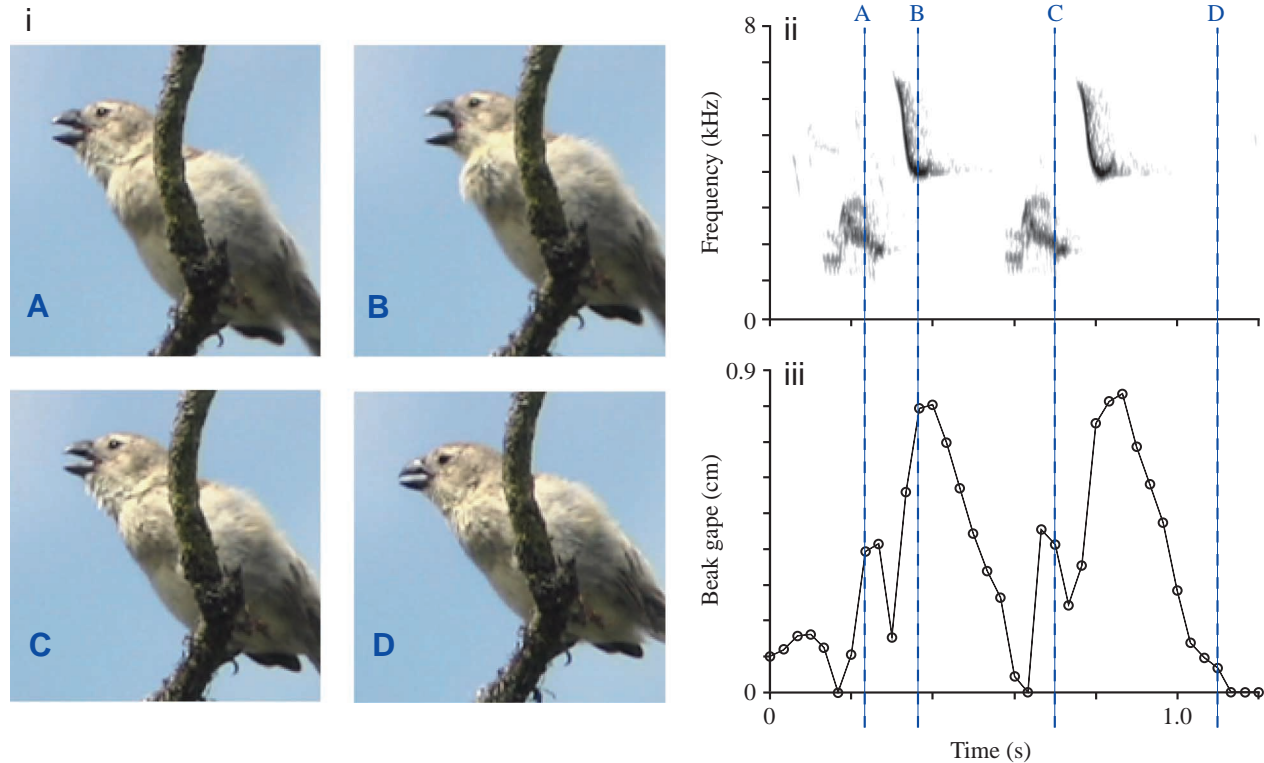


Fig. 1. (i) Four video frames from a song sequence in a large tree finch (*Camarhynchus psittacula*). The bird adjusts beak gape during the production of this song. This bird also appears to adjust vocal tract volume using head extension (frame A) and retraction (frame B). (ii) Sound spectrogram of the song produced. Rapid and large-scale changes in fundamental frequency are evident. (iii) Beak gape profile, calculated from video frames and aligned with the sound spectrogram. Video frames A–D are indicated by broken vertical lines. The birds' gape is ~0.4 cm at low frequencies (frames A and C), ~0.8 cm at high frequencies (frame B) and nearly closed at song completion (frame D). Two movie files of this song sequence, the first at normal speed ('psittacula.mov') and the second at one-third speed ('psittacula-slow.mov'), are included online as supplementary material.

we calculated exposed culmen length using three known measurements: actual beak length, the pixel length of beak length and the pixel length of exposed culmen. After calibration, we plotted beak gape at 33.33 ms intervals over the course of each vocal sequence (e.g. Figs 1–4).

Calculation of song frequencies and amplitudes

We used the sound analysis program SIGNAL 3.1 (Beeman, 1999) to measure acoustic frequency and amplitude values from audio clips of song sequences. Audio tracks were imported directly into SIGNAL (25 kPt sample rate) from the video camera to maximize audio quality. Audio clips were synchronized to their respective iMovie video sequences (Figs 1–4).

Peak acoustic frequencies and amplitudes were calculated for each 33.33 ms interval using customized macros in SIGNAL. The first and last 16.67 ms intervals of each audio track were omitted from this analysis in order to 'center' audio intervals around their corresponding video frames. This optimized the correspondence of audio data to video frames. We did not attempt to correct for any offset between the reception of audio and video signals by our camera, because most of our samples were taken within 10 m of the singing bird

(a distance at which video and audio signals recorded at 30 frames s^{-1} are expected to be synchronized within the error of a single video frame). Frequency values were obtained using 256 point fourier frequency transforms, which yielded a frequency resolution of 97.7 Hz. Amplitude (root mean square) values were obtained from oscillograms using an automated function in SIGNAL. The maximum amplitude in each song sequence was standardized to 0 dB, and remaining amplitude values were calculated with reference to this standard.

A second customized SIGNAL macro generated sound spectrograms with vertical lines transposed over them at 33.33 ms intervals. This allowed us to determine which video frames in each sequence contained vocal output and which frames corresponded to pauses between notes. Only video frames and audio data in which birds were vocalizing were used in regression analyses.

Gape by frequency regressions

Statistical analyses were conducted using JMP (Version 4.04; SAS Institute Inc., Cary, NC, 2002). Our first goal was to test the hypothesis that birds modify beak gape in correspondence with changing song frequencies in the positive direction predicted by the vocal tract resonance model. As a

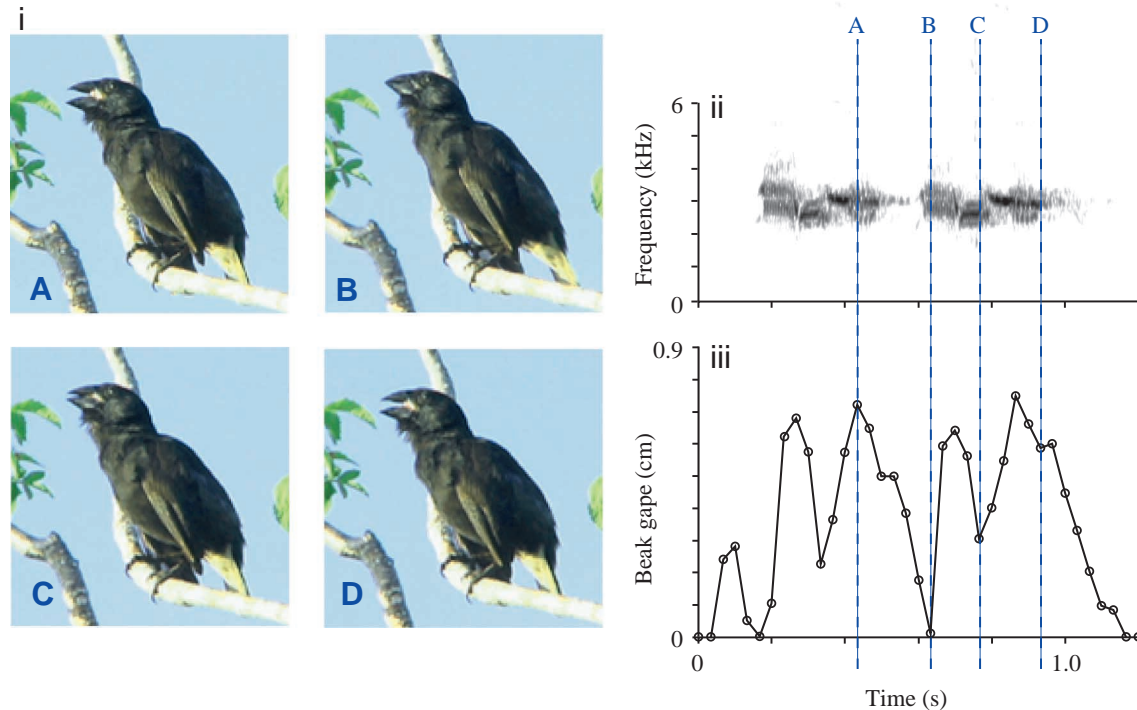


Fig. 2. (i) Four video frames from a song sequence in a medium ground finch (*Geospiza fortis*). (ii) Sound spectrogram of the song produced. (iii) Beak gape profile, calculated from video frames and aligned with the sound spectrogram. Video frames A–D are indicated by broken vertical lines. Each syllable consists of three notes, the second of which is produced at slightly lower frequencies. These lower frequencies are matched by reduced gapes (e.g. frame C). Two movie files of this song sequence, the first at normal speed ('fortis.mov') and the second at one-third speed ('fortis-slow.mov'), are included online as supplemental material.

preliminary step, we plotted acoustic frequency as a function of beak gape for all song sequences ($N=164$). In approximately 40 song sequences, we detected one or two conspicuous outliers in the upper-left quadrants of bivariate plots (i.e. low gape and high frequency). Further inspection indicated that these 'low gape–high frequency' outliers were almost always introductory frames within song sequences and were thus likely to be a result of autocorrelation error (Sokal and Rohlf, 1995). That is, birds' beaks were generally closed before they started to sing and apparently had not achieved normal gape by the first frame of some song sequences. To minimize this error we applied the 'Density Ellipse' algorithm of JMP (99% confidence interval) to identify outliers for removal from subsequent analysis. The outliers identified by this algorithm (59 of 3665 total data points) corresponded closely to our own impressions of outlying points on bivariate plots.

We next calculated least-squares regressions of acoustic frequency as a function of beak gape for data pooled by individuals. Our pooling of data within individuals is justified by the observation that different song sequences produced by any individual were always of the same song type. We then calculated regressions at the species level, after excluding non-significant individual regressions (as in Westneat et al., 1993). For individual and species-level analyses, we applied sequential Bonferroni adjustments to regression P -values to account for the high number of calculations performed.

Our second goal was to characterize species differences in gape–frequency correlations among the Darwin's finches. A preliminary analysis of the interaction between gape and species, in which frequency was the dependent variable, revealed significant heterogeneity in regression slopes ($F_{6,3035}=13.85$, $P<0.001$). We thus could not apply analysis of covariance (ANCOVA) in our species comparisons (Sokal and Rohlf, 1995). As an alternative, we conducted one-way tests on slope and intercept values as they varied across our sample. We detected unequal variances among species for both slope and intercept data and thus used non-parametric tests. We ran two sets of one-way Kruskal–Wallis main effect tests (JMP 4.04) and pairwise *post-hoc* tests (Conover, 1999). Our first set of tests examined only our Darwin's finch sample. We used individual slope and intercept values as replicates within species. Our second set of tests also included data from swamp sparrows (*Melospiza georgiana*) and white-throated sparrows (*Zonotrichia albicollis*). Original regression data on sparrow species were provided by Mark Westneat and colleagues (see Westneat et al., 1993). To facilitate this analysis, we pooled the sparrow data by bird ($N=5$ for each species) across all note types analyzed for each bird.

Next, we calculated correlations between body mass (compiled from our own data and from Dunning, 1993) and regression y -intercepts and slopes across the Darwin's finches only and then including the two sparrow species.

Finally, we tested the contribution of between-individual variation to species regression values. For this analysis, we examined variation in slope and intercept values among the nine *Geospiza fortis* individuals with the largest sample sizes. We again used Kruskal–Wallis tests on regression slopes and y-intercepts, with different song sequences as replicates.

Gape by amplitude regressions

We calculated least-squares regressions of song amplitude as a function of beak gape for data pooled by individuals. The goal of this analysis was to explore the possible influence of gape modulations on song amplitude. The predictions of the vocal tract model concerning the effects of gape on amplitude are specific to given frequencies, stating that deviations from particular gapes should cause reductions in amplitude for acoustically matched frequencies. By contrast, the vocal tract resonance model makes no predictions about the relationship between gape and amplitude across a broad song sample with wide variation in source frequencies, such as ours here. Our

analyses are intended to provide a point of comparison with those of Westneat et al. (1993), who identified a consistent influence of beak gape on song amplitude in sparrows for one of five note types examined. Outlier data points were identified as above, using the Density Ellipse algorithm of JMP at 99% confidence intervals, and removed from regression analysis.

Results

Gape by frequency regressions

Regressions of acoustic frequency on beak gape were statistically significant for 38 of 56 individuals analyzed (Table 2) and for all seven species (Table 3; Fig. 5). The slopes of all significant regressions were positive. The likelihood that the regression of an individual bird would achieve statistical significance depended largely on sample size (Table 2). As an illustration, regressions of 19 of the 20 individuals with the largest sample sizes achieved significance, compared with nine

of the 20 individuals with the smallest sample sizes. r^2 values of gape by frequency regressions averaged 0.48 ± 0.23 (mean \pm S.D.) for individuals with significant regressions (Table 2).

The y-intercepts of gape by frequency regressions were significantly variable among the seven Darwin's finch species (Kruskal–Wallis test, $\chi^2=15.07$, d.f.=6, $P=0.0197$). Pairwise comparisons at the level of $\alpha=0.05$ revealed that intercepts of two species, *Camarhynchus psittacula* and *Geospiza fortis*, were significantly lower than intercepts in two other species, *Camarhynchus parvulus* and *Certhidea olivacea*. Intercepts also differed between *C. psittacula* and *Platyspiza crassirostris*. When sparrow data were included, intercepts again showed significant variation among species (Kruskal–Wallis test, $\chi^2=22.51$, d.f.=8, $P=0.0041$). Previously identified contrasts among Darwin's finch intercepts were preserved, with the addition of a significant contrast between *G. fortis* and *P. crassirostris*

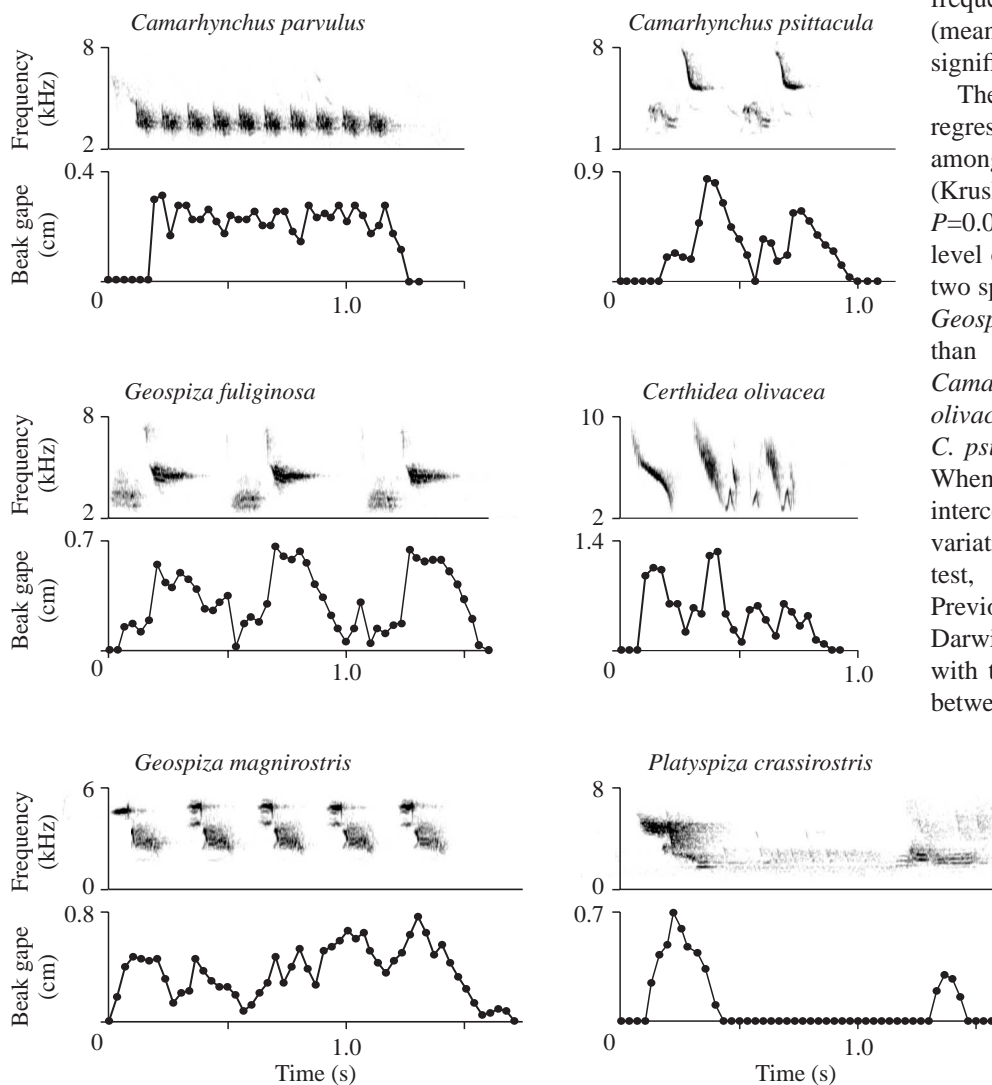


Fig. 3. Representative sound spectrograms and gape profiles for six species in this study. Changes in gape generally correspond to shifts in song frequency.

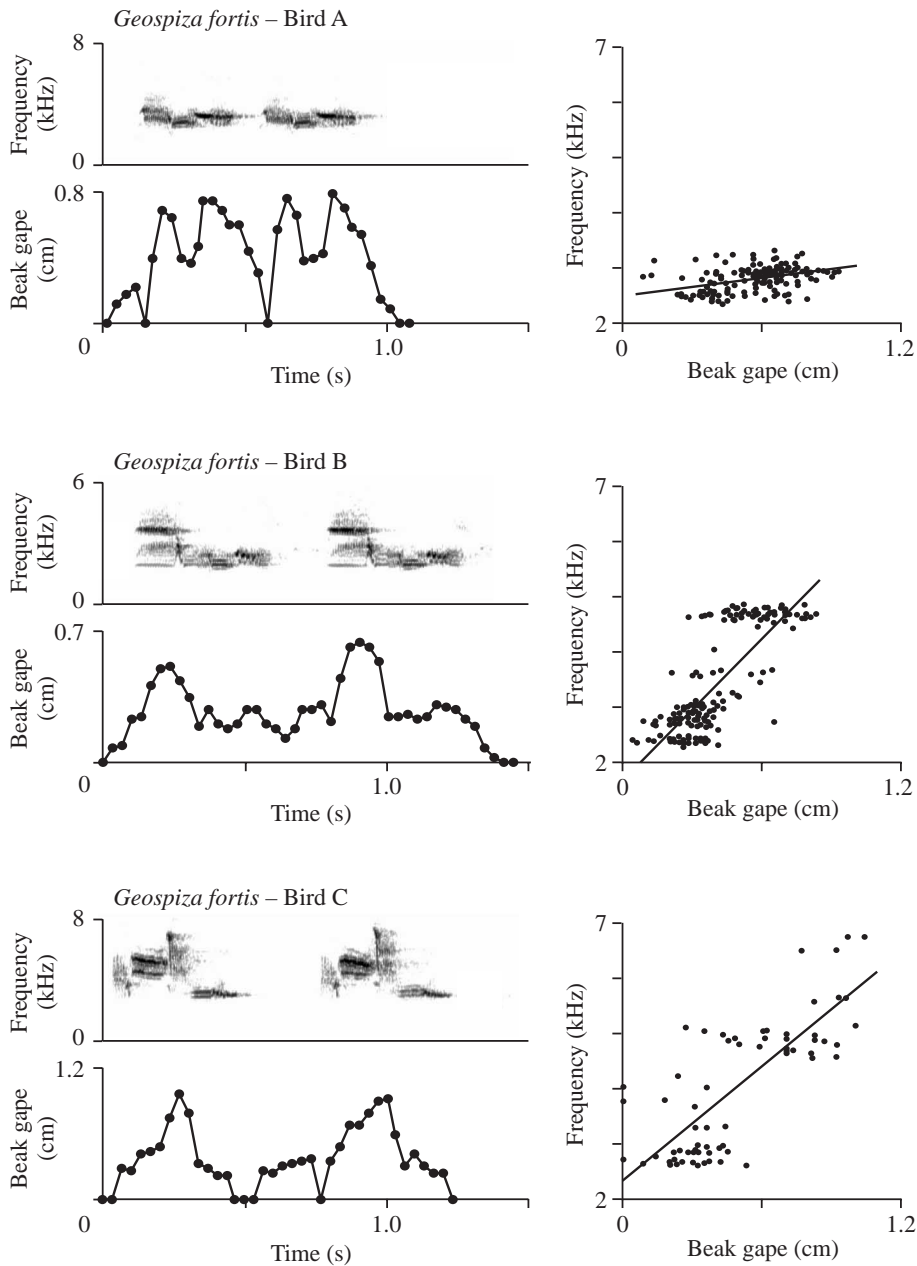


Fig. 4. Sound spectrograms, gape profiles and gape \times frequency plots for three *Geospiza fortis* individuals. These birds represent the range of within-species variation in regression slopes and y-intercepts; our sample varied significantly in y-intercepts and especially slopes. We failed to detect any significant correlations, however, between regression parameters, song parameters and age (as indicated by plumage – see text).

species (*Geospiza fuliginosa*, *C. parvulus*, *C. psittacula* and *M. georgiana*), and the *M. georgiana* slopes exceeded those of *G. fortis* and *Z. albicollis*. There were no significant contrasts between the regression slopes of any of the Darwin's finch species.

Within the Darwin's finches, both intercepts and slopes of gape–frequency regressions correlated negatively with body mass (Pearson product moment correlation, $R=-0.427$ and -0.209 , respectively), although not at statistically significant levels (Spearman's Rho, $P>0.30$ in both tests). With the addition of the two sparrow species, the correlation of body mass by intercepts weakened ($R=-0.270$), and the correlation of body mass by slope strengthened ($R=-0.325$), although again neither achieved statistical significance (Spearman's Rho, $P>0.55$ in both instances).

Within our *Geospiza fortis* sample, we found significant variation among birds in y-intercepts (Kruskal–Wallis test, $\chi^2=19.24$, d.f.=8, $P=0.014$; Fig. 4) and especially regression slopes

(Table 4). *Zonotrichia albicollis* y-intercepts were significantly greater than those of *C. psittacula* and *G. fortis*, and *Melospiza georgiana* intercepts were significantly lower than those of *C. parvulus* and *C. olivacea* (Table 4).

Analysis of slopes failed to reveal significant differences among Darwin's finch species alone (Kruskal–Wallis test, $\chi^2=5.24$, d.f.=6, $P=0.5128$, power=0.844). However, inclusion of sparrow data led to an overall effect of slope that approached significance (Kruskal–Wallis test, $\chi^2=15.41$, d.f.=8, $P=0.0517$). We applied *post-hoc* tests to this data set, not as an explicit test of species contrasts (given the borderline significance of the overall effect) but as a preliminary analysis of trends (Table 4). Slopes of the *Zonotrichia albicollis* regressions were significantly lower than slopes of four other

(Kruskal–Wallis test, $\chi^2=37.50$, d.f.=8, $P<0.0001$; Fig. 4). To examine possible causes of between-individual variation in the *G. fortis* sample, we ran two analyses. First, we calculated correlations between regression parameters (slope, y-intercept and r^2 values) and song parameters (minimum frequency, peak frequency, maximum frequency and frequency bandwidth). Second, we calculated correlations between regression parameters and plumage scores. For each bird in this analysis, we scored plumage on a scale of 1–5, as described in Grant (1999), using video images and field annotations. The extent of coverage of dark plumage provides a general indicator of age, with older birds possessing more dark plumage. None of these correlations were statistically significant (Spearman's Rho, $P>0.05$).

Table 2. Regression analyses for frequency data pooled by individuals (x-axis=cm, y-axis=Hz)

Species	N clips	n points [†]	y-intercept	Slope	r ²	F-ratio
<i>Camarhynchus parvulus</i>	7	203	3350	1111	0.09	19.56***
<i>Camarhynchus parvulus</i> [‡]	7	153	2433	4226	0.51	159.06***
<i>Camarhynchus parvulus</i>	2	60	2945	3302	0.59	83.18***
<i>Camarhynchus parvulus</i>	2	41	2116	3930	0.57	51.26***
<i>Camarhynchus parvulus</i>	2	27	2054	5541	0.25	8.37 NS
<i>Camarhynchus parvulus</i>	1	32	4709	1240	0.29	12.22*
<i>Camarhynchus parvulus</i>	1	31	3265	1299	0.16	5.61 NS
<i>Camarhynchus parvulus</i>	1	14	3267	327	0.02	0.26 NS
<i>Camarhynchus parvulus</i>	1	12	3677	-1744	0.10	1.06 NS
<i>Camarhynchus psittacula</i> [‡]	2	31	1789	4089	0.51	29.92***
<i>Camarhynchus psittacula</i> [‡]	1	13	2650	4101	0.39	7.12 NS
<i>Certhidea olivacea</i> [‡]	4	66	4377	2370	0.35	34.33***
<i>Certhidea olivacea</i>	1	11	4796	1463	0.13	1.38 NS
<i>Geospiza fortis</i>	12	267	2504	374	0.04	11.99*
<i>Geospiza fortis</i> [‡]	9	168	2487	541	0.17	35.02***
<i>Geospiza fortis</i> [‡]	8	181	1682	4256	0.65	326.57***
<i>Geospiza fortis</i>	8	153	2251	2226	0.17	31.74***
<i>Geospiza fortis</i>	7	114	2378	1160	0.11	13.36**
<i>Geospiza fortis</i>	5	156	1816	1815	0.35	81.14***
<i>Geospiza fortis</i>	5	125	2267	2221	0.40	82.93***
<i>Geospiza fortis</i>	5	116	3070	212	0.01	0.96 NS
<i>Geospiza fortis</i>	4	93	1754	4269	0.53	102.62***
<i>Geospiza fortis</i>	4	84	1975	2958	0.43	61.13***
<i>Geospiza fortis</i> [‡]	4	72	2346	3422	0.61	109.03***
<i>Geospiza fortis</i>	3	98	2312	2766	0.27	34.67***
<i>Geospiza fortis</i>	3	73	2088	2488	0.69	158.88***
<i>Geospiza fortis</i>	3	68	2176	2782	0.46	56.10***
<i>Geospiza fortis</i>	3	66	2524	1108	0.07	4.45 NS
<i>Geospiza fortis</i>	3	56	2230	1403	0.45	44.37***
<i>Geospiza fortis</i>	3	39	2755	-391	0.14	5.81 NS
<i>Geospiza fortis</i>	2	63	2679	35	0.00	0.02 NS
<i>Geospiza fortis</i>	2	62	1913	2135	0.26	21.14***
<i>Geospiza fortis</i>	2	46	2317	1062	0.13	6.56 NS
<i>Geospiza fortis</i>	2	37	2244	2579	0.58	49.09***
<i>Geospiza fortis</i>	1	33	1038	3118	0.89	260.15***
<i>Geospiza fortis</i>	1	31	1396	4084	0.71	69.58***
<i>Geospiza fortis</i>	1	26	2388	1767	0.39	15.03*
<i>Geospiza fortis</i>	1	26	2191	3714	0.48	21.88***
<i>Geospiza fortis</i>	1	25	1854	2648	0.74	67.12***
<i>Geospiza fortis</i>	1	24	2102	2240	0.59	31.33***
<i>Geospiza fortis</i>	1	19	2403	929	0.24	5.21 NS
<i>Geospiza fortis</i>	1	19	1802	3758	0.72	43.62***
<i>Geospiza fortis</i>	1	17	-261	7613	0.83	74.56***
<i>Geospiza fortis</i>	1	15	1954	1462	0.68	27.58***
<i>Geospiza fortis</i>	1	14	2306	1064	0.14	1.99 NS
<i>Geospiza fortis</i>	1	12	8	7992	0.55	12.35 NS
<i>Geospiza fortis</i>	1	11	2193	3436	0.68	19.41*
<i>Geospiza fuliginosa</i>	5	154	2684	3598	0.10	17.17***
<i>Geospiza fuliginosa</i> [‡]	4	126	2858	3328	0.77	425.00***
<i>Geospiza fuliginosa</i>	1	23	4031	1180	0.03	0.63 NS
<i>Geospiza fuliginosa</i>	1	16	2923	4545	0.39	9.09 NS
<i>Geospiza fuliginosa</i>	1	13	1979	12251	0.67	21.92*
<i>Geospiza magnirostris</i> [‡]	5	109	1976	2567	0.20	26.87***
<i>Geospiza magnirostris</i>	1	19	3369	-399	0.04	0.75 NS
<i>Geospiza magnirostris</i>	1	16	2386	648	0.09	1.38 NS
<i>Platyspiza crassirostris</i> [‡]	3	27	3145	3407	0.60	37.52***

[†]Number of data points after removal of outliers.

[‡]Example songs and gape profiles for these birds are illustrated in Figs 1–4.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$ (significance after Bonferroni correction); NS, not significant.

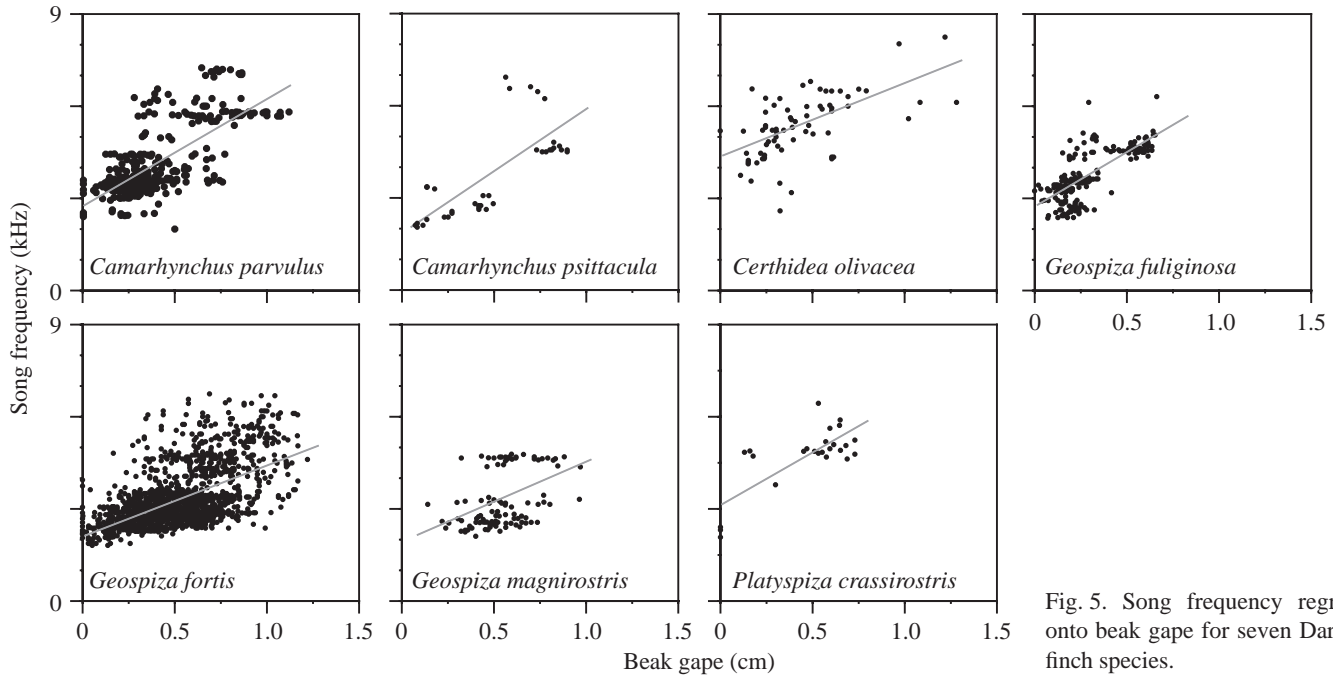


Fig. 5. Song frequency regressed onto beak gape for seven Darwin's finch species.

Gape by amplitude regressions

Regressions of amplitude as a function of beak gape were positive and statistically significant for 17 of 56 song sequences (Table 5). Again it appeared that the probability that regressions would be significant depended upon sample size; regressions from seven of the 20 individuals with the largest sample sizes achieved statistical significance, compared with only two of the 20 individuals with the smallest sample sizes. r^2 values of significant gape by amplitude regressions averaged 0.35 ± 0.23 (Table 5).

Discussion

The resonance model of vocal tract function predicts that songbirds will adjust vocal tract volume while singing so as to track changes in source frequencies (Nowicki and Marler,

1988; Westneat et al., 1993; Gaunt and Nowicki, 1998; Fletcher and Tarnopolsky, 1999). Songbirds might adjust vocal tract volume in a number of ways, such as through changes in the position of the glottis, larynx and tongue, through changes in beak gape and through postural changes such as head extension or retraction (Westneat et al., 1993; e.g. Fig. 1). Beak

Table 3. Regression analyses for data pooled by species* (units: x-axis=mm, y-axis=kHz)

Species	n*	y-intercept	Slope	r ²	F-ratio
<i>Camarhynchus parvulus</i>	489	2733	3516	0.56	611.70**
<i>Camarhynchus psittacula</i>	31	1789	4089	0.51	29.92**
<i>Certhidea olivacea</i>	66	4377	2370	0.35	34.33**
<i>Geospiza fuliginosa</i>	293	2765	3489	0.58	397.10**
<i>Geospiza fortis</i>	2034	2113	2283	0.33	1004.75**
<i>Geospiza magnirostris</i>	109	1976	2567	0.20	26.87**
<i>Platypiza crassirostris</i>	27	3145	3407	0.60	37.52**

*Calculations exclude data from individuals with NS (not significant) regressions (see Table 2).

** $P < 0.0001$ (after Bonferroni correction).

Table 4. Regression y-intercepts and slopes for nine species

Species	Mean	S.E.M.
y-intercept		
<i>Melospiza georgiana</i>	1545	572
<i>Camarhynchus psittacula</i>	1789	—
<i>Geospiza fortis</i>	1965	111
<i>Geospiza magnirostris</i>	1976	—
<i>Geospiza fuliginosa</i>	2507	269
<i>Zonotrichia albicollis</i>	3016	302
<i>Camarhynchus parvulus</i>	3111	452
<i>Platypiza crassirostris</i>	3145	—
<i>Certhidea olivacea</i>	4377	—
Slope		
<i>Zonotrichia albicollis</i>	1158	209
<i>Geospiza fortis</i>	2740	285
<i>Certhidea olivacea</i>	2370	—
<i>Geospiza magnirostris</i>	2567	—
<i>Camarhynchus parvulus</i>	2762	665
<i>Platypiza crassirostris</i>	3407	—
<i>Camarhynchus psittacula</i>	4089	—
<i>Melospiza georgiana</i>	4228	664
<i>Geospiza fuliginosa</i>	6392	2930

Values are means \pm S.E.M. Significant contrasts from *post-hoc* tests are indicated by separations between vertical lines.

Table 5. Regression analyses for amplitude data pooled by individuals (x-axis=cm, y-axis=dB)

Species	<i>N</i> clips	<i>n</i> points [†]	y-intercept	Slope	<i>r</i> ²	<i>F</i> -ratio
<i>Camarhynchus parvulus</i>	7	203	-18.38	26.75	0.13	31.12***
<i>Camarhynchus parvulus</i>	7	153	-12.90	11.60	0.16	28.62***
<i>Camarhynchus parvulus</i>	2	60	-17.06	7.18	0.05	3.02 NS
<i>Camarhynchus parvulus</i>	2	41	-13.96	21.60	0.26	12.66*
<i>Camarhynchus parvulus</i>	2	27	-18.03	38.13	0.14	4.22 NS
<i>Camarhynchus parvulus</i>	1	32	-33.61	26.01	0.80	123.03***
<i>Camarhynchus parvulus</i>	1	31	-16.55	9.59	0.03	0.90 NS
<i>Camarhynchus parvulus</i>	1	14	-7.09	-6.71	0.01	0.09 NS
<i>Camarhynchus parvulus</i>	1	12	-11.78	10.74	0.03	0.29 NS
<i>Camarhynchus psittacula</i>	2	30	-17.08	13.67	0.47	24.80***
<i>Camarhynchus psittacula</i>	1	13	-21.94	19.03	0.31	4.93 NS
<i>Certhidea olivacea</i>	4	64	-15.92	15.34	0.24	19.15***
<i>Certhidea olivacea</i>	1	11	-3.49	-9.67	0.22	2.58 NS
<i>Geospiza fortis</i>	12	269	-10.94	6.58	0.02	6.20 NS
<i>Geospiza fortis</i>	9	172	-15.39	-15.39	0.04	7.70 NS
<i>Geospiza fortis</i>	8	178	-14.85	14.40	0.23	51.10***
<i>Geospiza fortis</i>	8	156	-9.75	0.87	0.00	0.05 NS
<i>Geospiza fortis</i>	7	112	-16.77	23.69	0.10	11.99*
<i>Geospiza fortis</i>	5	153	-9.50	-4.17	0.01	1.52 NS
<i>Geospiza fortis</i>	5	125	-12.79	3.96	0.05	6.21 NS
<i>Geospiza fortis</i>	5	119	-9.11	-0.20	0.00	0.01 NS
<i>Geospiza fortis</i>	4	96	-13.04	4.19	0.01	1.05 NS
<i>Geospiza fortis</i>	4	84	-3.24	-13.45	0.10	9.38 NS
<i>Geospiza fortis</i>	4	71	-13.77	4.83	0.04	2.55 NS
<i>Geospiza fortis</i>	3	100	-8.14	-10.77	0.05	5.42 NS
<i>Geospiza fortis</i>	3	74	-12.04	12.47	0.16	14.08**
<i>Geospiza fortis</i>	3	67	-10.95	13.83	0.12	8.98 NS
<i>Geospiza fortis</i>	3	66	-23.90	59.67	0.35	34.24***
<i>Geospiza fortis</i>	3	56	-14.95	20.30	0.31	24.48***
<i>Geospiza fortis</i>	3	39	-11.11	14.39	0.10	3.94 NS
<i>Geospiza fortis</i>	2	62	-18.01	29.42	0.09	5.99 NS
<i>Geospiza fortis</i>	2	34	-6.01	-2.56	0.02	0.61 NS
<i>Geospiza fortis</i>	2	47	-16.64	25.55	0.32	21.26***
<i>Geospiza fortis</i>	2	37	-9.45	5.44	0.02	0.63 NS
<i>Geospiza fortis</i>	1	33	-14.52	9.55	0.20	7.65 NS
<i>Geospiza fortis</i>	1	31	-8.94	0.13	0.00	0.00 NS
<i>Geospiza fortis</i>	1	27	-3.58	-7.74	0.16	4.69 NS
<i>Geospiza fortis</i>	1	26	-2.18	-8.31	0.20	5.86 NS
<i>Geospiza fortis</i>	1	24	-10.67	5.69	0.05	1.08 NS
<i>Geospiza fortis</i>	1	24	-17.53	12.16	0.13	3.17 NS
<i>Geospiza fortis</i>	1	19	-27.44	28.23	0.20	4.35 NS
<i>Geospiza fortis</i>	1	19	-16.02	8.50	0.12	2.41 NS
<i>Geospiza fortis</i>	1	17	-0.37	-11.73	0.09	1.41 NS
<i>Geospiza fortis</i>	1	15	-15.90	8.11	0.04	0.66 NS
<i>Geospiza fortis</i>	1	14	-24.87	30.49	0.22	3.38 NS
<i>Geospiza fortis</i>	1	12	-11.02	1.82	0.00	0.00 NS
<i>Geospiza fortis</i>	1	11	-4.60	-16.05	0.20	2.21 NS
<i>Geospiza fuliginosa</i>	5	158	-16.21	16.85	0.01	1.83 NS
<i>Geospiza fuliginosa</i>	4	137	-22.52	24.06	0.33	67.85***
<i>Geospiza fuliginosa</i>	1	23	-44.05	69.14	0.74	59.17***
<i>Geospiza fuliginosa</i>	1	15	-34.81	202.58	0.71	32.17***
<i>Geospiza fuliginosa</i>	1	13	-16.52	50.06	0.22	3.16 NS
<i>Geospiza magnirostris</i>	5	109	-20.07	13.37	0.13	16.13***
<i>Geospiza magnirostris</i>	1	19	-4.86	-4.50	0.12	2.29 NS
<i>Geospiza magnirostris</i>	1	16	-15.16	19.97	0.29	5.77 NS
<i>Platyspiza crassirostris</i>	3	44	-18.47	25.91	0.59	59.36***

[†]Number of data points after removal of outliers.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$ (significance after Bonferroni correction); NS, not significant.

gape changes are the easiest of these to quantify and are predicted to have particularly strong effects on vocal tract resonances (Fletcher and Tarnopolsky, 1999; Hoese et al., 2000). Prior studies in a diversity of songbird species have shown a positive relationship between beak gape and acoustic frequencies during song production, in accordance with the predictions of the vocal tract resonance model (Westneat et al., 1993; Podos et al., 1995; Moriyama and Okanoya, 1996; Williams, 2001; see also Hausberger et al., 1991; Patterson and Pepperberg, 1994). Our study extends this finding to include Darwin's finches. We found that song frequency regressed significantly onto beak gape for over two-thirds of individuals examined and for all seven species examined. Furthermore, all significant regressions between gape and frequency had positive slopes.

Prior studies of beak gape kinematics in songbirds have been conducted in laboratory settings. Our study demonstrates the feasibility of conducting such a study in the field, at least for tame birds such as Darwin's finches. Close approaches to singers allowed us to maximize sound and video quality and to minimize the timing offset between audio and video signals. Perhaps the most severe limitation of our field method was the difficulty we had in identifying exact calibration standards within video frames for some of our clips. Fortunately, the availability of measurement data for these populations allowed us to use images of the birds themselves for calibration. Most of our birds studied here were not banded, so we estimated measurements of individuals using population means. Resulting errors are expected to exert only minimal effects on the species-level regressions, with the exception of *Geospiza fortis*, which shows extensive variation in morphology (Grant, 1999). We have recently discovered that *G. fortis* at one of our field sites, El Garrapatero, occurs in two morphs ('small') and ('large') that are highly distinct in beak size, shape and bite-force capacities (J. Podos, A. Hendry, A. Herrel and S. Huber, unpublished data). These morphs are identified readily on video clips, and by taking average beak length measurements for each morph we were able to reduce our calibration error for *G. fortis* at this site. For species-level regressions, calibration errors were most likely expressed as slight inaccuracies in regression intercept and slope values (Table 3). In spite of this error, the uniformly high *F*-ratios (Table 3) suggest that improved calibration accuracy would not change the overall finding that gape and frequency are positively related in these birds.

Our study thus supports the generality of the resonance model of song production. Furthermore, our study provides an opportunity to explore the effect of morphological variation on patterns of beak use during song production. Darwin's finches show particularly extensive variation in beak morphology and body size (Grant et al., 1985; Grant and Grant, 2002b). How might variation in these attributes influence the relationship between beak gape and song production? As a start, it is useful to consider the relationship between beak function and the potential for beak movements (Nowicki et al., 1992; Podos and Nowicki, in press). Because of a tradeoff between force and

speed in jaw mechanics, beak size and presumed force application potential are expected to correspond negatively to the maximum potential speed of gape adjustments (Podos, 2001). Birds with large beaks are expected to have difficulty performing rapid gape changes, whereas small-beaked birds should be relatively free of this constraint. We might therefore predict that birds with small beaks will undergo more rapid and/or precise beak gape adjustments while singing. However, the frequency and timing features of Darwin's finch songs have evolved in apparent compensation – with larger-beaked birds in effect evolving simpler songs – presumably in order to retain the filtering function of the vocal tract as beaks have diverged (Podos, 2001). As a result, we actually expected in this study that variation in beak size and function would exert only minimal effects on the expression of gape by frequency relationships.

This expectation is supported by our analysis of regression slopes, which failed to demonstrate any distinctions among the Darwin's finches (Fig. 5). Our confidence in the validity of this finding is supported by the high statistical power of the test employed. Uniformity among Darwin's finches is also suggested by their contrast as a group to the two sparrow species, as shown by the near-significant result of the test that included all species and by the *post-hoc* contrasts (Table 4). The conserved relationship in regression slopes within the Darwin's finches is consistent with their recent common ancestry and suggests that the gape–frequency relationship has not been influenced by the large-scale variations these birds express in beak morphology and body size.

Our expectation that body size variation should correspond to the *y*-intercepts of beak gape by frequency regressions received mixed support. We found a significant effect of species on regression intercepts, both including and excluding the sparrow species (Table 4). Furthermore, *post-hoc* tests revealed distinct categories of species based on intercept data. Several of these designations were consistent with the body size hypothesis. The two species with the smallest body masses, *Certhidea olivacea* (warbler finch) and *Camarhynchus parvulus* (small tree finch), for instance, were in the category of birds with the highest intercepts. However, other designations deviated from the body size hypothesis, particularly the placement of *Platyspiza crassirostris* (vegetarian finch), one of the two largest species, in this same category of high intercept species. The overall correlation between body mass and *y*-intercept was negative, as predicted, although not at a statistically significant level. One possible explanation for this result is the relatively low sample size for some of our species, four of which were represented by only a single bird (after we had excluded from analysis those individuals with non-significant regressions). There may be additional functional hypotheses, yet to be identified, to explain the diversification of regression intercepts.

Plots of beak gape by frequency, pooled by species, showed substantial scatter around regression lines (Fig. 5). This variation might arise from within-individual and inter-individual sources. In our analysis of *Geospiza fortis*, the

detection of significant differences in regression parameters among individuals indicates that, at least in this species, inter-individual variation exceeds within-individual variation. This is consistent with our impressions that gape profiles from within the same bird, across different renditions, tended to be very similar [for example, compare the gape profiles in Figs 2 and 4 (Bird A), both of which are from the same bird]. The acoustic stereotypy of Darwin's finch songs across renditions (Bowman, 1983) thus appears to be matched by stereotypy in patterns of beak movement.

Variations in regression parameters among conspecific birds might be caused by a number of factors. Errors in the calculation of gape, due to imprecise estimates of beak lengths in the calibration process, could lead to variation in regression intercepts but presumably not slopes. Ideally, we would have minimized calibration errors by obtaining direct beak length measurements from all subjects, although this was not possible given the opportunistic nature of our sampling procedure. More significantly, within-species variations in gape by frequency relationships may be caused by variation in biological factors such as age, condition and the features of songs produced. For example, perhaps birds with more experience are better able to match song patterns with precise adjustments in beak gape. However, we failed to detect significant correlations between regression values and plumage score (as an indicator of age) or between regression values and song frequency features. In one suggestive trend, birds that sang songs with higher frequencies and wider bandwidths tended to have higher regression slopes (e.g. Fig. 4, compare Birds A and C). This makes sense insofar as wider gapes should be required to help filter higher frequency notes.

Beak gape changes might conceivably play a functional role in amplitude as well as frequency modulation, although the vocal tract resonance model makes no such prediction. Support for a relationship between gape and amplitude was relatively weak; 17 of 56 song sequences showed significant relationships. Nevertheless, all of these significant regressions were positive. A likely explanation for positive relationships between amplitude and gape was identified by Westneat et al. (1993), who noted for their sparrow data that frequency and amplitude were often positively correlated and that gape might thus correlate to amplitude values as a secondary consequence. Indeed, from among the 17 song sequences in our sample for which amplitude and gape were correlated, 15 showed positive correlations between frequency and amplitude, nine to statistically significant degrees (Pearson product moment correlations, $P < 0.05$).

In summary, we find that seven Darwin's finch species match beak gape to peak frequencies during song production (e.g. Figs 1, 2) and, furthermore, that this matching is done in a similar way across species (Fig. 5). This finding provides potential insights into the evolution of song structure in these birds. Different species of Darwin's finches are expected to vary in the versatility of their beak movements because of a tradeoff in jaw mechanics between force and speed. Tradeoffs between force and speed are common in vertebrate motor

systems and arise from biomechanical parameters (e.g. lever arm position) as well as muscle architecture (e.g. degrees of muscle pennation; see Herrel et al., 2002 for an overview of force–speed tradeoffs). Darwin's finches that have evolved the ability to apply strong crushing forces are thus expected to have evolved, as a necessary consequence, lower maximal speeds of gape change. Thus, in order to conduct accurate vocal tract matching, as characterized in the present study, birds that have evolved strong force potential should have evolved, as a secondary response, songs that are comparatively 'easy' to produce in terms of vocal performance (Podos and Nowicki, in press). Low-performance songs, according to our restricted definition, would require only low-speed vocal tract reconfigurations. By contrast, birds with beaks not adapted for strong crushing abilities should be free to evolve songs that require greater vocal versatility. This hypothesis is supported by the demonstration that beak morphology and song features have evolved in correlated fashion in Darwin's finches, with smaller-beaked birds evolving songs with more rapid trill rates and wider frequency bandwidths (Podos, 2001).

This is not to say that the evolution of beak form and function will necessarily cause evolutionary changes in song structure (Slabbekoorn and Smith, 2000; Grant and Grant, 2002a,b). The probability of beak–song co-evolution depends on many factors, including patterns of diversification in jaw mechanics and the extent to which birds' performance abilities are challenged during song production (Podos and Nowicki, in press). Moreover, songs evolve through other mechanisms, including adaptation to distinct acoustic habitats (Bowman, 1979) and through the accumulation of copy errors (Grant and Grant, 1996). The mechanism we have proposed – song parameters evolving as an incidental consequence of adaptation for feeding – should apply most directly to those song parameters such as trill rate that are influenced by vocal performance and the ability to conduct rapid vocal tract reconfigurations. The evolution of other song parameters such as note phonology may be influenced more directly by other mechanisms such as copy error (Grant and Grant, 1996). It is still an open question as to which song parameters are most relevant in song function in Darwin's finches. If song function turns out to rely upon performance-related parameters, particularly in the context of species recognition, then the linked evolution of beaks and songs could facilitate reproductive isolation and speciation in these birds (Podos, 2001).

In the long term, an in-depth understanding of beak use in Darwin's finch song production will require a greater sampling effort that includes more individuals and populations from additional islands. The strength of our regression data suggests that the vocal tract resonance model will receive further support with larger samples. Additionally, a greater sampling effort should provide improved resolution on patterns of diversity in y -intercepts. Video analysis of singing Darwin's finches can also be expanded to address additional questions. It would be useful to evaluate beak movements for a wider diversity of vocal forms than the songs studied here, especially the high-frequency 'whistles' (in the range of 12–15 kHz)

produced by Darwin's finches (Bowman, 1983). We predict that whistles would be accompanied by gapes exceeding levels shown here, although there is some evidence that the precision of the relationships between gape and vocal tract resonances drops off at higher frequencies (Fletcher and Tarnopolsky, 1999; Hoese et al., 2000; R. A. Suthers, F. Goller, R. Bermejo, J. M. Wild and H. P. Zeigler, unpublished). It would also be useful to obtain video clips of gape patterns using the higher sampling rates (e.g. 500 frames s⁻¹) now available in portable field cameras. High-speed video data would allow us to evaluate the relationship between gape and frequency with greater precision and would also enable us to characterize the velocity and acceleration of beak movements during song production as a way to test the hypothesis that beak force capacities co-vary negatively with the speed and precision of beak gape changes (Podos, 2001).

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