Persistence of song types in Darwin's finches, *Geospiza fortis*, over four decades

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Learned bird songs evolve via cultural evolution, with song patterns transmitted across generations by imitative learning. In Darwin's finches of the Galápagos Islands, males learn songs from their fathers, and song types can be maintained across multiple generations. However, little is known about the time frame over which specific song types are preserved, in the face of copy errors and corresponding modifications to song structure. Here we investigate cultural evolution in songs of male *Geospiza fortis*, at Academy Bay, Santa Cruz Island, comparing songs recorded in 1961 by R. Bowman (20 individuals) to those recorded in 1999 by J. Podos (16 individuals). For each individual, we characterized four timing and six frequency parameters, and assessed inter-individual variation in song structure using multivariate analysis. Several 1961 song types persisted into 1999, some with remarkable fidelity. Variation among song types was extensive during both years, and we detected no changes in 10 vocal parameters across the sampling period. These results illustrate temporal continuity in a culturally acquired trait, and raise questions about mechanisms that promote stability in song structure.

Keywords: bird song; cultural evolution; Darwin's finches; Galápagos Islands; *Geospiza fortis*

1. INTRODUCTION

Studies of bird songs have provided numerous insights into the process of cultural evolution (e.g. Mundinger 1980; Freeberg 2000). Population-level changes in culturally acquired traits accrue through mechanisms analogous to those regulating genetic evolution (Lynch 1996; Payne 1996). Some mechanisms may cause songs to diverge over time, whereas others may stabilize song structure. Divergence may occur in the acoustic structure of specific song types, driven by copy inaccuracy, improvisation or rearrangement of existing song units (Slater & Ince 1979; Payne 1996; Nelson *et al.* 2004). Alternatively, song types may remain stable if learning, production or perceptual mechanisms restrict song divergence (Podos *et al.* 2004). Song evolution may also proceed as different

song types become more or less prevalent, for instance through immigration, emigration or drift (Baker & Jenkins 1987; Lynch 1996), or if some song types endow their singers with elevated fitness (Gibbs 1990; Baker & Gammon 2008).

The study of song evolution has profited from research on island birds, including Darwin's finches of the Galápagos Islands, Ecuador. The Galápagos medium ground finch *Geospiza fortis* has been particularly well studied, with three notable features documented: males sing only a single song type throughout their lives (Bowman 1983), within-population heterogeneity in song structure is high (Ratcliffe 1981; Huber & Podos 2006), and young males usually copy songs directly from their fathers (Grant & Grant 1996). These observations suggest conflicting pressures on song evolution. On the one hand, learning from fathers suggests that song types would remain structurally stable, because young males would be less likely to combine material learned from multiple neighbour tutors, as it happens in some songbird species (Beecher 2008). On the other hand, observed variability within populations suggests that novel song patterns are generated readily. Earlier analyses suggested that *G. fortis* singing certain song types were selectively favoured, a phenomenon that could change song type prevalence (Gibbs 1990). Long-term research, however, found that the prevalence of multiple song types remains relatively stable over time (Grant & Grant 1996). Moreover, specific song types appear to remain fairly stable in structure, at least for up to five generations (Grant & Grant 1996). It is unknown whether song types persist over longer time periods, in the face of copy errors and corresponding modifications to song structure.

We studied long-term cultural evolution in *G. fortis* on Santa Cruz Island, capitalizing on Robert Bowman's pioneering recordings from 1961. Bowman (1983) observed that *Geospiza* sp. songs show greater variability on large islands than on small islands, with the population on the large island of Santa Cruz being particularly variable. Here, we assess potential changes in the acoustic structure of song types between 1961 and 1999.

2. MATERIAL AND METHODS

All birds were recorded on Santa Cruz Island, within the Galapagos National Park and in the vicinity of the Charles Darwin Research Station (00°44'15"–30" S, 90°18'05"–09" W; see Bowman (1983) for information about the study location). Bowman recorded unbanded birds between November 1961 and February 1962, using Nagra III-B or IV reel-to-reel recorders and an American D-33 microphone in a 24-inch parabola. Podos recorded colour banded birds in February and March 1999 using a Sony TCD-5M tape recorder and a Sennheiser ME66 shotgun microphone (Podos 2001). Differences in recording equipment across samples might presumably bias our acoustic analyses. In particular, directional microphones typically have more linear frequency responses than do parabolic microphones, an effect that can be exacerbated with increasing recording distances. However, recording equipment differences seem unlikely to have influenced our analyses, for two reasons: (i) Darwin's finches are tame and easily approached, in our experience as close as 2 m and typically within 5 m, thus minimizing recording distances and associated equipment effects, and (ii) frequency nonlinearities from parabolic recorders are typically manifest at frequencies outside of the range within which Darwin's finches sing. Tape degradation is another potential confounding factor, as Bowman stored the tapes himself and not in a sound archive. However, the Bowman recordings, when digitized in 2000, showed exceptional sound quality, and a recent study that compared

Figure 1. The measured acoustic parameters for a typical *G. fortis* song. Parameter no. 1 = number of notes; other parameters listed in text.

historical reel-to-reel tapes with current cassette recordings did not uncover any negative effects owing to degradation (Derryberry 2007).

We selected songs of 20 individuals recorded by Bowman (4.3 ± 1.3 (mean $\pm$ s.d.) song exemplars per bird) and 16 by Podos (3.6 ± 1.6). Songs were digitized (25 kHz sampling rate, 16-bit encoding) and analysed using RAVEN Pro 1.3 (Cornell Laboratory of Ornithology, 2004), constructing the spectrograms with a 256 fast Fourier transform length and a Hanning Window. For each song, we measured 10 parameters (figure 1). (1) Number of notes (a note being a continuous trace on a spectrogram), (2) trill rate (notes per second) (3) note duration (averaged across notes, if there was more than one note) and (4) song duration. For individual notes, we measured (5) peak frequency and the (6) minimum and (7) maximum frequencies at which the amplitude exceeded -24 dB relative to peak frequency (as in Podos 2001). We also calculated (8) frequency bandwidth (maximum–minimum frequency) over entire notes, and measured peak frequency for the (9) first 10 ms and the (10) last 10 ms of individual notes.

Measurements were averaged across all exemplars for each individual. We conducted principal components analysis (PCA) using SYSTAT version 12 (SPSS Inc., 2007), to more readily compare song type variation across years, retaining only principal components (PCs) with eigenvalues greater than 1.0. PC scores and raw parameter values were compared between years using Mann–Whitney *U*-tests, with *p*-values adjusted using the Dunn–Sidak method for multiple comparisons (Sokal & Rohlf 1995). We also assessed natural song type groupings using *k*-means cluster analysis to assess whether songs from different years tended to cluster together. PCA scores were entered into the *k*-means cluster analysis, solutions were derived for $2 \leq k \leq 10$, and the *k*-value that maximized the sum of *F*-ratios was selected as the most natural grouping (Nowicki & Nelson 1990).

3. RESULTS

The structure of some song types was highly conserved between 1961 and 1999, as indicated by the PCA. PC1 and PC2, representing aspects of song frequency (PC1) and timing (PC2), explained 60.5 per cent of total variance (table 1). In a plot of these two

Table 1. Principal components weightings on 10 acoustic parameters, combining the 1961 and 1999 data. (Significant (at $\alpha = 0.05$) weightings are indicated in bold print.)

per cent of variance explained	principal components			
	1	2	3	4
frequency bandwidth	0.95	0.17	0.08	−0.08
whole note, max. frequency	0.95	0.12	0.09	0.18
whole note, peak frequency	0.73	0.10	−0.06	0.17
end note, peak frequency	0.51	−0.36	0.05	0.59
trill rate	−0.12	−0.96	0.04	0.04
note duration	0.17	0.94	0.14	−0.09
number of notes	−0.05	−0.76	0.62	0.09
song duration	0.08	0.11	0.99	0.05
whole note, min. frequency	0.02	−0.18	0.06	0.91
beginning note, peak frequency	0.19	0.47	0.01	0.61

components, some 1961 song types lie very close to some 1999 song types, despite wide variation within years (figure 2). PC3 and PC4, representing aspects of duration (PC3) and frequency (PC4), explained an additional 25 per cent of the variance.

Song types from 1961 and 1999 overlapped in all individual acoustic parameters, and no significant changes were detected across years in any individual parameters or PCA axes (table 2).

When *k*-means cluster analysis was conducted on the first two PCs only, the optimal number of groups (*k*) was 2 (division indicated by the blue line in figure 2). Both groups included exemplars from both 1961 and 1999. When the *k*-means cluster analysis was repeated using all PCs with eigenvalues greater than 1 (PC1–PC4), the optimal *k* was 10 (using such a *k*, there were only few exemplars per cluster). Of these 10 groups, five included both 1961 and 1999 songs.

4. DISCUSSION

Some song types of the Darwin’s finch *G. fortis* persisted over 37 years with remarkable fidelity. An example appears in figure 2, just to the right of label A: one song is from 1961, and the other from 1999. Numerous other cases of close overlap are apparent (purple shading in figure 2). More generally, the acoustic space of *G. fortis* songs changed little over the four decades, with no significant changes detected either in raw parameters or PCs, despite some trends bordering on statistical significance (table 2).

While our data document persistence of some song types, we cannot assess with confidence whether novel song types emerged over the four-decade span. For illustrative purposes, we have labelled three song types of 1999 as B, C and D in figure 2. These song types are relatively isolated on the PCA diagram. While it is possible that these song types arose after 1961, it is also possible that these song types existed in 1961 but had just not been sampled. If these song types indeed emerged after 1961, it seems likely that they did not emerge *de novo*, but rather as

Figure 2. Representative spectrograms of song types from the 20 males recorded in 1961 (blue boxes) and the 16 recorded in 1999 (pink boxes), superimposed on the graph of principal component (PC)1 versus PC2. The blue line divides the two main groups defined by the k -cluster analysis of PC1 and PC2. Letter labels refer to particular song types mentioned in §4.

Table 2. Mann–Whitney tests for differences in song parameters and principal component analysis (PCA) scores between 1961 and 1999.

parameter	W	p	Dunn–Sidak cor
original parameters			
numnotes	140.5	0.43	1
trill rate	79	0.009	0.088
notedur	226	0.036	0.31
songdur	228	0.030	0.27
freqmin	223	0.047	0.38
freqpeak	215.5	0.080	0.57
freqmax	210	0.12	0.71
band	195	0.28	0.96
beginning	209	0.12	0.73
end	185	0.44	1
derived PCA axes			
PC1	188	0.39	0.86
PC2	233	0.020	0.076
PC3	215	0.082	0.29
PC4	225	0.039	0.15

modifications of the pre-existing song types. For example, song B is similar to song types from 1961 directly to the right of it on figure 2, except that it has more note repetitions. Likewise, song C is similar to 1961 song types directly below it on figure 2, except with more notes. Finally, song D looks similar to a cluster of 1961 and 1999 songs labelled E, but with the high and low-frequency components reversed in order. Hence, novelty in *G. fortis* might emerge more from a recombination of elements, parallel to that described by Nelson *et al.* (2004) than from a gradual modification of specific song types owing to inaccurate copying and improvisation (e.g. Payne 1996).

Mechanisms favouring the temporal stability of song types include preferences for specific (e.g. local) song types, or selection against songs with divergent acoustic features (songs that feature copy error or innovation or songs from a distant population, Wright *et al.* 2008). In the case of *G. fortis*, individuals appear not to have a choice of what song to copy; it is that of their social father. However, individuals may fail to copy their

father's song with fidelity, and consequently suffer mating costs, to the extent that other individuals do not respond to their songs (Lachlan *et al.* 2004). This hypothesis is consistent with data from Podos (2007), who found that male *G. fortis* in the El Garrapatero population on Santa Cruz respond much more strongly to songs from their own population than to songs from the Bahia Academia population, 11 km distant. This discrimination occurred despite the fact that songs from the two populations overlap acoustically, an observation that suggests these birds respond most strongly to song types that are familiar.

Other mechanisms might favour novelty in songs of Darwin's finches. For example, Grant & Grant (1996) showed that female *G. fortis* tend to select males whose songs differ from their (the females') fathers. This tendency recalls the finding by Grant (1984) that female *G. conirostris* on Isla Genovesa avoid mates with songs similar to their fathers, perhaps a result of selection to avoid inbreeding. If females indeed avoid males singing paternal songs, males singing novel songs would presumably benefit. In order to balance familiarity and novelty, one strategy of *G. fortis* males might be to recombine familiar song elements in novel ways. More data are needed to document the accuracy of copying and the prevalence of improvisation/recombination in this species, and more widely across the genus *Geospiza*.

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