Singing in the sky: song variation in an endemic bird on the sky islands of southern India

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Birdsong structure is known to vary across different scales of geographical separation, from differences between neighbours in a habitat to populations across continents. The high-elevation regions of the Western Ghats mountains in southern India form 'sky islands' containing the unique Shola habitat. Bird species on such sky islands are often specifically adapted to habitats typical of these islands while populations on different islands may have been geographically isolated over varying periods of time. Forest fragmentation can intensify the effects of such isolation by affecting species dispersal processes. We examined the effects of genetic differentiation across populations on the song of a threatened, endemic bird, the white-bellied shortwing, *Brachypteryx major*, on different islands of this sky island system. We compared songs from three populations, one of which on one island was genetically distinct from the other two populations on another island. These two populations were genetically similar but separated by recent deforestation. We recorded songs from 23 individuals and characterized 572 songs by 13 parameters. Multivariate analyses revealed significant differences in song between the three populations, with the genetically distinct populations across the two islands being the most differentiated. This was supported by a visual and aural examination of spectrograms that revealed characteristic qualitative differences in songs across these populations. Finally, this study corroborates accepted patterns of congruence between song and genetic divergence across islands and also highlights the difference in song between anthropogenically fragmented, but genetically similar populations, possibly owing to cultural drift.
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Variation in birdsong, which plays a critical role in widely different phenomena such as species recognition, territoriality and mate choice (Catchpole & Slater 1995; Gil & Gahr 2002) could result from innate genetic differences (Slabbekoorn & Smith 2002) or unpredictable cultural variation (Grant & Grant 2002). Such variation is most likely to occur in geographically isolated populations that may or may not be genetically differentiated. Although the origin and evolution of birdsong in isolated populations remain largely unexplored, they may have far-reaching implications for complex processes such as speciation (Price 1998, 2008).

Geographical variation in song is known to exist on different scales, from the microgeographical (e.g. white-crowned sparrow, *Zonotrichia leucophrys*: Nelson 1998) to continent-wide (e.g. blue

tit, *Cyanistes caeruleus*: Doutrelant & Lambrechts 2001). Such variation can arise either from genetic variation in innate vocalizations or cultural differences in learned components of song or a combination of these factors. Some studies have shown congruence in genetic and song differentiation in certain taxa such as reed warblers, *Acrocephalus* sp. and *Hippolais* sp. (Helbig & Seibold 1999), kinglets, *Regulus* sp. (Päckert et al. 2003), winter wrens, *Troglodytes troglodytes* (Drovetski et al. 2004), golden-spectacled warblers, *Seicercus burkii* (Päckert et al. 2004) and yellow-billed bush warblers, *Cettia acanthizoides* (Alstrom et al. 2007). However, in certain other taxa such as white-crowned sparrows (MacDougall-Shackleton & MacDougall-Shackleton 2001) and Darwin's finches, *Geospiza* sp. (Grant & Grant 2002), song variation across isolated populations was found to have a significant cultural basis. Songbirds are known to learn many of their vocalizations in a manner analogous to human vocal learning (Doupe & Kuhl 1999) and in such cases, songs, like memes, may differ even if populations are not genetically different. Songs, for example, are known to be more divergent culturally on small isolated islands (Gammon et al. 2005).

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At the smallest geographical scale, individual songs have a certain level of similarity with one another while they can differ in other features. Variation in individual songs is thought to provide an important basis for sexual selection (Price 1998) that can even lead to speciation. What has, however, been poorly documented is individual variation in song within and across populations caused by cultural differences (but see Grant & Grant 1996; Laiolo & Tella 2005, 2007).

Sky islands are a terrestrial island system of high-elevation mountain-top habitats that may display different levels of landscape connectivity. Such a system provides us with a natural system to examine geographical variation in birdsong across populations with and without genetic connectivity. The Western Ghats mountains in southern India harbour one such tropical sky island system (Warshall 1994). It is noteworthy that studies of cultural variation in birdsong dialects have largely been restricted to temperate species (Nelson et al. 2004), while songs of species in tropical biodiversity hotspots, such as the Western Ghats, remain virtually unexplored. The white-bellied shortwing, *Brachypteryx major*, a songbird endemic to this system, exhibits high population genetic divergence across islands, while populations on a single island could be genetically similar, although ecologically isolated (Robin et al. 2010).

In this study, we asked the following questions. (1) Do songs of the white-bellied shortwing differ across and within sky island populations and if they indeed vary, do they correspond to the level of genetic differentiation between these populations? (2) Which song parameters lead to differences in birdsong, if any, across and within islands?

METHODS

Study Area

This study was conducted on two islands, Ooty and Grasshills–Kodaikanal in the sky island complex of the Western Ghats mountains of southern India. The breeding song of the shortwing was recorded from two sites, Kodaikanal and Grasshills, on a single island and from one population, Ooty, on another island separated from the first by a deep, 500-million-year-old geographical and genetic barrier (Robin et al. 2010; Fig. 1). The shortwing populations on these two islands differed significantly in combined mitochondrial DNA (cytochrome b, cytochrome oxidase 1 and control region) distance (Kimura-2parameter distance = 9.5%, $F_{ST} = 0.97$; Robin et al. 2010). In contrast, Grasshills and Kodaikanal, two populations on the same island, showed little genetic differentiation using the same markers (Kimura-2parameter distance = 0.22%, $F_{ST} = 0.11$). Lands deforested at least 100 years ago, however, separate Kodaikanal and Grasshills from one another (Fig. 1). All three populations have similar habitat structure characterized by stunted montane evergreen Shola forests (described in Meher-Homji 1984; Shanker & Sukumar 1999).

Study Species

The white-bellied shortwing, considered to be a rare species until recently, is a threatened, endemic, understory bird (Collar et al. 2001) found uniquely in the Shola forests on the sky islands in the Western Ghats (Robin & Sukumar 2002; Robin et al. 2006). The species is rather cryptic and is most often detected by its characteristic breeding song (Robin & Sukumar 2002; Robin et al. 2006). Our recent study on its population dynamics at Grasshills with marked birds indicates that individuals are territorial and could hold territories for up to 4 years or longer (V. V. Robin & A. Sinha, unpublished data).

Data Collection

Songs were recorded from 23 males including three colour-banded and five unmarked individuals at Grasshills, 10 unmarked individuals at Kodaikanal and five unmarked individuals at Ooty.
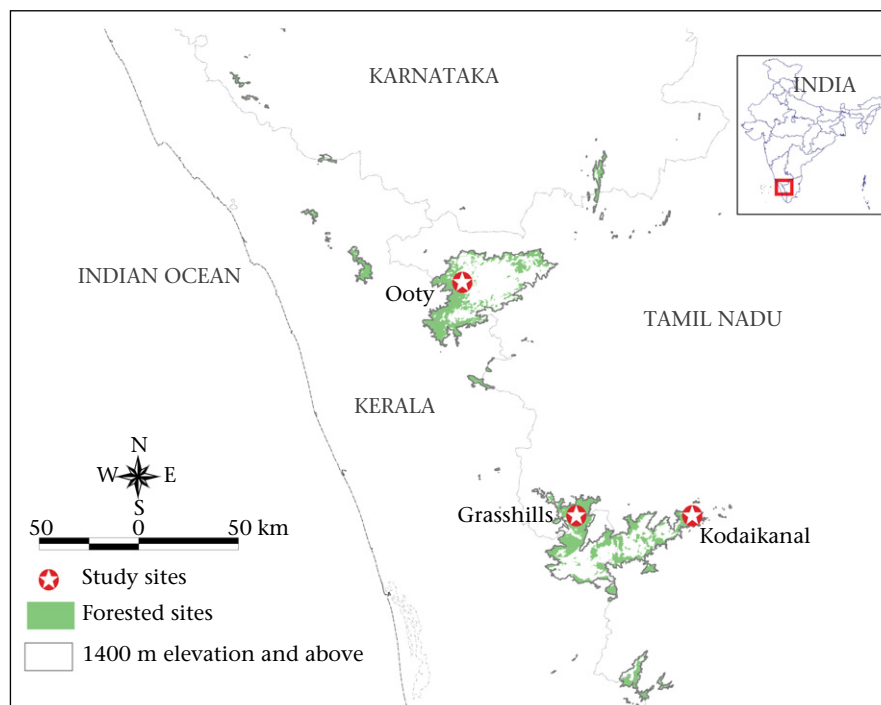

Figure 1. Map of the study locations on the sky islands of the Western Ghats mountains. The forested areas are indicative of present Shola-grassland habitat.

While recording unmarked individuals, we took care to record only a single continuous bout from one individual in each location to avoid repeated recording of the same individual. All recordings were made within a forest patch with closed canopy cover and at a distance of 8–20 m from the bird, depending on its visibility and accessibility. All recordings were made on audiotapes (TDK-90) in an analogue tape recorder (Marantz PMD222) using a directional microphone (Sennheisser ME66 shotgun microphone with K6 powering module).

A total of approximately 2000 songs were recorded and digitized with RAVEN PRO 1.3 (www.birds.cornell.edu/raven) at a sampling rate of 48 kHz. Songs that were of poor recording quality or had high background noise from rain or other birds were discarded and 1312 songs were retained for further analysis. Individual notes within each song were digitized from the spectrogram and we also examined the power spectrum. This allowed us to inspect the relative power at a particular frequency and locate more precisely the bounds of the highest and lowest frequencies of a note. The lowest frequency (denoted as 'Low Frequency'), highest frequency (denoted as 'High Frequency'), start time and end time for each note were recorded (Koetz et al. 2007; Liu et al. 2008; also reviewed in Slabbekoorn & Smith 2002). The length of each note was computed as the difference between its end time and start time, and its bandwidth as that between its High and Low Frequencies. From these basic measurements, we derived 13 variables for each song (Fig. 2, Appendix Table A1) and these were used in the final analysis. Thus, our final data had a nested structure with 13 variables for each song computed from their respective notes, with several songs for each individual and several individuals from each population being analysed.

Data Analysis

Data selection and initial analysis

We recorded a mean + SE of 104.1 + 46.8 (range 14–403) songs from each marked individual ($N = 8$) over several recording sessions at Grasshills. In contrast, a mean of 31.9 + 4.7 (range 11–75) songs were recorded from single recording sessions of unmarked individuals ($N = 15$) at Kodaikanal and Ooty. To make the data comparable across populations, we selected a maximum of 30 songs (mean + SE = 24.87 + 1.3, range 11–30) from each individual, wherever possible. Additionally, for each marked individual, we chose only the first 30 songs from a single bout, which, in turn, was chosen randomly from among its multiple bouts that had

a minimum number of 30 songs. Ultimately, we used a data set of 572 songs for analysis.

All statistical analyses were conducted using JMP version 8.0.1 (SAS Inc 2009) and SPSS version 16 (Norüsis 1992). Our initial analyses with 13 chosen variables revealed a high level of collinearity with 45 of the 55 pairs of variables being significantly correlated with one another (Spearman rank correlation: $P < 0.05$). We therefore conducted a principal components analysis (PCA) and, following examination of the scree plot, found that five components (PC), with Eigenvalues greater than 1, accounted for 86.37% of variation in the data (Table 1). The variables that loaded maximally onto these five PC were standard deviation (SD) in High and Low Frequency onto PC1, Note Bandwidth (mean and SD) onto PC2, Mean Low and High Frequency onto PC3, Notes Per Song and Song Length onto PC4 and Note Length (mean and SD) onto PC5. We then extracted these component scores (PC1–PC5) for each data point and used these five reduced, uncorrelated variables for further analysis. We also ensured that there were no obvious nonlinear associations between the extracted component scores.

Final data analysis

To test for differences in song between and within islands, we conducted a nested MANOVA with all five PC scores, with individuals nested within a population and songs nested within an individual. We additionally conducted a discriminant function analysis (DFA) to examine and validate whether songs could be grouped according to populations based on the relationship between the five PC scores (Blumstein & Munos 2005; Podos 2007). To investigate whether the selection of 30 songs from each individual was adequate for the complete resolution of the discriminant model, we repeated the entire analysis (PCA and subsequent DFA with the four significant PC scores that emerged) with the complete Grasshills data set (mean + SE = 104.1 + 46.8, range 14–403 songs per individual). We found no effect of sample size in this analysis, as the inclusion of the additional songs did not improve the discriminant model.

To examine which parameters led to differences in song between and within populations, we conducted a nested ANOVA for each of the five PC scores separately and post hoc Student's t and Tukey's honestly significant difference (HSD) tests to examine the effect details. We also examined the contribution of the different song parameters to the discriminant model.

Finally, we visually and aurally examined the spectrograms of all individuals from all three populations to describe any qualitative similarities or differences between the songs of these populations.
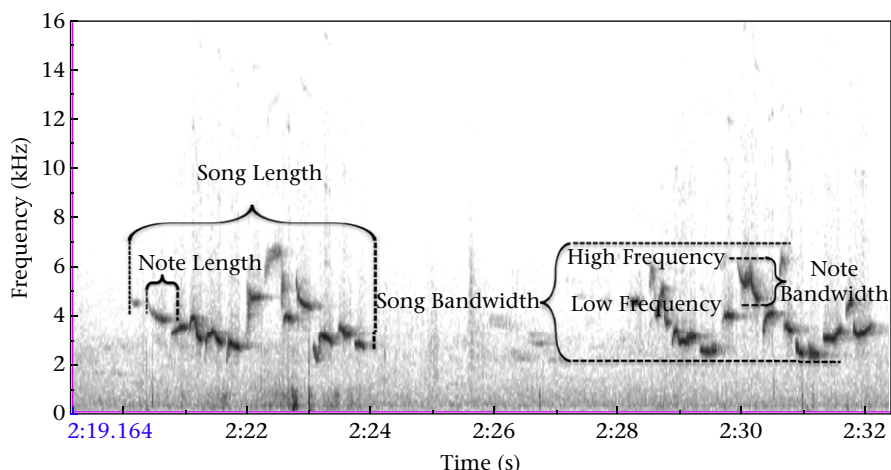

Figure 2. Spectrogram of a typical song of the white-bellied shortwing with some of the key variables used for the final analysis.

Table 1
Principal component scores for variables of the white-bellied shortwing song used in the final analysis

Rotated factor pattern	PC1	PC2	PC3	PC4	PC5
Notes Per Song	0.2994166	0.0991273	−0.057982	0.8451714	−0.254883
Mean Low Frequency	0.207815	−0.175274	0.9371506	0.0115094	−0.053687
Mean High Frequency	0.2815473	0.5355666	0.7318569	0.0688674	−0.048818
Mean Note Bandwidth	0.1488233	0.9089015	−0.048518	0.0795311	−0.006443
Mean Note Length	−0.194793	−0.078647	0.086458	−0.083725	0.8288841
SD Low Frequency	0.9108075	−0.030605	0.1307009	0.0392139	−0.06422
SD High Frequency	0.7301477	0.4902194	0.1018798	0.10318	0.0400019
SD Note Bandwidth	0.182815	0.887056	−0.092035	0.0685369	0.0448643
SD Note Length	0.1047906	0.0951858	−0.109226	−0.016418	0.8151395
Minimum Song Low Frequency	−0.566028	−0.176561	−0.6708375	−0.211107	0.1011315
Maximum Song High Frequency	0.6685764	0.5202873	0.2631521	0.2767535	−0.034125
Song Length	0.0440427	0.0930999	0.0106081	0.9422663	0.0771328
Song Bandwidth	0.7708745	0.4966142	−0.046289	0.3100215	−0.067617

RESULTS

Does Song Vary across a Genetic Barrier?

We found that songs from all three sampled populations (Grasshills, Ooty and Kodaikanal) differed significantly from one another (MANOVA: $F_{4,546} = 10.23$, $P < 0.0001$) and that the greatest difference was across these populations (groupwise ANOVA, Table 2). We were also able to classify 67.5% of the songs to the correct population of their origin based on a discriminant model (Fig. 3), indicating that there were significant differences between all the groups sampled.

Two canonical discriminant functions significantly contributed to separating all three populations (canonical correlation = 0.64, 0.39, respectively). The first function was better at discriminating the genetically different populations, that is, Ooty from other populations (Fig. 3; variance explained = 79.9%; canonical correlation = 0.64; Wilk's lambda = 0.5, $P < 0.05$), than the second function, which separated the two genetically similar populations (Grasshills from Kodaikanal), albeit to a lesser extent (variance explained = 20.1%; canonical correlation = 0.39; Wilk's lambda = 0.85, $P < 0.05$).

There was no direct linear correlation between the difference in song across populations and the genetic distance between these populations, as genetically similar populations (Kodaikanal and Grasshills) within an island differed significantly in their songs. The magnitude of song differences, however, corresponded to genetic differentiation, as more genetically divergent populations differed more in their songs than did more genetically similar ones.

Although the largest differences in shortwing songs were across populations, there were also significant individual differences within a population, but to a lesser extent (Table 2).

Basis for Differences between Populations

In discerning which variables contributed most to differences in songs between populations, all the five variables, PC1–PC5,

Table 2
Contribution of different parameters and grouping to differences in white-bellied shortwing song

	Population	Between individuals within population
PC1	58.12*	2.93*
PC2	18.96*	4.51*
PC3	5.43*	4.77*
PC4	13.69*	3.32*
PC5	99.93*	10.11*

ANOVA groups effects test (F ratio, $df = 2, 20$).
* $P < 0.0001$.

displayed significant differences across the three populations (nested ANOVA: $F_{22,549} = 8.33$, 6.13, 5.18, 4.30 and 20.70 for PC1 to PC5 respectively, $P < 0.05$). All the variables also contributed significantly (Wilk's lambda: 0.830, 0.935, 0.972, 0.956, 0.748 for PC1 to PC5, $P < 0.05$) to differentiating populations in the discriminant model. However, PC5 (maximally correlated with Note Length) was the variable that best discriminated between populations compared to the other variables. In the DFA, the first discriminant function that best differentiated between populations was also maximally correlated with PC5 (Appendix Table A2). It is noteworthy that this function also separated the songs of genetically different populations in the study area most effectively (Ooty from Grasshills and Kodaikanal). In contrast, PC1 (maximally correlated with variation in Low and High Frequency) correlated with the second canonical function, which separated the genetically similar populations (Grasshills from Kodaikanal; Appendix Table A2).

We also examined which song parameters contributed to the differences between each of the sampled populations by examining their effect details (Student's t and Tukey's HSD tests; Table 3). We found that PC1 and PC5 were different across all the populations while Ooty was different from both Grasshills and Kodaikanal for PC4 (maximally correlated with Song Length and Notes Per Song). Grasshills and Kodaikanal, however, did not differ for the same variable. Ooty and Grasshills were not different for PC2 (maximally correlated with Mean Note Bandwidth) and PC3 (maximally correlated with Mean High and Mean Low Frequency) while Kodaikanal was different from both populations for this variable. Certain song parameters such as mean and SD of Note Length and SD of High and Low Frequency thus appeared to be more important in discriminating songs across different populations in this sky island system.

A qualitative, visual and aural examination of spectrograms revealed that Ooty songs were most different from those of the Kodaikanal and Grasshills populations, while these two were more similar to one another. In the Ooty population, certain notes were short and repeated often, while the songs were fairly simple with no complex, long notes (Fig. 4). The Grasshills and Kodaikanal populations had longer and more variable notes in their repertoire. Songs from these populations, although largely similar in structure, nevertheless exhibited certain differences. The Grasshills songs were characterized by a series of marginally overlapping, alternating high- and low-frequency notes, perhaps produced by alternating syrinxes (Fig. 5). This pattern was not observed in Kodaikanal (Fig. 6). The Grasshills songs also had very few repetitive notes, while those from Kodaikanal had more repetitive notes, although not as much as the Ooty songs. Aurally, the Kodaikanal song was very similar to the Grasshills song. These qualitative differences in song thus support the quantitative conclusion that songs of the most genetically differentiated Ooty
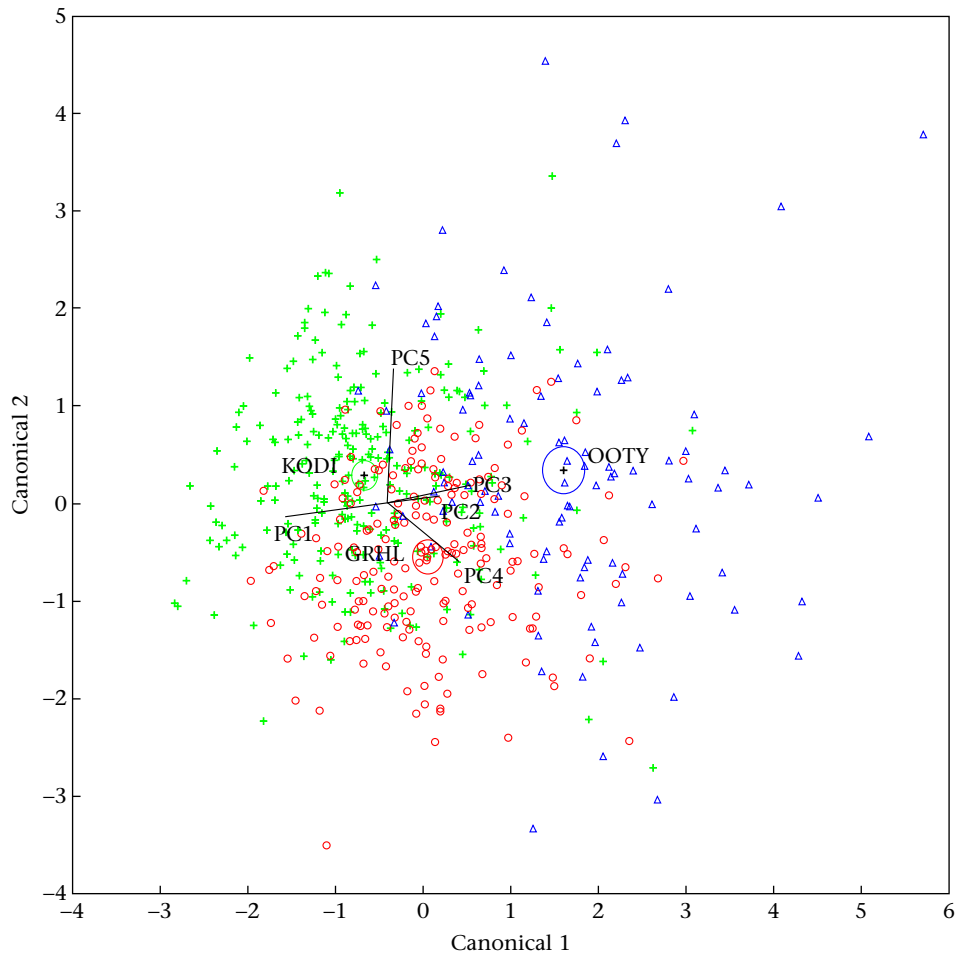
Figure 3. Canonical plot with five principal components of 572 songs from the three white-bellied shortwing populations. Each point represents a single song and circles represent 95% confidence intervals of the multivariate means of the three respective populations. GRHL: Grasshills; KODI: Kodaikanal; OOTY: Ooty. PC1–PC5 represent the five principal components.

population were most different from those of the other two genetically similar, although ecologically fragmented, Kodaikanal and Grasshills populations.

DISCUSSION

We found that shortwing songs from all three study populations on the two sky islands of the Western Ghats were different from one another. Populations that showed maximal genetic differentiation (Ooty from Grasshills and Kodaikanal) differed the most in their songs, while populations that were genetically similar (Grasshills and Kodaikanal) were also different, but by a smaller magnitude. Individuals exhibited considerable variation in their songs, which

Table 3
Effect details describing the difference in reduced white-bellied shortwing song parameters (PC1–PC5) between the three study populations

	KODI	GRHL	OOTY
PC1	A	B	C
PC2	A	B	B
PC3	A	B	B
PC4	A	A	B
PC5	A	B	C

For each parameter, groups with different letters are significantly different from one another (Student's *t* and Tukey's HSD test: $P < 0.05$). KODI: Kodaikanal; GRHL: Grasshills; OOTY: Ooty.
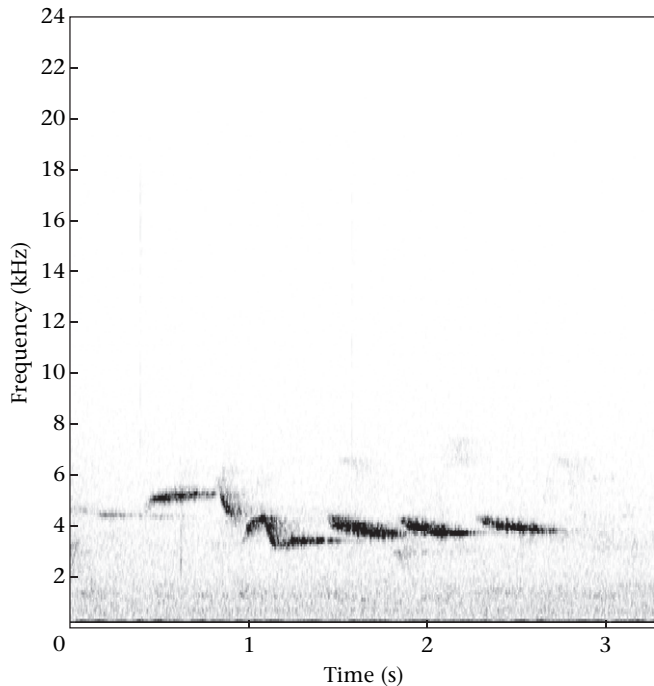
could not always be unambiguously assigned to specific populations or individuals. The genetically different populations varied most in Note Length, while genetically similar groups were separated by the variance in High and Low Frequency of their song.

The largest geographical barrier in the Western Ghats, the Palghat Gap, also serves as a 5-million-year-old genetic barrier for the white-bellied shortwing (Robin et al. 2010). The taxon looks distinctly different in plumage across this Gap, with the northern population (Ooty) exhibiting a rufous belly while the southern populations (Grasshills and Kodaikanal) have a white belly. Our study shows that populations across this Gap are clearly divergent not just in their genetic structure and plumage but also in their song. The greatest difference in song characters, examined aurally and spectrally, was across this genetic divide. The longer, complex notes seem to characterize the population south of the Palghat Gap (Grasshills and Kodaikanal), corroborating the role of note length in differentiating song. Song differentiation, strongly correlated with levels of genetic variation, has also been well documented in golden-spectacled warblers (Päckert et al. 2004) and yellow-billed bush warblers (Alstrom et al. 2007).

Some studies (e.g. Baptista 1996) suggest that certain traits such as song length show high genetic heritability. Dawson et al. (2006), on the other hand, found that note length and maximum frequency were the important variables in differentiating chickadee species. It is perhaps noteworthy that our study too has revealed note length to be an important variable in differentiating the song of genetically divergent populations.

Figure 4. Representative spectrogram of the Ooty song, north of the Palghat Gap, with repetitive short notes that characterize the songs of this population.
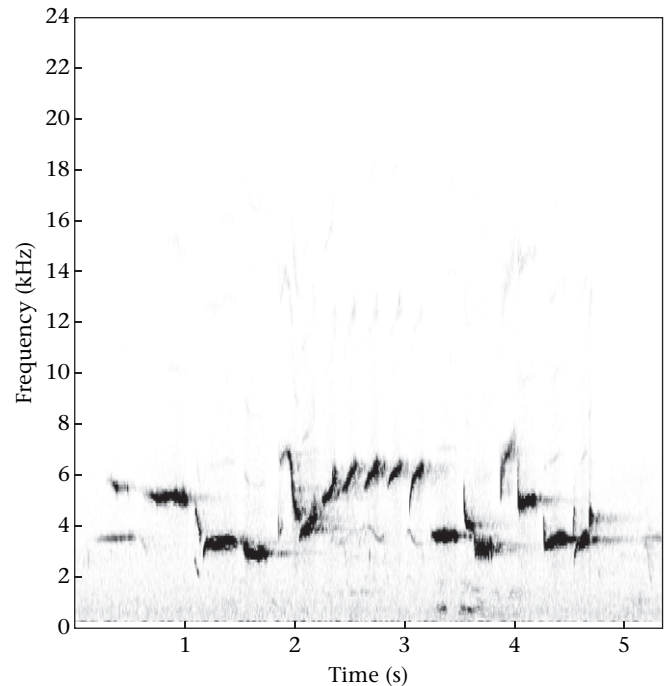

Figure 6. Representative spectrogram of the Kodaikanal song with long notes characteristic of individuals south of the Palghat Gap.

On a single sky island, the Anamalai–Palni Hills, the Grasshills and Kodaikanal populations are similar genetically, although they have been separated by deforested lands for over a century. The birds of these populations are also morphologically similar with no significant plumage difference. These birds, however, differ significantly in their song with the variance in the highest and lowest frequencies being the most discriminating variables. This difference is probably

Figure 5. Representative spectrogram of the Grasshills song, with repeated high- and low-frequency notes in the middle of the song, characteristic of individuals from this region.

due to the presence of certain, consecutive high- and low-frequency notes in the Grasshills population. Evidence for such differences in genetically similar populations is increasing (Grant et al. 2000; MacDougall-Shackleton & MacDougall-Shackleton 2001; Nicholls et al. 2006). Laiolo & Tella (2007) have recently demonstrated how Dupont's larks, *Chersophilus duponti*, across fragmented landscapes in Spain vary significantly in their song repertoire size. Podos et al. (2004), in a review, suggested that song dialects are easily formed in geographically separated groups where the species have certain life history traits such as limited dispersal, similar to what shortwings are presumed to exhibit (V. V. Robin & A. Sinha, unpublished data). Support for such a phenomenon appears to emerge from our results as well, as genetically segregated populations (Ooty and Grasshills–Kodaikanal) clearly showed divergence in their song patterns. Two genetically similar populations separated by habitat fragmentation, Grasshills and Kodaikanal, however, displayed several distinct song characteristics, an indication that some components of the shortwing song could differ, possibly caused by cultural drift. Nevertheless, we have so far only examined variation in ancient, slow-evolving mitochondrial DNA sequences. More detailed investigations with fast-mutating nuclear microsatellite markers may provide much deeper insights into recent genetic differentiation and its correlation with song variability.

Individual differences in song are known from several species (Williams & MacRoberts 1977; also reviewed in Podos et al. 1992). The factors that may have led to individual variation in shortwing song, especially cultural drift, in our study populations need further exploration. Birdsong has long been recognized as a classic example of a cultural trait in a nonhuman taxon (Catchpole & Slater 1995). It is believed that variation in birdsong could arise from individual behavioural traits that subsequently give rise to cultural differences caused by either drift or sexual selection of particular song characters (reviewed in Laiolo & Tella 2007), sometimes even leading to speciation (Ryan 2006).

In the shortwing, it appears that there are different processes that could be driving speciation. Genetic differentiation clearly
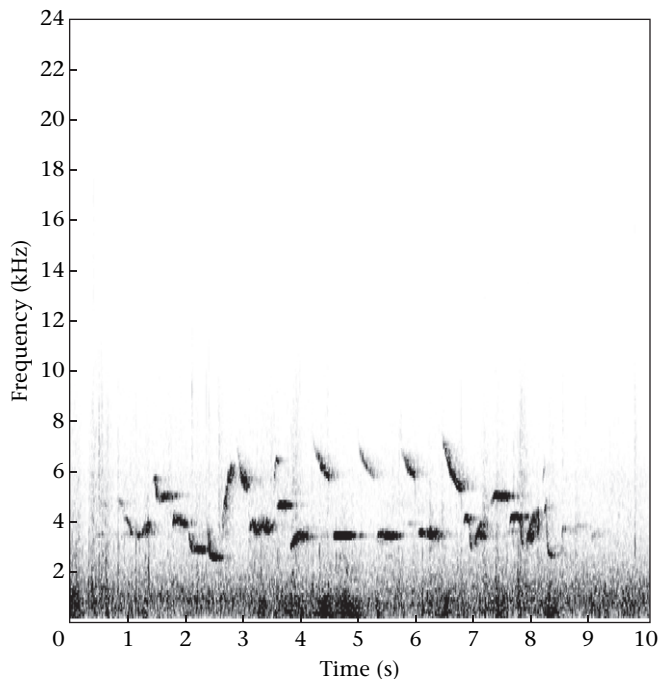
underlies the observed morphological and plumage differences between the two shortwing populations across the Palghat Gap. Similar differentiation following isolation has also been shown to lead to speciation correlated with inherent song differences in ground finches (Grant et al. 2000). We are of the opinion that certain elements of the shortwing song could have similarly differentiated during the process of speciation across the Gap. However, we are uncertain whether similar processes have driven differentiation in song between two populations (Grasshills versus Kodaikanal) within an island. As these populations have recently lost forest connectivity, it is possible that the differences between their songs reflect cultural variation. Thus, our documentation of variation in shortwing song, driven largely by genetic but also possibly cultural differentiation in the sky islands of the Western Ghats, could serve as a model system to test similar processes of differentiation in other species as well.

The study populations of the white-bellied shortwing continue to be under severe threat of habitat loss, fragmentation and degradation from human activities (Collar et al. 2001). In addition to threatening their survival, such fragmentation may impact these populations in several hitherto undiscovered ways, one of which could be the generation of cultural divergence in birdsong. It has been strongly suggested that, in addition to ecosystem, species and genetic diversity, populations with culturally differentiated traits be considered for conservation as a fourth level of biodiversity (Caro 2007; Laiolo & Tella 2007). While conservation attention should clearly be directed towards the two newly discovered shortwing species across the Palghat Gap (Robin et al. 2010), such efforts must also take into account the protection of populations with unique songs, including that in Kodaikanal, south of the Gap.

Acknowledgments

References

Alstrom, P., Olsson, U., Rasmussen, P., Yao, C., Ericson, P. & Sundberg, P. 2007. Morphological, vocal and genetic divergence in the *Cettia acanthizoides* complex (Aves: Cettiidae). *Zoological Journal of the Linnean Society*, **149**, 437–452.

Baptista, L. 1996. Nature and its nurturing in avian vocal development. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. Kroodsma & K. Miller), pp. 39–60. Ithaca, New York: Cornell University Press.

Blumstein, D. & Munos, O. 2005. Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. *Animal Behaviour*, **69**, 353–361.

Caro, T. 2007. Behaviour and conservation: a bridge too far? *Trends in Ecology & Evolution*, **22**, 394–400.

Catchpole, C. & Slater, P. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.

Collar, N., Crosby, R. & Crosby, M. 2001. *Threatened Birds of Asia: the BirdLife International Red Data Book*. Cambridge: BirdLife International.

Dawson, M., Bloomfield, L., Charrier, I. & Sturdy, C. 2006. Statistical classification of black-capped (*Poecile atricapillus*) and mountain chickadee (*Poecile gambeli*) call notes. *Journal of Comparative Psychology*, **120**, 147–152.

Doupe, A. & Kuhl, P. 1999. Birdsong and human speech: common themes and mechanisms. *Annual Review of Neuroscience*, **22**, 567–631.

Doutrelant, C. & Lambrechts, M. 2001. Macrogeographic variation in song: a test of competition and habitat effects in blue tits. *Ethology*, **107**, 533–544.

Drovetski, S. V., Zink, R. M., Rohwer, S., Fadeev, I. V., Nesterov, E. V., Karagodin, I., Koblik, E. A. & Red'kin, Y. A. 2004. Complex biogeographic history of a Holarctic passerine. *Proceedings of the Royal Society B*, **271**, 545–551.

Gammon, D., Baker, M., Tipton, J. & Yasukawa, K. 2005. Cultural divergence within novel song in the black-capped chickadee (*Poecile atricapillus*). *Auk*, **122**, 853–871.

Gil, D. & Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, **17**.

Grant, B. R. & Grant, P. R. 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution*, **50**, 2471–2487.

Grant, P. & Grant, B. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**, 707–711.

Grant, P., Grant, B. & Petren, K. 2000. The allopatric phase of speciation: the sharp beaked ground finch (*Geospiza difficilis*) on the Galapagos islands. *Biological Journal of the Linnean Society*, **69**, 287–317.

Helbig, A. J. & Seibold, I. 1999. Molecular phylogeny of Palearctic-African *Acrocephalus* and *Hippolais* warblers (Aves: Sylviidae). *Molecular Phylogenetics and Evolution*, **11**, 246–260.

Koetz, A. H., Westcott, D. A. & Congdon, B. C. 2007. Geographical variation in song frequency and structure: the effects of vicariant isolation, habitat type and body size. *Animal Behaviour*, **74**, 1573–1583.

Laiolo, P. & Tella, J. 2005. Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's lark. *Journal of Applied Ecology*, **42**, 1183–1193.

Laiolo, P. & Tella, J. L. 2007. Erosion of animal cultures in fragmented landscapes. *Frontiers in Ecology and the Environment*, **5**, 68–72.

Liu, I., Lohr, B., Olsen, B. & Greenberg, R. 2008. Macrogeographic vocal variation in subspecies of swamp sparrow. *Condor*, **110**, 102–109.

MacDougall-Shackleton, E. & MacDougall-Shackleton, S. 2001. Cultural and genetic evolution in mountain white-crowned sparrows: song dialects are associated with population structure. *Evolution*, **55**, 2568–2575.

Meher-Homji, V. 1984. Udhagamandalam (Ootacamund): a biogeographic perspective. *Indian Geographical Journal*, **59**, 205–213.

Nelson, D. 1998. Geographic variation in song of Gambel's white-crowned sparrow. *Behaviour*, **135**, 321–342.

Nelson, D., Hallberg, K. & Soha, J. 2004. Cultural evolution of Puget Sound white-crowned sparrow song dialects. *Ethology*, **110**, 879–908.

Nicholls, J. A., Austin, J. J., Moritz, C., Goldizen, A. W. & Webster, M. 2006. Genetic population structure and call variation in a passerine bird, the satin bowerbird, *Ptilorhynchus violaceus*. *Evolution*, **60**, 1279–1290.

Norüsis, M. 1992. *SPSS/PC+ Professional Statistics Version 5.0*. Chicago: SPSS Inc.

Päckert, M., Martens, J., Kosuch, J., Nazarenko, A. & Veith, M. 2003. Phylogenetic signal in the song of crests and kinglets (Aves: Regulus). *Evolution*, **57**, 616–629.

Päckert, M., Martens, J., Sun, Y. & Veith, M. 2004. The radiation of the *Seicercus burkii* complex and its congeners (Aves: Sylviidae): molecular genetics and bioacoustics. *Organisms Diversity and Evolution*, **4**, 341–364.

Podos, J. 2007. Discrimination of geographical song variants by Darwin's finches. *Animal Behaviour*, **73**, 833–844.

Podos, J., Peters, S., Rudnicky, T., Marler, P. & Nowicki, S. 1992. The organization of song repertoires in song sparrows: themes and variations. *Ethology*, **90**, 89–106.

Podos, J., Huber, S. K. & Taft, B. 2004. Bird song: the interface of evolution and mechanism. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 55–87.

Price, T. 1998. Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society B*, **353**, 251–260.

Price, T. 2008. *Speciation in Birds*. Greenwood Village, Colorado: Roberts.

Robin, V. V. & Sukumar, R. 2002. Status and habitat preference of white-bellied shortwing *Brachypteryx major* in the Western Ghats (Kerala and Tamilnadu), India. *Bird Conservation International*, **12**, 335–351.

Robin, V. V., Sukumar, R. & Thiollay, J. 2006. Status and distribution of the white-bellied shortwing *Brachypteryx major* in the Western Ghats of Karnataka and Goa, India. *Bird Conservation International*, **16**, 345–351.

Robin, V. V., Sinha, A. & Ramakrishnan, U. 2010. Ancient geographical gaps and paleo-climate shape the phylogeography of an endemic bird in the sky islands of southern India. *PLoS ONE*, **5**, e13321.

Ryan, S. J. 2006. The role of culture in conservation planning for small or endangered populations. *Conservation Biology*, **20**, 1321–1324.

SAS Inc 2009. *JMP, Version 8.0.1*. Cary, North Carolina: SAS Institute Inc.

Shanker, K. & Sukumar, R. 1999. Synchrony in small mammal populations of montane forest patches in southern India. *Journal of Animal Ecology*, **68**, 50–59.

Slabbekoorn, H. & Smith, T. 2002. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society B*, **357**, 493–503.

Warshall, P. 1994. The Madrean Sky Island Archipelago: a planetary overview. In: *Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico* (Ed. by F. L. DeBano, P. F. Ffolliott, A. Ortega–Rubio, G. J. Gottfried & R. H. Hamre), pp. 6–18. Fort Collins, Colorado: United States Department of Agriculture.

Williams, L. & MacRoberts, M. 1977. Individual variation in songs of dark-eyed juncos. *Condor*, **79**, 106–112.

APPENDIX

Table A1
The primary variables of white-bellied shortwing song used in the final analysis

No.	Variable	Description
1	Mean Low Frequency	Mean of low frequency measurements of all notes in a phrase
2	Mean High Frequency	Mean of high frequency measurements of all notes in a phrase
3	Mean Note Bandwidth	Mean of delta frequency (high frequency−low frequency) of all notes in a phrase
4	Mean Note Length	Mean of the lengths of all notes in a song
5	SD Low Frequency	Standard deviation from mean of low frequency measurements of all notes in a song
6	SD High Frequency	Standard deviation from mean of high frequency measurements of all notes in a song
7	SD Note Bandwidth	Standard deviation from mean of delta frequency (high frequency−low frequency) of all notes in a song
8	SD Note Length	Standard deviation from mean of the lengths of all notes in a song
9	Notes Per Song	Number of notes in a song
10	Song Length	The length of a song from the start of the first note to the end of the last note
11	Song Bandwidth	Calculated as the difference between the highest and lowest frequencies of all notes in a song
12	Minimum Song Low Frequency	The lowest frequency of all notes in a song
13	Maximum Song High Frequency	The highest frequency of all notes in a song

Table A2
Pooled within-population correlations between discriminating variables (PC1–PC5) and the standardized canonical discriminant functions

Variable	Discriminant function	
	1	2
PC5	−0.665*	0.403
PC4	0.255*	0.050
PC1	0.405	0.722*
PC2	0.216	−0.462*
PC3	−0.130	−0.312*

Variables are ordered by the absolute size of correlation within the respective functions.

* Largest absolute correlation between each variable and a discriminant function.