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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.

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.

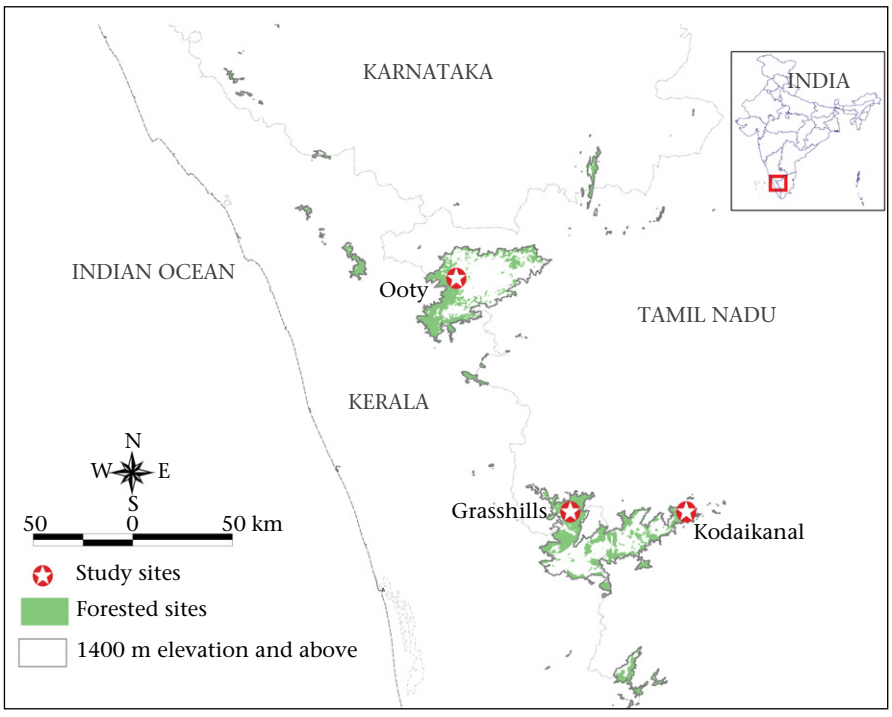

Figure 1. Map of the study locations on the sky islands of the Western Ghats mountains. The forested areas are indicative of present Shola-grassland habitat.