



Short Communication

Genome-wide data help identify an avian species-level lineage that is morphologically and vocally cryptic



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ABSTRACT

Species identification has traditionally relied on morphology. However, morphological conservatism can lead to a high incidence of cryptic species, as characters other than morphological ones can be biologically important. In birds, the combined application of bioacoustic and molecular criteria has led to an avalanche of cryptic species discoveries over the last two decades in which findings of deep vocal differentiation have usually been corroborated by molecular data or vice versa. In this study, we use genome-wide DNA data to uncover an unusual case of cryptic speciation in two species within the South-east Asian Streak-eared Bulbul *Pycnonotus blanfordi* complex, in which both morphology and vocalizations have remained extremely similar. Despite a considerable pre-Pleistocene divergence of these two bulbul species, bioacoustic analysis failed to uncover differences in their main vocalization, but examination of live birds revealed important differences in eye color that had been overlooked in museum material. Our study demonstrates that genome-wide DNA data can be helpful in the detection of cryptic speciation, especially in species that have evolved limited morphological and behavioral differences.

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1. Introduction

Cryptic species provide a challenge to taxonomists because they lack features differentiating them from other, better-known species, leading to serious underestimates of global animal diversity (Bickford et al., 2007). While knowledge about the planet's invertebrate fauna is relatively fragmentary, certain vertebrate groups such as birds were thought to be understood in great detail (Mayr, 1946) until the application of DNA barcoding techniques demonstrated an unexpected incidence of cryptic bird species diversity even in extremely well-explored regions such as North America and Europe (Hebert et al., 2004; Kerr et al., 2007). However, the barcoding approach has its own limitations, especially in cases where cryptic species are unusually young (Wagner et al., 2013), or where genetic introgression has resulted in a reduction of raw sequence divergence in the barcoding gene, COI (cytochrome oxidase I), leading species to be overlooked by barcoders

(Rheindt and Edwards, 2011). In these instances, the use of genome-wide markers is called for to disentangle patterns of potential gene flow (McCormack et al., 2013).

In birds, plumage coloration and external morphology have been the main taxonomic guiding lights for the last few centuries. However, many bird lineages use vocal cues as their main agents of mate selection, and bioacoustic characters have been shown to be of greater taxonomic importance than plumage characters in some lineages (e.g. Irwin et al., 2001; Isler et al., 1998; Rheindt et al., 2008). Bird vocalizations were only occasionally recruited for species diagnosis before the 1980s (Stein, 1963; Thielcke, 1970); their routine application for this purpose is a relatively new phenomenon (Alström and Ranft, 2003) that has led to the discovery of high levels of cryptic species especially across tropical bird genera from less well-explored regions.

Coincidentally, many of the cryptic species-level lineages first exposed by mtDNA sequencing have been quickly confirmed by field ornithologists familiar with their vocalizations. In some cases, mtDNA has alerted ornithologists to bird forms that are highly likely to exhibit distinct vocalizations (Rheindt et al., 2013). In

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other cases, vocal distinctions were pointed out first but then quickly corroborated by mtDNA studies (Isler et al., 2007; Tobias et al., 2008). It is extremely rare to find cases in which bird lineages deeply diverged in mtDNA fail to exhibit some sort of pronounced differentiation either in plumage or vocalizations upon closer inspection.

In this study, we used genome-wide DNA markers along with mtDNA, vocal and observational data to examine subspecific differentiation within the Streak-eared Bulbul *Pycnonotus blanfordi* from South-east Asia. The species is divided into two subspecies: nominate *blanfordi* (mostly confined to Myanmar) and *conradi* (from Thailand and Indochina) (Fig. 1A). The two taxa are reported to be poorly differentiated in coloration, with *conradi* having slightly yellower underparts than *blanfordi* (Fishpool and Tobias, 2005; Robson, 2008), and nothing is published about potential vocal differences. We present data showing *conradi* to be a rare example of a genetically deeply-diverged avian lineage with limited differentiation in plumage and vocalizations. However, we expose a diagnostic morphological trait (eye color) that has previously been overlooked by museum taxonomists (probably because eyes are not preserved in dry museum skins). Differences in eye color may serve as a reproductive barrier in this complex and may partly account for the deep genomic differentiation.

2. Methods

2.1. Field observations and morphological comparisons

We carried out detailed observations of the less well-known nominate taxon on the occasion of two field expeditions to Myanmar, one from 25–31 May 2014 around Bago (17.3333° N, 96.4833°

E) and the second from 21–28 February 2015 around Bagan (21.1667° N, 94.8667° E). We also examined online photo collections of Asian birds (e.g. www.orientalbirdimages.org) to compare images of live individuals with our own observational data from Myanmar. As detailed plumage comparisons have previously failed to reveal pronounced differentiation in coloration, we restricted ourselves to morphological comparisons of live birds (as opposed to museum specimens).

2.2. Bioacoustic sample collection and analysis

We collected seven recordings of the species' main vocalization from six individual streak-eared bulbuls from our own fieldwork as well as from other sound recordists (Table 1). Streak-eared bulbuls, like many other *Pycnonotus* bulbuls, have inconspicuous and non-stereotypical call notes (Fishpool and Tobias, 2005; Robson, 2008) that are challenging to use for field identification and taxonomic purposes. While the streak-eared bulbul's vocalizations have not been studied in great detail, the call type we are comparing is the main vocalization known in this species. It may serve as a general contact call, while additional vocalizations are rarely heard. We are confident that all recordings belong to the same homologous vocalization. Of the six individuals, three were from nominate *blanfordi* (Myanmar) and three were from *conradi* (Thailand: 1, Vietnam: 1, Cambodia: 1; Fig. 1, Table 1).

We used the program RavenPro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA) under default settings to measure vocal parameters in these recordings. Each streak-eared bulbul call bout comprises of a series of short, serially repeated vocal elements (Fig. 1D). We measured four vocal characters: (1) element duration, (2) inter-element duration, (3) pace, and (4) dominant frequency (Table 1). For all recordings containing multiple call

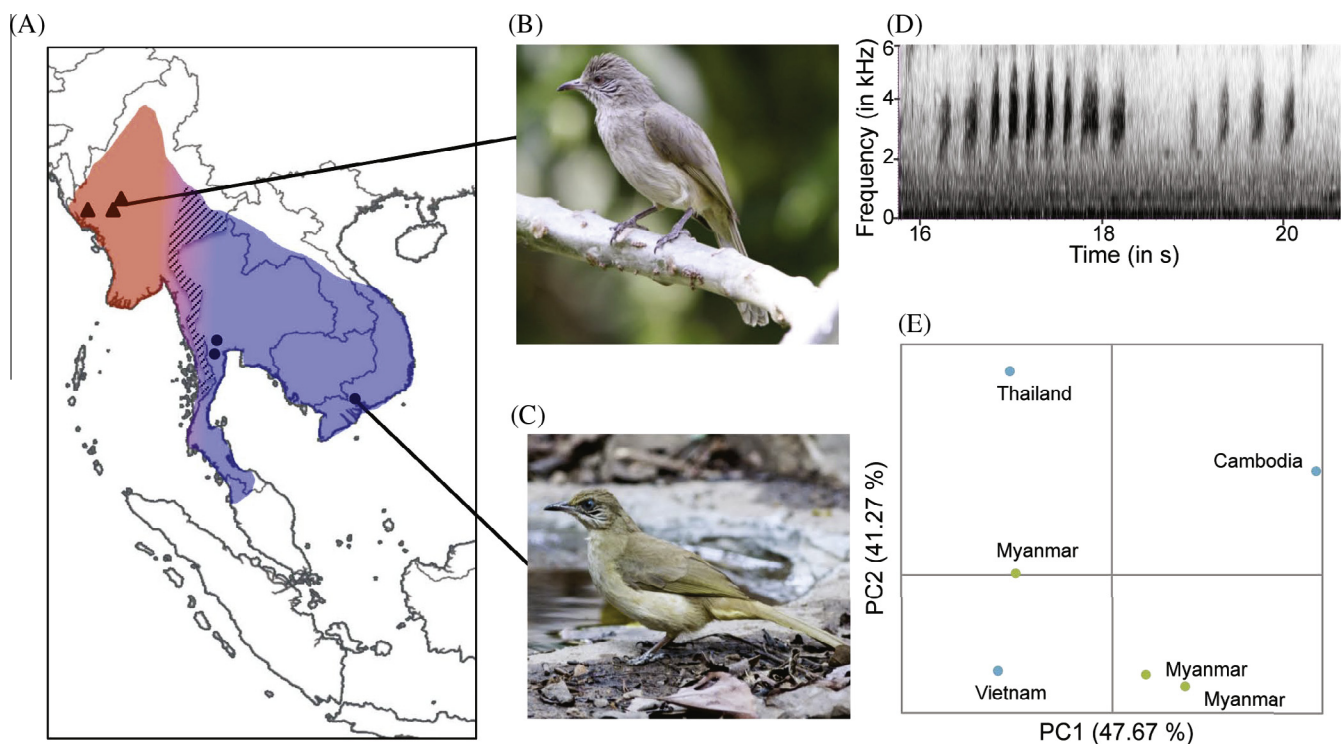


Fig. 1. (A) Streak-eared bulbul distribution and vocal collection localities. Distribution of the nominate *blanfordi* from Myanmar is denoted in red and *conradi* in blue. Diagonal lines denote montane areas largely uninhabited by either form, but may encompass possible areas of overlap; (B and C) streak-eared bulbul *blanfordi* from Myanmar (© James Eaton) and *conradi* from Thailand (© Simon van der Meulen), respectively, with lines pointing to the approximate locality where photos were taken; (D) example sonogram of a main vocalization given by nominate *blanfordi* showing the succession of nine and four song elements, respectively, making up two successive song bouts; (E) principal component analysis of four bioacoustic parameters on six individuals (*conradi* blue, *blanfordi* green), also showing the amount of variation explained by each principal component (PC). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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