Morphological, vocal and genetic divergence in the *Cettia acanthizoides* complex (Aves: Cettiidae)

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We used morphological, vocal and molecular (one mitochondrial and two nuclear loci) data to re-evaluate the taxonomic status of the taxa *acanthizoides*, *concolor*, and *brunnescens* in the *Cettia acanthizoides* (J. Verreaux, 1871) complex. We conclude that all three are valid taxa, and that *acanthizoides* of China and *concolor* of Taiwan are best treated as conspecific, whereas *brunnescens* of the Himalayas is better considered as a separate species. The degree of morphological, vocal, and genetic differentiation is variably congruent among all taxa; the recently separated *acanthizoides* and *concolor* differ slightly in plumage and structure but are indistinguishable in vocalizations, whereas the earlier diverged *brunnescens* and *acanthizoides/concolor* differ only slightly more in morphology but to a much greater degree in vocalizations. We stress the essential nature of taxonomic revisions as a prerequisite for the biodiversity estimates required for conservation planning. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **149**, 437–452.

ADDITIONAL KEYWORDS: cytochrome *b* – evolution – glyceraldehyde-3-phosphodehydrogenase (G3PDH) intron 11 – myoglobin intron 2 – phylogeny – taxonomy.

The Yellowish-bellied Bush Warbler *Cettia acanthizoides* (J. Verreaux, 1871) in the avian family Cettiidae (Alström *et al*., 2006) is a small (~10–11 cm), mostly brownish, and rather 'featureless' skulking warbler occurring in the Himalayas, central and south-east China, and Taiwan (Watson, Traylor & Mayr, 1986; Dickinson, 2003; Fig. 1). Despite its drab appearance, the songs of *C. acanthizoides* are among the most remarkable and arresting of all Asian birds. Probably partly as a result of its phenotypic similarity to two more widely distributed and common polytypic congeners, Strong-footed Bush Warbler *Cettia fortipes* (Hodgson, 1845) and Aberrant Bush Warbler *Cettia flavolivacea* (Blyth, 1845), *C. acanthizoides* has remained relatively poorly known, and records may be unreliable if unaccompanied by either voucher specimens or tape recordings. *C. acanthizoides* breeds in broad-leaf scrub and, especially, in bamboo thickets in forest at 2000–3660 m in the Himalayas (Ali & Ripley, 1997; Grimmett, Inskipp & Inskipp, 1998; Rasmussen & Anderton, 2005), 2600–3965 m in central China (Meyer de Schauensee, 1984; Cheng, 1987; P. Alström & U. Olsson, pers. observ.), 1500–1830 m in south-east China (Meyer de Schauensee, 1984), and *c*. 1950–3500 m in Taiwan (Chang, 1980; Koh & Lee, 2003). All populations probably move altitudinally, at least slightly, and the species has been recorded down to 1350 m in the Himalayas (Ali & Ripley, 1997), although this altitudinal record requires confirmation. Earlier sources list and map *C. acanthizoides* for parts of the hills south of the Brahmaputra, but this has been found to be without basis (Rasmussen & Anderton, 2005), and records from Hong Kong (Carey *et al*., 2001) are no longer considered reliable (G. J. Carey,

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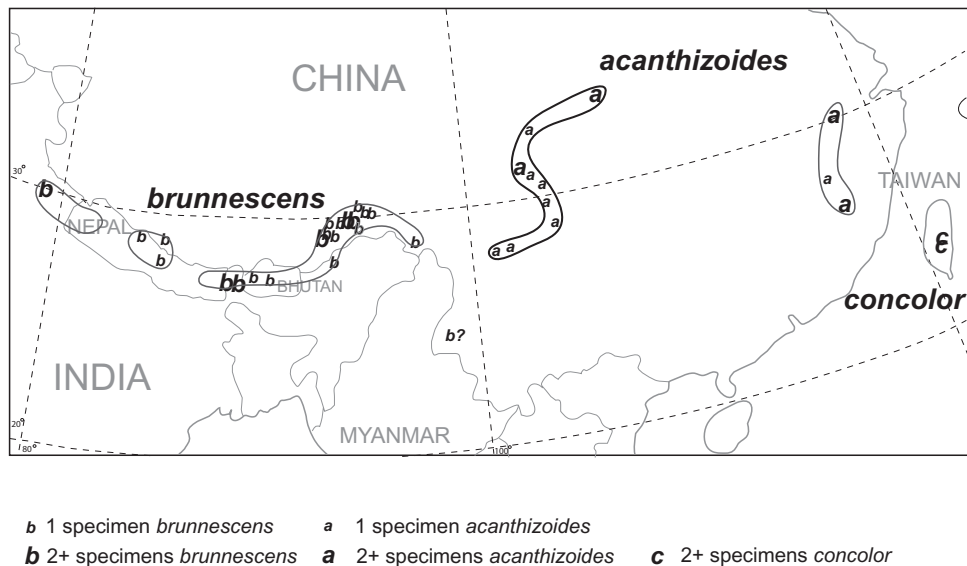
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Figure 1. Point map and extrapolated distributional ranges of the taxa in the *Cettia acanthizoides* complex. One-letter abbreviations indicate specimen localities, either studied by us or reported by museums and/or in the literature (Ludlow & Kinnear, 1944; Vaurie, 1972; Cheng, 1987; Inskipp & Inskipp, 1991; Wang *et al*., 1991; Rasmussen & Anderton, 2005; Spierenburg, 2005). See text for specimen locality marked 'b?'.

pers. comm.). Watson *et al*. (1986) and Sibley & Monroe (1990) erroneously called the species *Cettia robustipes* (Swinhoe, 1866), a mistake rectified in Sibley & Monroe (1993). Three subspecies are usually recognized: *acanthizoides* (J. Verreaux, 1871) in China except the south and south-east Xizang province; *concolor* Ogilvie-Grant, 1912 in Taiwan; and *brunnescens* (Hume, 1872) in the Himalayas, south-east Xizang province, China, and possibly northern Myanmar (where the species 'should' occur according to Robson, 2000) (Dickinson, 2003; Fig. 1).

In this paper we analyse geographical variation in morphology, vocalizations, and three molecular markers [mitochondrial cytochrome *b* gene, nuclear myoglobin intron 2, and glyceraldehyde-3-phosphodehydrogenase (G3PDH) intron 11] in the *C. acanthizoides* complex and discuss the taxonomic implications of our findings. We also discuss the evolution of morphological and vocal traits, and stress the importance of taxonomic studies in the context of biodiversity estimates and conservation.

MATERIAL AND METHODS

MORPHOLOGY AND VOCALIZATIONS

Morphological data were taken from specimens in the collections of the American Museum of Natural History, New York, USA (AMNH: two *brunnescens*, five *acanthizoides*, and nine *concolor*), The Natural History Museum, Tring, UK (BMNH: 18, 10, and 3), and the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM: 2, 9, and

11). Plumage colour comparisons were made in all collections. Measurements were taken at the AMNH and BMNH with digital calipers as follows (to the nearest mm): culmen from skull base, bill height and width at distal edge of nares, maximum skull width (where the skull was unpadded and intact), length of flattened and stretched wing, length of primary 1 (primaries numbered from outermost inwards), maximum width of primary 1, shortfalls from folded wing tip of each primary, tarsus length, distal width of tarsus, tail length, tail graduation (distance between shortest and longest rectrices), and width of central rectrix (where relatively fresh). Statistics were performed using SYSTAT 8.0. Means of untransformed measurements were compared between taxa using two-way ANOVA, with sex as the covariate. A discriminant function analysis was performed to determine which variables best distinguish between the taxa.

We have field experience with the song of *acanthizoides* from Sichuan (May/June 1986, 1987, 1989, 1990, and 1994), Shaanxi (June 1995), and Fujian (May 1993) provinces, China; *concolor* from Taiwan (May 1999); and *brunnescens* from West Bengal (May 1997) and Uttaranchal (May 1998) provinces, India. We have tape recorded the song of *acanthizoides* in Sichuan (three individuals), Shaanxi (one) and Fujian (one), *brunnescens* in West Bengal (four), and *concolor* (one), and calls of *acanthizoides* in Sichuan (three), Shaanxi (one) and Fujian (two), *brunnescens* in West Bengal (3), and *concolor* (two). All tape recordings were made using a Sony WM-D6 cassette or DAT TCD-D3 recorder and a Telinga Pro parabolic reflector/

microphone. In addition, we obtained published recordings of song of *brunnescens* from Bhutan (one; Connop, 1995) and *concolor* (two; Liu, 1994, 1995), and unpublished recordings by Pratap Singh of *brunnescens* from Uttaranchal (four) and Arunachal Pradesh (one) provinces, India. The sonograms were made using RAVEN 1.1 (Charif, Clark & Fristrup, 2003).

We use the following voice terminology: song strophe – a continuous flow of notes, separated from other strophes by pauses (either silent or filled with calls); element – a discrete, unbroken unit in a sonogram; note – a sound that may or may not consist of more than one element; phrase – two or more different notes forming a unit that is given at least twice in succession; trill – a fast multiple repetition of a phrase; tremolo – a fast multiple repetition of identical elements.

DNA COLLECTION, EXTRACTION, SEQUENCING, AND PHYLOGENETIC ANALYSES

We obtained blood samples from four *acanthizoides*, one *concolor* and one *brunnescens* (Table 1). DNA extraction and sequencing was performed as described in Olsson *et al.* (2005). The G3PDH intron 11 (along with 36 and 18 bp of exons 11 and 12, respectively),

which was not used in Olsson *et al.*, was amplified using primers G3P13b and G3P14b, and the following PCR cycling parameters: 5 min at 95 °C; followed by 40 cycles of 40 s at 95 °C, 40 s at 57 °C, and 1 min at 72 °C; terminated by 8 min at 72 °C. It was sequenced using the primers G3P14b and G3PintL1.

The phylogenetic analyses were performed as described in Olsson *et al.* (2005), with the following exceptions. The models selected for the Bayesian analyses were the general time-reversible model (Lanave *et al.*, 1984; Tavaré, 1986; Rodríguez *et al.*, 1990), with an estimated proportion of invariant sites (Gu, Fu & Li, 1995) (GTR + I) for cytochrome *b*; the Hasegawa, Kishino & Yano (1985) model (HKY) for the myoglobin intron 2; and the latter model with an estimated proportion of invariant sites (HKY + I) for the G3PDH intron 11. Parsimony bootstrapping was performed with the branch and bound method and the 'MulTrees' option in effect; no indels were coded as characters.

RESULTS

MORPHOLOGY

All three taxa are similar in plumage, differing only in minor but consistent ways; *brunnescens* is the most

Table 1. DNA samples used

Taxon	Locality	Sample id. number	GenBank number
Phylloscopus chloronotus simlaensis	NW Frontier Prov., Pakistan	NRM 20046808	Myo: DQ008556 G3P: DQ364120 Cytb: DQ008504
Cettia cetti albiventris	Punjab, India	NRM 20046810	Myo: DQ008561 G3P: DQ364121 Cytb: DQ008509
Cettia acanthizoides acanthizoides 1	Sichuan, China (*c.* 29.5°N, 103°E)	NRM 20056598	Cytb: DQ364116
Cettia acanthizoides acanthizoides 2	Sichuan, China (*c.* 29.5°N, 103°E)	NRM 20056599	Myo: DQ364129 G3P: DQ364124 Cytb: DQ364117
Cettia acanthizoides acanthizoides 1	Fujian, China (*c.* 27.5°N, 117.5°E)	NRM 20056600	Myo: DQ364127 G3P: DQ364122 Cytb: DQ364114
Cettia acanthizoides acanthizoides 2	Fujian, China (*c.* 27.5°N, 117.5°E)	NRM 20056601	Myo: DQ364128 G3P: DQ364123 Cytb: DQ364115
Cettia acanthizoides concolor	Taiwan (*c.* 24°N, 121°E)	TESRI 344	Myo: DQ364130 G3P: DQ364125 Cytb: DQ364118
Cettia brunnescens	West Bengal, India (*c.* 27°N, 89°E)	NRM 20056602	Myo: DQ364131 G3P: DQ364126 Cytb: DQ364119

Cytb, cytochrome *b*; G3P, G3PDH intron 11; Myo, myoglobin intron 2; NRM, Swedish Museum of Natural History; TESRI, Taiwan Endemic Species Research Institute.

divergent taxon. Compared with the other taxa, the upperparts of *brunnescens* are brighter, ruddier brown; the upperparts of *concolor* are darker and richer than in *brunnescens*; whereas those of *acanthizoides* have a noticeably more olive cast than the previous two. These differences have been apparent in all specimens examined. Specimens from the Fujian province that are considered to be *acanthizoides* (in the BMNH) are a brighter rufous colour above compared with those from Sichuan province. The wing and tail edgings of *brunnescens* and *concolor* are a distinctly brighter rufous than in the nominate subspecies. Below, *brunnescens* is paler, duller, and more washed out in colour than either of the other taxa, and in worn plumage the yellowish tinge of the belly can be virtually lacking; even in fresh plumage, *brunnescens* typically has a relatively weakly yellow-tinged belly (just one specimen, USNM 519886, shows a relatively strong yellow tint on the belly). The nominate subspecies and *concolor* are both fairly richly coloured below, although *concolor* has bright fulvous-buff flanks and undertail-coverts, and a browner centre of breast, whereas the nominate subspecies is more uniformly yellowish on the belly, and dingier and greyer on the throat and breast; these distinctions hold for all specimens examined. Specimens of *acanthizoides* from the Fujian province are brighter yellow below than birds from Sichuan; effects of wear have not been eliminated as the cause of this difference.

Mensurally the taxa are also very similar (Table 2), with the most distinct difference being in bill length. The shorter bill of *acanthizoides* is noticeable in direct comparison with the other taxa, although there is overlap in bill length among all taxa [*brunnescens* range, 12.8–14.4 mm; *acanthizoides* range, 12.1–13.1 mm (13.6 mm in one individual); *concolor* range, 12.8–13.7 mm) (Table 2)]. The bill of *brunnescens* is also slightly narrower and shallower at the base than in *acanthizoides* and *concolor*, giving it a relatively spike-like appearance. Otherwise, the taxa are remarkably similar in structure. Although samples of females are small, all three taxa show marked sexual size dimorphism, particularly in wing and tail length (Table 2).

Stepwise discriminant function analysis (Wilks' $\lambda = 0.15$, approximate $F = 2.57$, d.f. = 16, 26, $P = 0.016$) confirmed the importance of bill length in distinguishing the taxa, but bill width, height, and length of the outer primary were also important (Table 3). Most individuals of both sexes were correctly identified to group membership using these measurements (Fig. 2).

A specimen from north-west Yunnan (Yongping; USNM 312581; Fig. 1, marked b?) that has heretofore been considered to be *acanthizoides* matches *brunnescens* better in bill length, and in having paler, brighter rufous upperparts, and a whiter (vs. dingy grey) breast. We tentatively consider it to be *brunnescens*.
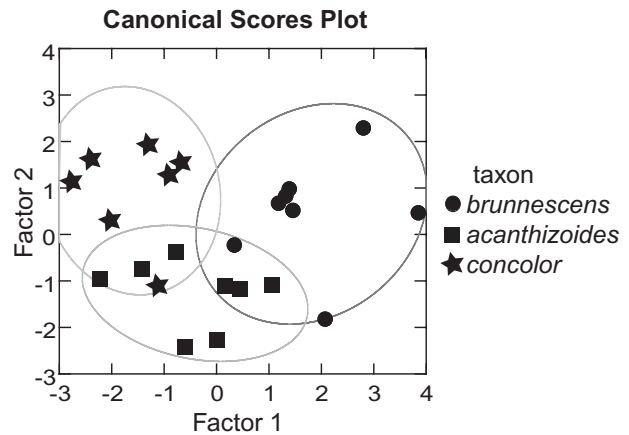

Figure 2. Plot of canonical scores from discriminant functions analysis between members of the *Cettia acanthizoides* group.

VOICE

The song of *acanthizoides* consists of a long series of drawn-out 'straight' high-pitched whistles on a slightly ascending scale (part I), followed by a prolonged either descending or, uncommonly, rather 'straight', fast hammering tremolo (part II) (Figs 3–6). The strophes are usually separated by long pauses, but when the bird is excited several strophes can follow immediately after one another, or they may be separated by a series of rapidly repeated call notes. There is variation in the number and appearance of the individual song elements, both within and between strophes sung by the same male. In our sample there is also individual variation in these variables, but larger samples are needed to determine whether there are consistent differences between individual males. We have not detected any consistent geographical variation. The song of *concolor* is indistinguishable from that of *acanthizoides*.

The most common song type of *brunnescens* (Figs 7–11) also begins with a series of drawn-out whistles on an ascending scale (part I), but compared with *acanthizoides/concolor* the number of whistles is much smaller and less variable (usually between three and five), and the individual whistles are on average nearly twice as long, and usually differ more in frequency from each other (they are more 'stepped', although less commonly the final two, three, or four whistles can be similar in pitch). The second part (part II) of the song of *brunnescens* is a rather slow melodious 'wobbling' trill, which is generally distinctly shorter than the tremolo noted in *acanthizoides/concolor*. Unlike the tremolo in *acanthizoides/concolor*, which consists of a single, very short, and rapidly repeated element, the trill of *brunnescens* is made up of a repeated phrase of two, three, or four whistled

Table 2. Untransformed measurements (mean ± standard deviation, *N* in parentheses) for taxa in the *Cettia acanthizoides* complex

Variable	*brunnescens*		*acanthizoides*		*concolor*	
	Male	Female	Male	Female	Male	Female
Culmen l from skull	13.40 ± 0.67 (16)	13.35 ± 0.48 (4)	12.95 ± 0.41 (10)***	12.35 ± 0.17 (4)***	13.39 ± 0.35 (9)	13.13 ± 0.31 (3)
Bill h	2.22 ± 0.11 (13)*	2.27 ± 0.06 (3)*	2.32 ± 0.14 (9)	2.22 ± 0.10 (4)	2.33 ± 0.09 (8)	2.37 ± 0.21 (3)
Bill w	2.24 ± 0.10 (13)*	2.10 ± 0.10 (3)*	2.23 ± 0.18 (11)	2.40 ± 0.26 (4)	2.34 ± 0.17 (9)	2.47 ± 0.15 (3)
Skull w	12.19 ± 0.38 (11)	11.95 ± 0.21 (4)	12.34 ± 0.46 (8)	12.08 ± 0.35 (3)	12.35 ± 0.42 (8)	12.3 ± 0.10 (3)
Wing l (flattened)	53.25 ± 0.91 (16)	49.5 ± 1.00 (4)	52.82 ± 1.33 (11)	48.50 ± 1.00 (4)	51.56 ± 1.68 (9)	48.67 ± 3.05 (3)
P1 L	17.13 ± 0.88 (12)	15.55 ± 1.20 (4)	16.83 ± 0.62 (11)	14.25 ± 1.42 (4)	15.90 ± 0.61 (8)*	14.60 ± 1.51 (3)*
P1 w	3.90 ± 0.43 (10)*	3.95 ± 0.37 (4)*	3.66 ± 0.43 (11)	3.33 ± 0.35 (3)	3.59 ± 0.26 (8)	3.67 ± 0.11 (3)
P1 s	24.73 ± 1.49 (11)	22.75 ± 0.96 (4)	24.83 ± 0.69 (9)	23.00 ± 1.63 (4)	24.62 ± 1.06 (8)	23.00 ± 0 (3)
P2 s	13.09 ± 1.22 (11)	11.50 ± 0.58 (4)	12.81 ± 0.64 (9)	11.25 ± 0.50 (4)	12.62 ± 0.52 (8)	12.00 ± 1.00 (3)
P3 s	4.88 ± 0.64 (8)	4.75 ± 0.96 (4)	5.49 ± 1.58 (9)	4.25 ± 0.50 (4)	4.94 ± 0.56 (8)	5.00 ± 0 (2)
P4 s	1.36 ± 0.38 (7)	1.25 ± 0.29 (4)	1.60 ± 0.54 (9)*	1.12 ± 0.25 (4)*	1.07 ± 0.61 (7)	1.17 ± 0.29 (3)
P5 s	0 ± 0 (8)	0 ± 0 (4)	0 ± 0 (9)	0 ± 0 (4)	0 ± 0 (7)	0 ± 0 (2)
P6 s	0 ± 0(8)	0 ± 0 (3)	0 ± 0 (9)	0 ± 0 (4)	0 ± 0 (7)	0 ± 0 (2)
P7 s	1.43 ± 0.45 (7)	2.00 ± 0 (2)	1.39 ± 0.43 (9)	1.00 ± 0 (4)	1.43 ± 1.13 (7)	0.75 ± 0.35(2)
P8 s	3.35 ± 0.54 (8)	3.50 ± 0.71 (2)	3.87 ± 0.54 (9)	3.00 ± 0 (4)	3.57 ± 0.73 (7)	3.00 ± 0 (2)
P9 s	4.87 ± 0.79 (8)	5.00 ± 0 (2)	5.14 ± 0.44 (9)	4.25 ± 0.50 (4)	4.86 ± 0.69 (7)	4.00 ± 0 (2)
P10 s	6.97 ± 0.73 (8)	6.75 ± 0.35 (2)	6.97 ± 0.86 (9)	5.75 ± 0.96 (4)	6.57 ± 0.61 (7)	6.00 ± 1.41 (2)
Tarsus l	21.67 ± 0.78 (15)	20.70 ± 1.04 (4)	21.11 ± 0.87 (11)	20.10 ± 0.50 (4)	21.12 ± 0.98 (8)	20.67 ± 0.67 (3)
Tarsus distal w	2.30 ± 0.12 (12)	2.15 ± 0.13 (4)	2.11 ± 0.22 (11)	2.20 ± 0.08 (4)	2.28 ± 0.12 (9)	2.07 ± 0.06 (3)
Tail l	46.91 ± 1.96 (15)	41.95 ± 2.27 (4)	47.27 ± 2.45 (11)	43.15 ± 2.59 (4)	47.17 ± 2.05 (9)	43.1 ± 2.09 (3)
Tail graduation	9.39 ± 0.85 (10)	8.07 ± 0.83 (3)	8.38 ± 1.17 (9)	8.67 ± 1.15 (3)	9.16 ± 1.90 (8)	9.63 ± 1.18 (3)
Central rectrix w	6.00 ± 0.60 (7)	4.98 ± 0.31 (3)	6.36 ± 0.88 (5)	5.77 ± 0.45 (4)	6.56 ± 0.72 (5)	6.00 ± 0 (2)

Two-way ANOVAs between taxa with sex as covariate: *$P < 0.05$; **$P < 0.01$; ***$P < 0.05$. h, height; l, length; s, shortfall; w, width (see text for measurement methods).

Table 3. Summary statistics of discriminant function analysis between members of the *Cettia acanthizoides* group

Variable	F-to-remove	Tolerance
Culmen from skull	1.23	0.52
Wing l	0.71	0.40
Tarsus l	0.38	0.67
Tail l	0.94	0.41
Bill h at nares	3.37	0.32
Bill w at nares	1.09	0.88
Primary 1 l	6.56	0.62
Primary 1 w	0.67	0.51

Jackknifed classification matrix

Taxon	% correctly classified
brunnescens	63
acanthizoides	38
concolor	57
total	52

Eigenvalues

Factor 1	Factor 2
2.28	1.03

h, height; l, length; w, width (see text for measurement methods).

elements of alternating pitch. The trill is often immediately succeeded by a different, very thin high-pitched slow trill of either two or three elements of alternating pitch (part III) (Figs 7, 8); occasionally, the higher-pitched trill replaces the usual one. A second song type, which is sometimes heard interspersed between strophes of the first type, consists of one drawn-out high-pitched note followed by a trembling trill (Fig. 12). There is variation in the number and appearance of the individual song elements, both within and between strophes sung by the same male, as well as between individuals, but larger sample sizes are needed to determine whether the individual differences are consistent. With respect to the appearance of the individual elements, parts II and III are more variable than part I, and therefore probably are more important for individual recognition (cf. two species of pipits *Anthus* studied by Elfström, 1990). There is also variation between eastern and western populations (Table 4), but a larger sample size is required to confirm the differences. See Table 5 for a detailed comparison of the vocalizations of *acanthizoides/concolor* vs. *brunnescens*, and Martens (1975) for detailed descriptions and sonograms of the songs of two males from Nepal, which agree well with our data.
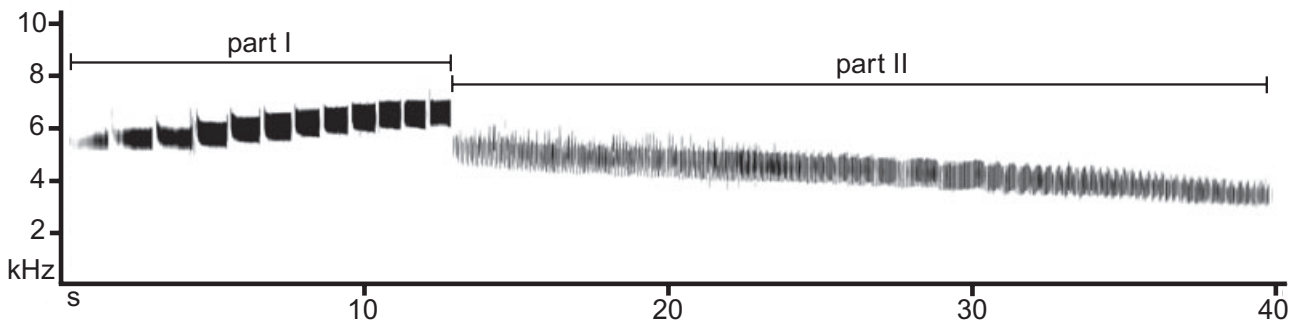
Figure 3. One song strophe of *Cettia a. acanthizoides*, Shaanxi, China, June; tape recording by Per Alström.
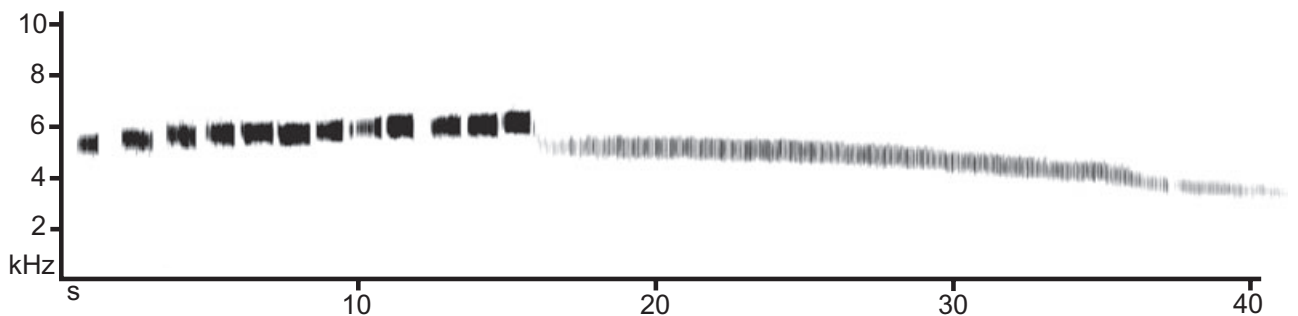
Figure 4. One song strophe of *Cettia a. acanthizoides*, Sichuan, China, May; tape recording by Per Alström.
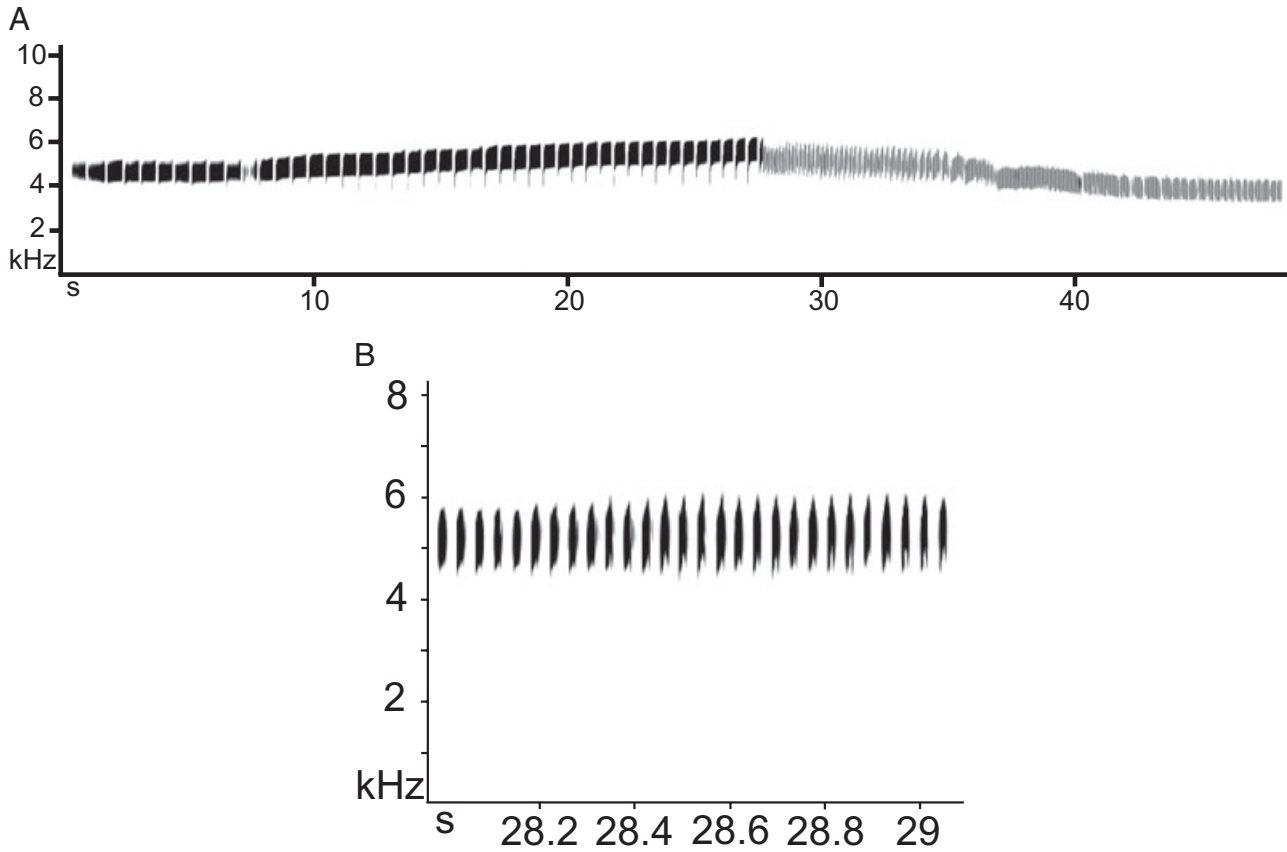
A

B

Figure 5. A, one song strophe of *Cettia a. acanthizoides*, Fujian, China, May; tape recording by Per Alström. B, the same recording as that shown in (A) but with the detail from part II at a higher time resolution.
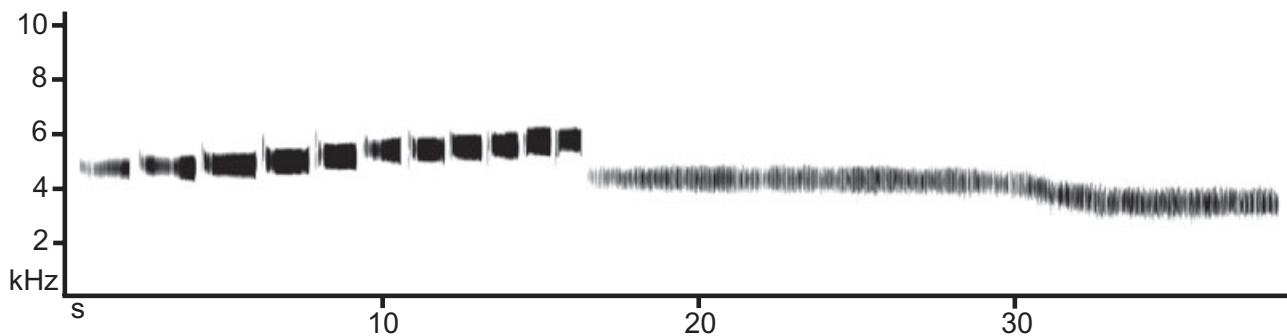

Figure 6. One song strophe of *Cettia a. concolor*, Taiwan, May; tape recording by Per Alström.

The call of all three taxa (Fig. 13) is a short note that consists of two, uncommonly one, elements that can be transcribed as either *tret* or *trit*. When the bird is alarmed or excited, it is often repeated at very short intervals for long periods, and then sometimes consists of multiple elements, sounding more like *trrrt*. The call of *acanthizoides* and *concolor* are indistinguishable, whereas the call of *brunnescens* is lower-pitched.

DNA

The cytochrome *b* gene tree (Fig. 14) shows a sister relationship between *acanthizoides* and *concolor*, with *brunnescens* as a sister to both of these. The myoglobin and G3PDH introns are unable to resolve the relationships among our six samples (not shown).

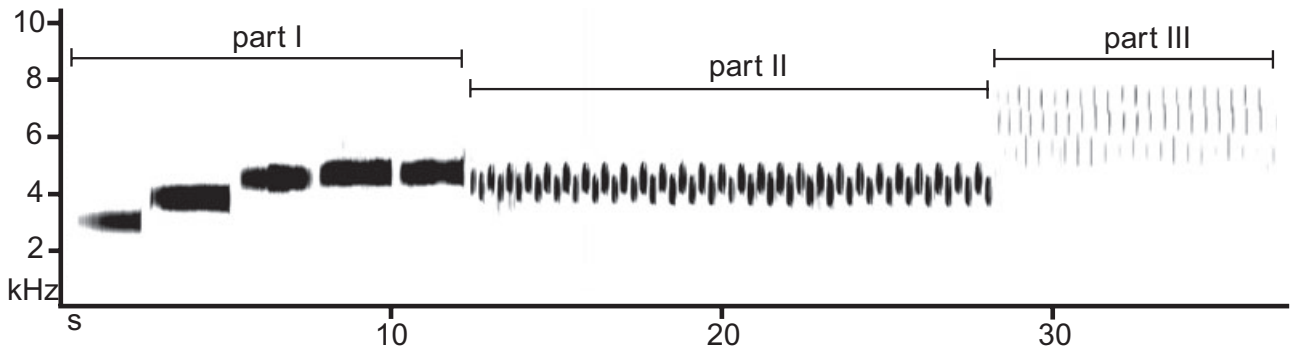The genetic divergences are shown in Table 6. The differences between *acanthizoides* and *concolor* are

Figure 7. One song strophe of *Cettia brunnescens*, Arunachal Pradesh, India, June; tape recording by Pratap Singh.
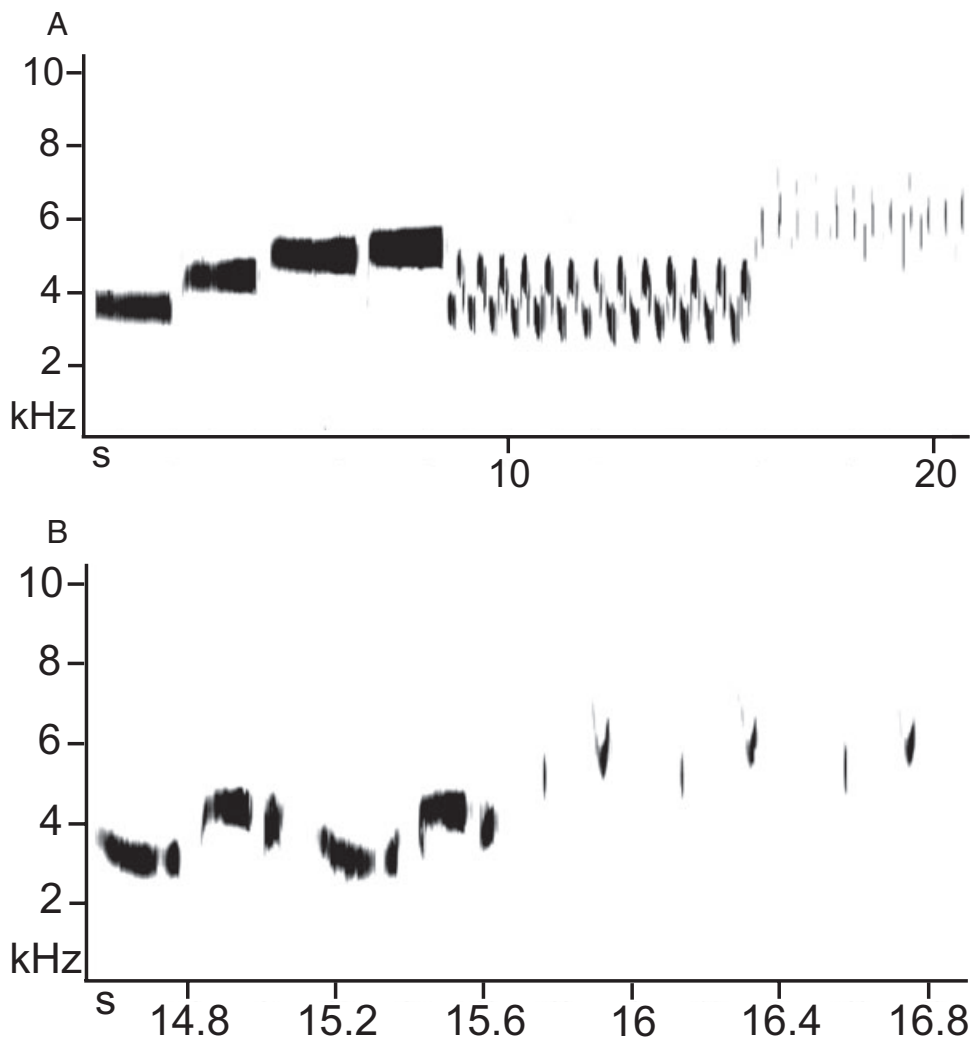

Figure 8. A, one song strophe of *Cettia brunnescens*, West Bengal, India, May; tape recording by Per Alström. This is from a different individual than the song strophe shown in Figure 9. B, the same recording as that shown in (A) but with the detail from part II and the beginning of part III at a higher time resolution.
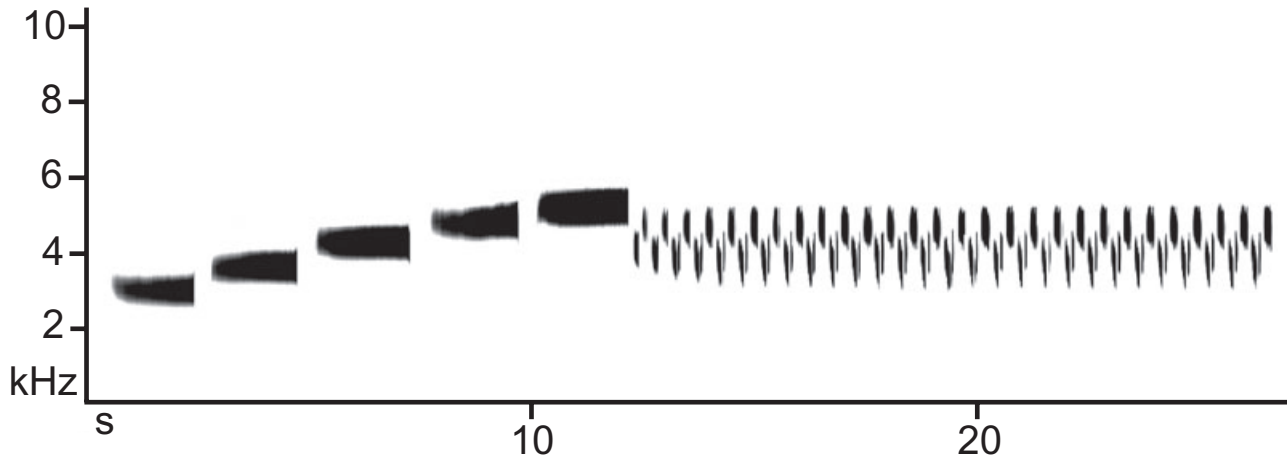
Figure 9. One song strophe of *Cettia brunnescens*, West Bengal, India, May; tape recording by Per Alström.
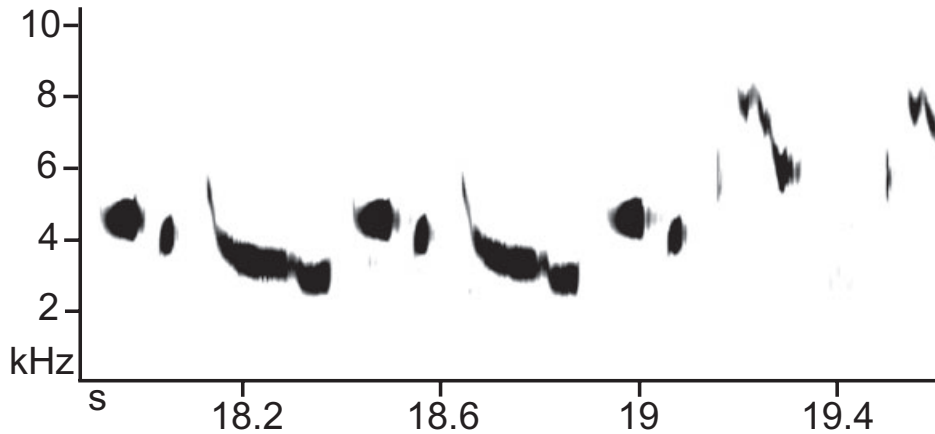

Figure 10. A cut from part II and the beginning of part III of the song of *Cettia brunnescens*, West Bengal, India, May, different individual compared with Figures 8 and 9. Tape recording by Per Alström.

Table 4. Main differences in song of *brunnescens* between Uttaranchal in the western part of the range ($N = 4$ males) and West Bengal, Arunachal Pradesh and Bhutan ($N = 6$) in the eastern part of the range. See Figure 3 for a definition of parts I and II, respectively. The third part of the song, which is not always sung, has not been included in the comparison

	Uttaranchal				West Bengal/Arunachal Pradesh (India)/ Bhutan			
	Mean	SD	Range	*N*	Mean	SD	Range	*N*
Length of strophe	10.7	1.7	7.7–14.1	13	20.3	5.5	12.8–29.6	25
Length of part I	5.5	0.5	4.9–6.8	13	9.7	2.2	4.3–14	25
No. of whistles in part I	2.9	0.3	2–3	14	4.4	0.9	2–6	25
Lengths of whistles in part I	1.5	0.2	1.3–2	39	1.9	0.3	1.1–2.8	109
Length of part II	5.1	1.8	2.6–8.7	13	10.3	4.3	4–19.7	25
No. of el. in part II	23.9	8.1	12–38	13	50.7	21.5	18–96	25
No. of different el. in part II	2.1	0.3	2–3	13	2.8	0.8	2–4	25

el., elements; *N* refers to the number of either strophes or whistles; all lengths are given in seconds.
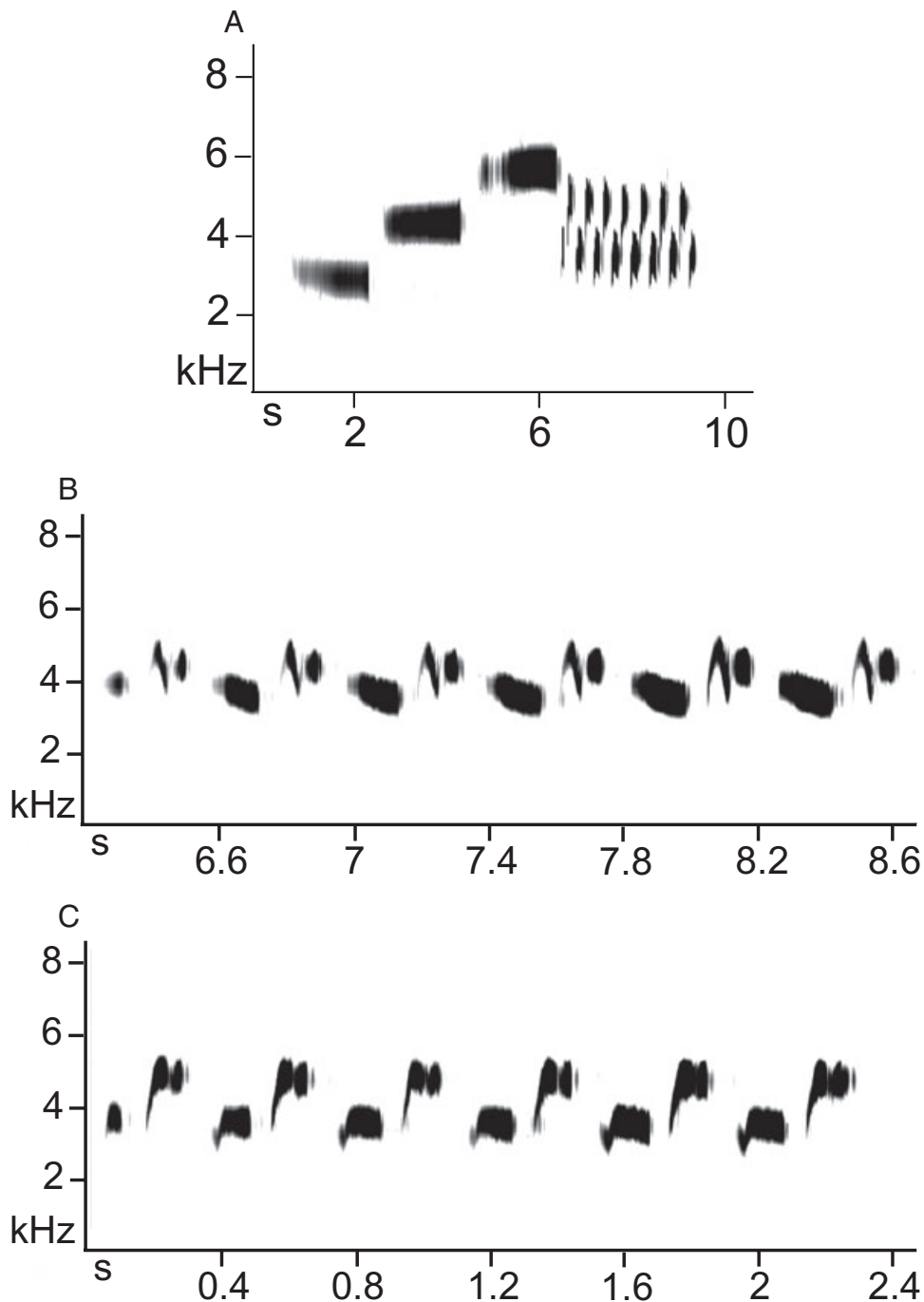
Figure 11. A, one song strophe of *Cettia brunnescens*, Uttaranchal, India, June; tape recording by Pratap Singh. B, the same recording as that shown in (A) but with the detail from part II at a higher time resolution. C, a different song strophe from the same individual. Detail from part II at a higher time resolution.

either zero or slight (0.5%), and are no greater than the variation within *acanthizoides* (0.6%); in fact, one of the cytochrome *b* haplotypes of *acanthizoides* from Sichuan is more similar to the *concolor* haplotype (0.1%) than to the other *acanthizoides* from Sichuan (0.2%). On the contrary, *brunnescens* differs consider-

ably more from *acanthizoides* and *concolor* in all three regions. The differences between *acanthizoides*/ *concolor* and *brunnescens* in the myoglobin and G3PDH introns are slight, although greater than between *acanthizoides* and *concolor* and intrataxon comparisons.

Table 5. Detailed comparison of the songs of the three taxa in the *Cettia acanthizoides* complex. The third part of the song of *brunnescens*, which is not always sung, has not been included in the comparison. See Figs 3 and 7 for a definition of parts I and II, respectively

	acanthizoides/concolor				*brunnescens*			
	Mean	SD	Range	*N*	Mean	SD	Range	*N*
Length of strophe	43.1	8.9	32.3–66.5	13	16.9	6.5	7.5–29.6	38
Freq. span of strophe	3842	496.5	3037–4944	13	3109	414.1	2520–4056	38
Top freq. of strophe	6805	429	6243–7529	13	5605	243.6	5103–6172	38
Bottom frequency of strophe	2963	236.9	2583–3529	13	2504	360.6	1843–3165	38
Length of part I	19.1	10.7	6–43.9	12	8.3	2.7	4.3–14	38
Frequency span of part I	2214	854.1	1357–3786	12	3047	434.2	2415–4056	38
Top frequency of part I	6812	476.5	6243–7795	13	5606	245.1	5103–6172	38
Bottom freq. of part I	4573	604	3483–5586	13	2537	399.8	1843–3165	38
No. of whistles in part I	17.2	10.3	7–45	13	3.9	1.0	2–6	38
Lengths of whistles in part I	1	0.3	0.3–1.8	149	1.8	0.3	1.1–2.8	148
Freq. span of whistles in part I	977	152	525–1379	150	989	113.9	633–1274	148
Length of part II	24.1	12.3	7.2–53.3	13	8.5	4.4	2.6–19.7	38
Freq. span of part II	2378	571	1219–2966	13	2183	396.8	1402–3106	38
Top freq. of part II	5339	464	4446–6044	13	5175	182.1	4738–5459	38
Bottom freq. of part II	2969	237.4	2583–3529	13	2982	354.5	2261–3605	38
No. of el. in part II	427	146.4	221–745	13	41.5	22.1	12–96	38
No. of different el. in part II	1	0	1–1	13	2.5	0.8	2–4	38

el., elements; freq., frequency (kHz); *N* refers to number of either strophes or whistles; all lengths are given in seconds. Number of individuals: *acanthizoides*, Sichuan, three; Shaanxi, one; Fujian, one; *concolor*, three; *brunnescens*, Uttaranchal, four; West Bengal, four; Arunachal Pradesh, one; Bhutan, one.
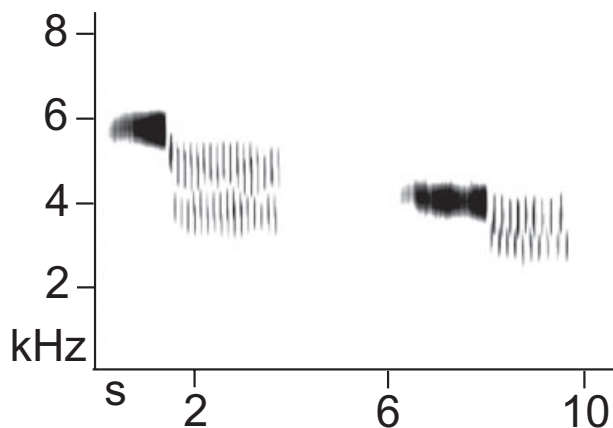

Figure 12. Two strophes of a less common type of song of *Cettia brunnescens*, West Bengal, India, May; same individual as in Figure 8; tape recording by Per Alström.

Table 6. Pairwise percentage sequence divergences among our samples in the *Cettia acanthizoides* complex. The uncorrected *P* and corrected (GTR + I for cytochrome *b*, HKY for the myoglobin intron 2, and HKY + I for the G3PDH intron 11) values are the same in all cases except one, where the corrected value is shown to the right of the slash

Cytochrome *b* (1038 bp)	**Divergence**
acanthizoides Sichuan–Sichuan	0.2
acanthizoides Fujian–Fujian	0.2
acanthizoides Sichuan–Fujian	0.2–0.6
acanthizoides–concolor	0.1–0.5
acanthizoides / concolor–brunnescens	3.8–4.3/4.3–4.8

Myoglobin intron 2 (714 bp)	
acanthizoides Fujian–Fujian	0
acanthizoides Sichuan–Fujian	0
acanthizoides–concolor	0–0.1
acanthizoides / concolor–brunnescens	0.4–0.6

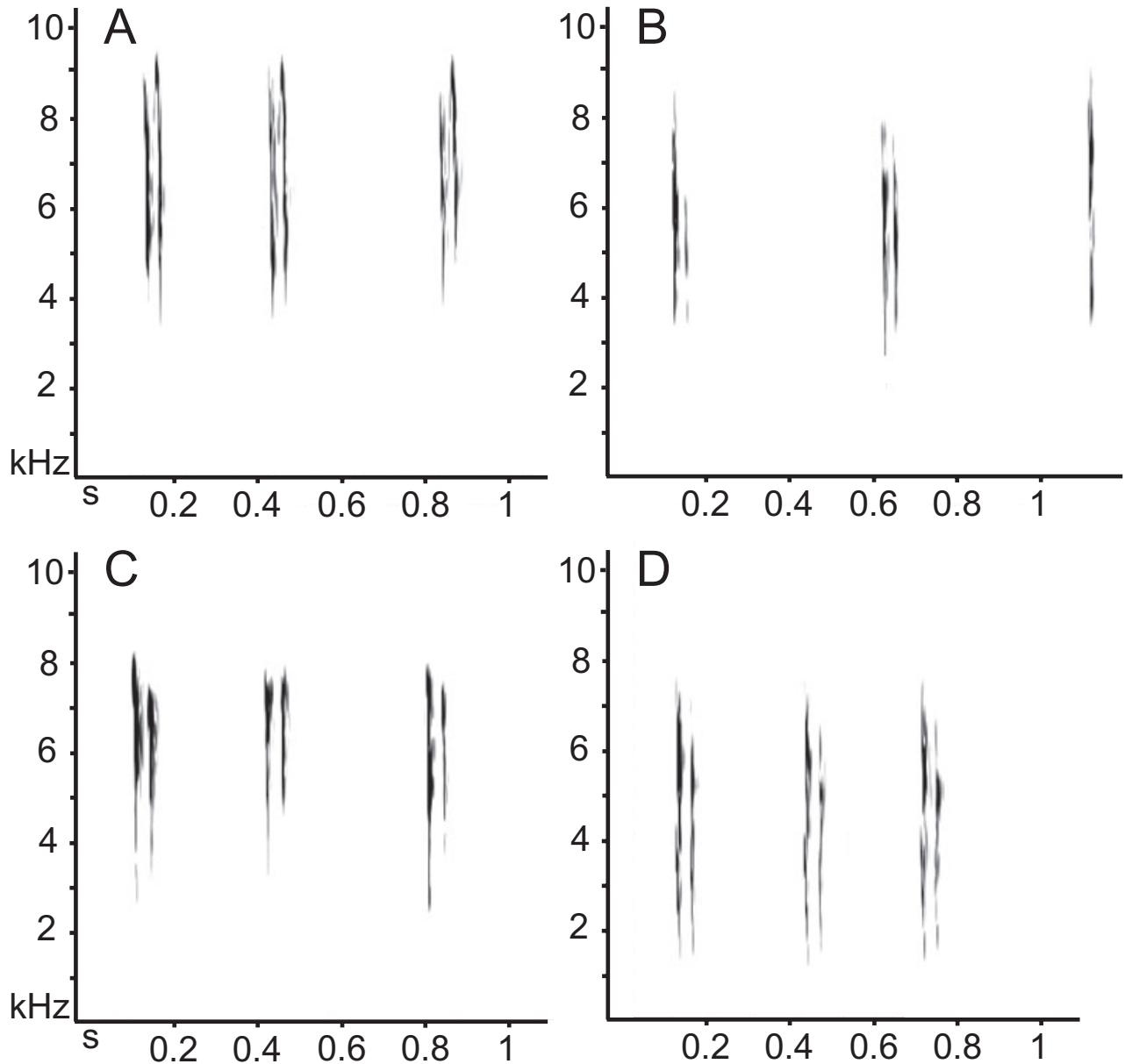| **G3PDH intron 11 (374 bp)**	
acanthizoides Fujian–Fujian	0
acanthizoides Sichuan–Fujian	0
acanthizoides–concolor	0
acanthizoides / concolor–brunnescens	0.3–0.6

Figure 13. Calls of *Cettia a. acanthizoides* (A: Shaanxi, China; B: Sichuan, China), *Cettia a. concolor* (C: Taiwan), and *C. brunnescens* (D: West Bengal, India). All tape recordings are by Per Alström, except for (C), which is from Liu (1995).

DISCUSSION

TAXONOMY

Although Watson *et al*. (1986) synonymised *concolor* with *acanthizoides*, we recognize *concolor* as a valid taxon based on its minor but consistent differences from *acanthizoides* in plumage colour and measurements. The lack of both vocal and genetic differentiation between these two taxa confirm their treatment as conspecific. The cytochrome *b* divergence between them is comparable to within-population variation in several *Phylloscopus* and *Seicercus* warblers (Helbig

et al., 1996; Martens *et al*., 2004; Olsson, Alström & Sundberg, 2004; Päckert *et al*., 2004; Olsson *et al*., 2005).

It is possible that the two disjunct populations of *acanthizoides* may be sufficiently different in plumage to warrant recognition of an additional subspecies, but further study is required to determine this.

In contrast, *brunnescens* is more divergent morphologically, genetically, and, especially, vocally from *acanthizoides* and *concolor*. The difference in song between *brunnescens* and the two others is obvious and striking, both audibly and spectrographically,
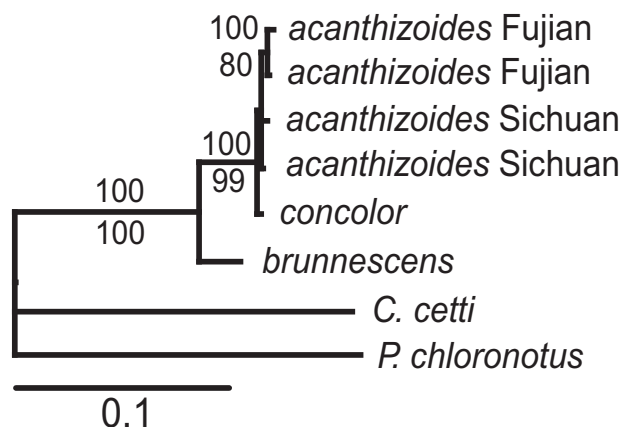
Figure 14. Cytochrome *b* tree of the three taxa in the *Cettia acanthizoides* complex and *Cettia cetti albiventris*, rooted with *Phylloscopus chloronotus*, estimated by Bayesian inference under the GTR + I model. Posterior probabilities (81 000 trees) are shown above nodes, and parsimony bootstrap values (1000 replicates) are shown below nodes.

unlike the intrataxon variation in *brunnescens* and *acanthizoides/concolor*, which is negligible over large geographical distances (spanning *c*. 15° and 18° longitudes, respectively, in our sample). The vocal differences between *brunnescens* and *acanthizoides/concolor* are considerably greater than between several other sympatric, non-interbreeding species in a number of different Old World warbler genera (Martens, 1980; Cramp, 1992; Rasmussen & Anderton, 2005). We predict that the song would act as a reproductive isolating barrier between *brunnescens* and *acanthizoides/concolor* were their ranges to come into contact. The cytochrome *b* tree and concordant divergences between the three unlinked loci, suggest that *brunnescens* has been separated from *acanthizoides/concolor* considerably longer than the two latter have been separated from each other. The cytochrome *b* divergence between *brunnescens* and *acanthizoides/concolor* is greater than between *Cettia diphone borealis* and *Cettia diphone cantans* (2.3%; Nishiumi & Kim, 2004), which are often treated as separate species (e.g. Sibley & Monroe, 1990; Rasmussen & Anderton, 2005), and comparable with differences among several *Phylloscopus* and *Seicercus* taxa that are treated as heterospecific (Helbig *et al*., 1995, 1996; Martens *et al*., 2004; Olsson, Alström & Sundberg, 2004; Päckert *et al*., 2004; Olsson *et al*., 2005).

The traditional classification of *acanthizoides/concolor* and *brunnescens* as conspecific is based on their morphological similarity, which is confirmed here. However, the pronounced differences between them in song and DNA show that they are better treated as separate species. This treatment was adopted by Rasmussen & Anderton (2005) with the intention that the present paper (cited therein as work in progress by P. Alström *et al*.) would provide full scientific rationale for doing so. Vocal characteristics have become increasingly important in taxonomic re-evaluations in birds, largely as a result of the growing knowledge of vocalizations resulting from the increased use of tape-recorders and sound analysis software, and the greater ease of travel to poorly studied areas in recent years (reviewed by Alström & Ranft, 2003). Molecular markers have often revealed large genetic divergences and nonmonophyletic relationships among taxa treated as conspecific in a wide range of birds (e.g. Friesen, Piatt & Baker, 1996; Pasquet & Thibault, 1997; Zink & Blackwell, 1998; Kennedy & Spencer, 2000; Zink & Blackwell-Rago, 2000; Liebers, Helbig & de Knijff, 2001; Zink *et al*., 2002; Drovetski *et al*., 2004; Martens *et al*., 2004; Olsson, Alström & Sundberg, 2004; Olsson *et al*., 2005). Such results have led to taxonomic revisions and the recognition of a larger number of species.

To conclude, based on the results from the present study, we propose the following taxonomic arrangement of the *C. acanthizoides* complex:

CETTIA ACANTHIZOIDES WITH SUBSPECIES
ACANTHIZOIDES (J. VERREAUX, 1871)
CONCOLOR OGILVIE-GRANT, 1912
CETTIA BRUNNESCENS (HUME, 1872) MONOTYPIC

We suggest retaining the English name Yellowish-bellied Bush Warbler for *C. acanthizoides*, as this is the most widely distributed species, and the one for which the name is most apt. For *C. brunnescens*, the English name Hume's Bush Warbler is appropriate and has been in long use, and for this reason was the name adopted in Rasmussen & Anderton (2005).

EVOLUTION OF MORPHOLOGICAL AND VOCAL TRAITS

Morphological differentiation is weakly congruent with genetic divergence in the *C. acanthizoides* complex. On plumage, the most recently separated taxa, *acanthizoides* and *concolor*, are more similar to each other than either of these is to *brunnescens*. However, structural differences are scarcely more evident between *brunnescens* and *acanthizoides/concolor* than between *acanthizoides* and *concolor*.

In contrast, there is a strong positive correlation between the degree of vocal and genetic divergence, as the vocally similar *acanthizoides* and *concolor* are genetically close to each other, whereas the vocally more differentiated *brunnescens* is more divergent genetically. The same has been demonstrated in the genera *Regulus* (Päckert *et al*. 2003), *Phylloscopus* (Helbig *et al*., 1996), and *Seicercus* (Päckert *et al*.,

2004; cf. Alström & Olsson, 1999; Olsson *et al*., 2004). However, as shown by Grant & Grant (2002) for two species of *Certhidea*, this is not always the case.

The vocal differences between *brunnescens* and *acanthizoides/concolor* have apparently evolved in allopatry. There are no indications that they have diverged as a result of selection against hybridization during secondary contact ('reinforcement of prezygotic isolation'; Dobzhansky, 1940; Butlin, 1989; Howard, 1993; Liou & Price, 1994; Servedio, 2000). First, the ranges of *acanthizoides* and *brunnescens* are not known to meet (although they could have met in the past). Second, each song type is uniform over a large geographical area, and the differences are not exaggerated where the ranges are in close proximity.

The recently separated *acanthizoides* and *concolor* are slightly divergent in plumage and structure, but not at all in vocalizations, whereas vocalizations are more differentiated than morphology between the earlier separated *brunnescens* and *acanthizoides/ concolor*. That plumage divergence precedes song differentiation in the early stages of speciation is common in passerine birds, as indicated by the many morphological subspecies that have indistinguishable songs (cf. e.g. Cramp, 1988, 1992; Cramp & Perrins, 1993), and by the many examples of presumably recently separated, not yet fully reproductively isolated, species that differ considerably more in plumage than in song, e.g. *Emberiza citrinella* and *Emberiza leucocephalos* (Byers, Olsson & Curson, 1995; Martens, 1996; Panov, Roubtsov & Monzikov, 2003), *Emberiza bruniceps*, and *Emberiza melanocephala* (Byers *et al*. (1995), and *Parus ater* and *Parus melanolophus* (Martens, 1996, and references therein).

IMPORTANCE OF TAXONOMIC REVISIONS

The number of recognized species of birds in the world was *c*. 8600 in 1946 (Mayr, 1946), *c*. 9000 in 1980 (Bock & Farrand, 1980), and *c*. 9700 in 1990 (Sibley & Monroe, 1990) and 2003 (Dickinson, 2003). This increase is mainly attributable to taxonomic rearrangements in which subspecies were elevated to the rank of species. Dickinson (2003) lists *c*. 26 400 least-inclusive taxa (monotypic species and subspecies of polytypic species). Many of these are very poorly known, especially with respect to vocalizations and relationships, and are in urgent need of taxonomic revision. Accordingly, there is great potential for a substantial increase in the number of recognized bird species. Collar (2003) estimated that the true number of species in Asia might be 20% higher than currently recognized, and he explicitly stressed the urgent need to revise the taxonomy of many rare, little-known Asian birds with limited distributions that are currently treated as subspecies of more widespread spe-

cies, and therefore are ranked as low priority and lack protection. As birds are excellent indicators of areas important for biodiversity conservation overall (Stattersfield *et al*., 1998), the underestimation of avian diversity has serious consequences. Hence, detailed and up-to-date studies of geographical variation in birds can have very important bearings on biodiversity conservation in general.

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