Species delimitation based on multiple criteria: the Spotted Bush Warbler *Bradypterus thoracicus* complex (Aves: Megaluridae)

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We demonstrate the importance of using multiple criteria in species delimitations, whatever the conceptual base for species delimitation. We do this by studying plumage, biometrics, egg coloration, song, mitochondrial DNA and habitat/altitudinal distribution in the Spotted Bush Warbler *Bradypterus thoracicus* (Blyth) complex, and by conducting playback experiments. Taxa that we suggest are best treated as separate species [*B. thoracicus* (Blyth), *B. davidi* (La Touche) and *B. kashmirensis* (Sushkin)] differ in most or all of these aspects, particularly in song and mitochondrial DNA, while those that we treat as subspecies (*suschkini*) or synonyms (*przevalskii*) differ slightly and only in morphology. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **154**, 291–307.

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INTRODUCTION

The 'biological' species concept (Mayr, 1942, 1963) has prevailed in ornithology for several decades, despite advocacy for alternatives in recent years (e.g. Cracraft, 1989, 1997; Zink & McKitrick, 1995; Sangster *et al*., 1999; Helbig *et al*., 2002; Alström & Mild, 2003: 30–35). For other groups of organisms, with the exception of mammals (Corbet, 1997), morphological or phylogenetic species concepts have long been dominant (e.g. Mishler, 1985; Gornall, 1997; Ruffing, Kocovsky & Stauffer, 2002; for recent reviews on species concepts, see Mayden, 1997; Wheeler & Meier, 2000), or species have been described without reference to a species definition; for example, Nelson (1999) noted that most fish species have been described without indication of which species concept was adopted. According to de Queiroz (1998) 'all modern species definitions are variations on the same general species concept', and the main discrepancies between them result from their focus on different stages in the differentiation of lineages. He proposed a 'unified' species concept based on the common element in all contemporary species definitions, namely that species are 'segments of population level lineages' (de Queiroz, 2005a; see also 2005b, c). Helbig *et al*. (2002) developed guidelines for the assignment of species rank to taxa in various degrees of geographical overlap, without adhering to any particular species concept.

Most proponents of 'phylogenetic' or 'morphological' species concepts, e.g. Rosen (1978, 1979), Nelson & Platnick (1981), Cracraft (1983, 1989), Donoghue (1985) and Zink & McKitrick (1995), reject infraspecific rank. A few advocates of 'phylogenetic' species

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concepts, such as Nixon & Wheeler (1990) and Davis & Nixon (1992), accept infraspecific taxa, but remark that these, unlike species, do not exhibit fixed differences from other conspecific taxa. In contrast, under the 'biological' species concept (Mayr, 1942, 1963), least-inclusive nominal taxa may be classified as either species or subspecies, depending on the degree of observed or inferred reproductive isolation from other taxa.

The subspecies category has been much criticised. Wilson & Brown (1953) argued that different subspecies may be mistakenly perceived as real entities, while in reality they may constitute a common gene pool, and the differences grade into each other. Mayr (1963, 1969) did not consider subspecies to be evolutionary units, except when geographically isolated. This was supported by Zink (2004), who reviewed studies of 230 subspecies of birds belonging to 41 species, and concluded that only 3% of these subspecies qualified as distinct evolutionary entities. However, Phillimore & Owens (2006) found that 36% of 259 subspecies belonging to 67 species were monophyletic. They suggested that the main reason for the discrepancy between their and Zink's (2004) results was that the earlier study included almost exclusively continental taxa from the Nearctic and Palearctic regions, which were shown by Phillimore & Owens to be significantly less likely to be monophyletic than subspecies from islands or other biogeographical regions.

Several methods for delimiting least-inclusive taxa, i.e. monotypic species or subspecies of polytypic species, have been proposed, including some based exclusively on DNA data (reviewed by Sites & Marshall, 2003). However, for most groups of organisms, new species and subspecies are described and taxonomic revisions are undertaken mainly based on morphology, because other attributes are generally not sufficiently well known to be useful. Birds are far better known than other major taxa with respect to the number of extant species, relationships, geographical variation in morphology and other traits, vocalizations, other behaviours, ecology, distribution, and degree of reproductive isolation. In spite of – or, perhaps, as a result of – this, species limits in birds are frequently the subject of continual debate (e.g. Isler, Isler & Whitney, 1999; Yésou, 2002; Baker *et al.*, 2003; Parkin *et al.*, 2004; Collinson *et al.*, 2006).

In the present paper we underline the importance of using multiple criteria in species delimitations, irrespective of the species definition adopted. We do this by using morphological, oological, vocal, behavioural, genetic and ecological criteria to review the taxonomy of the Spotted Bush Warbler *Bradypterus thoracicus* complex. Taxa which we suggest treating as separate species differ in most or all of these aspects, notably in song and mitochondrial DNA, while those that we consider to be conspecific differ, if at all, slightly and only in morphology.

MATERIAL AND METHODS

STUDY GROUP

The Old World warbler genus *Bradypterus* in the avian family Megaluridae (Alström *et al.*, 2006) comprises nearly 25 species, distributed in Africa and Asia (Dickinson, 2003; del Hoyo, Elliott & Christie, 2006). The species are mostly brown, paler below than above, usually with some darker spotting on the foreneck and breast. They are renowned for being similar morphologically. As a result of this, the genus has a long history of taxonomic instability and confusion (e.g. La Touche, 1926; Baker, 1930; Hartert & Steinbacher, 1934; Delacour, 1943; Ripley, 1982; Ali & Ripley, 1983; Dickinson *et al.*, 2000; Rasmussen *et al.*, 2000; del Hoyo *et al.*, 2006), and has recently been shown to be non-monophyletic (Drovetski *et al.*, 2004; Beresford *et al.*, 2005; Alström *et al.*, 2006). *Bradypterus thoracicus* (Blyth, 1845) is generally treated as a single species breeding in two main, disjunct areas (Fig. 1). Five or six (up to eight) subspecies are usually recognized (Hartert & Steinbacher, 1934; Watson, Traylor & Mayr, 1986; Round & Loskot, 1995; Dickinson, 2003; Fig. 1). From an assessment of morphological variation, Round & Loskot (1995) proposed that these be treated as two species: *B. thoracicus* (comprising *thoracicus*, *kashmirensis* and *przevalskii*) and *B. davidi* (including *davidi* and *suschkini*).

We studied all these taxa on their breeding grounds (Fig. 1, Table 1). We found territory-holding birds most closely matching *davidi* in central China in late spring and summer, well south of the previously known breeding range (Etchécopar & Hüe, 1983; Meyer de Schauensee, 1984; Cheng, 1987; Fig. 1, Table 1). Several individuals were caught, blood-sampled and tape-recorded; additional material was obtained for a few taxa, either on their breeding grounds, on migration or in their winter quarters (Table 1).

MORPHOLOGY AND EGGS

Specimens were studied in or were borrowed from the American Museum of Natural History (AMNH), New York: 24 *thoracicus*, two *przevalskii*; Academy of Natural Sciences (ANSP), Philadelphia: four *thoracicus*; The Natural History Museum (BMNH), Tring, UK: 11 *kashmirensis*, 57 *thoracicus*, three *przevalskii*, two *davidi*; Bombay Natural History Society (BNHS), Mumbai, India: one *thoracicus*; Field Museum of Natural History (FMNH), Chicago: one *thoracicus*,
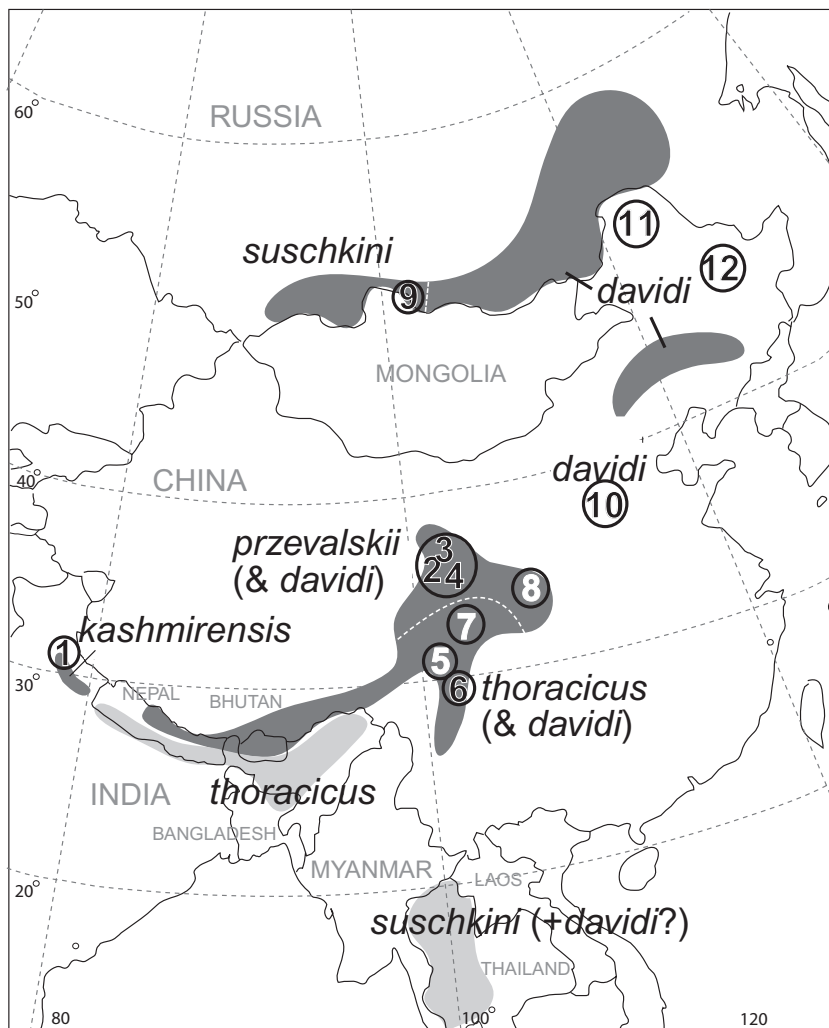
Figure 1. Distribution of the *Bradypterus thoracicus* complex compiled from previously published sources (grey; Dement'ev & Gladkov, 1968; Ali & Ripley, 1983; Flint *et al.*, 1984; Meyer de Schauensee, 1984; Watson *et al.*, 1986; Cheng, 1987; Round & Loskot, 1995; Rasmussen & Anderton, 2005) and the present study (numbers). Dark grey refers to breeding and pale grey to non-breeding. Field study sites are indicated by numbers (see Table 1 for details): (1) Manali, Himachal Pradesh; (2) Laoye Shan, Qinghai; (3) Huzu Bei Shan, Qinghai; (4) Mengda, Qinghai; (5) Wolong, Sichuan; (6) Emei Shan, Sichuan; (7) Jiuzhaigou, Gansu; (8) Taibai Shan, Shaanxi; (9) Listvyanka; (10) Panquengou, Shanxi; (11) Huzong, Heilongjiang; (12) Dailing, Heilongjiang. Localities where *thoracicus* and *davidi* and *przevalskii* and *davidi*, respectively, have been found sympatrically in the breeding season in the present study are indicated by white numbers. The winter distribution for *kashmirensis* has not been given in the literature, and the winter distribution for *davidi* has been considered uncertain.

one *davidi*; Museum of Comparative Zoology (MCZ), Harvard University: 13 *thoracicus*, two *przevalskii*, four *davidi*; Naturalis (NNM), Leiden, the Netherlands: two *davidi*; Royal Ontario Museum (ROM), Toronto: one *thoracicus*; University of Michigan Museum of Zoology (UMMZ), Ann Arbor: 11 *kashmirensis*, 20 *thoracicus*, two *davidi*; National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC: 19 *thoracicus*, four *davidi*; Yale Peabody Museum (YPM), New Haven: one *thoracicus*,

three *davidi*; Museum für Naturkunde (ZMB), Berlin, Germany: four *przevalskii*, one *davidi*; and Zoological Survey of India, Kolkata, India: three *thoracicus*.

Measurements taken from museum specimens include: culmen length from base of skull; maximum wing length (flattened and stretched); shortfalls from wing point of folded wing of each primary, numbered ascendantly; distance from notch in inner web of primaries 1 and 2 to their tips; lengths of primaries 1 and 2; width of primaries 1 and 2 just distal to notch;

Table 1. Birds studied in the field. All except one were singing males; all captured birds were measured, and most were photographed

Taxon	Location	Date	No. observed	No. caught/no. DNA samples	No. taped
kashmirensis	Manali, Himachal Pradesh, NW India (32.1°N, 77.1°E)	late June 1999	*c.* 10	1*	7†
thoracicus‡	Wolong, Sichuan, C China (30.5°N, 102.6°E)	late June 1990	3	1	1
thoracicus	Emei Shan, Sichuan, C China (29.3°N, 103.2°E)	May 1986	'a few'	–	–
thoracicus	Emei Shan, Sichuan, C China (29.3°N, 103.2°E)	mid-May 1987	*c.* 5	–	2
thoracicus	Emei Shan, Sichuan, C China (29.3°N, 103.2°E)	early May 1992	1	1	1
przevalskii	Huzu Bei Shan, NE Qinghai, NC China (*c.* 37°N, 102°E)	late June 1995	1	–	–
przevalskii	Mengda, NE Qinghai, NC China (*c.* 35.4°N, 102.4°E)	mid-June 1994	3	3	2
przevalskii	Laoye Shan, NE Qinghai, NC China (36.6°N, 101.4°E)	early June 1993	1	1	–
przevalskii	Laoye Shan, NE Qinghai, NC China (36.6°N, 101.4°E)	late June 1995	2	–	–
przevalskii	Taibai Shan, S Shaanxi, NC China (33.6°N, 107.4°E)	mid-June 1995	7	1	–
przevalskii	Jiuzhaigou, S Gansu, C China (33.1°N, 104.2°E)	mid-June 1989	3	–	–
przevalskii	Jiuzhaigou, S Gansu, C China (33.1°N, 104.2°E)	mid-June 1994	1	1	–
davidi§	Huzong, Heilongjiang, NE China (52.0°N, 123.6°E)	late June 1988	≥7	–§	2
davidi	Dailing, Heilongjiang, NE China (c.47.0°N, 129.0°E)	mid-June 1988	1	–	–
davidi	Panquengou, Shanxi, NC China (*c.* 37.3°N, 112°E)	early June 1993	1	–	1
davidi	Taibai Shan, S Shaanxi, NC China (33.6°N, 107.4°E)	mid-June 1995	9	1	–
davidi	Jiuzhaigou, S Gansu, C China (33.1°N, 104.2°E)	late May + mid-June 1989	1	–	–
davidi	Jiuzhaigou, S Gansu, C China (33.1°N, 104.2°E)	mid-June 1994	1	1	1
davidi	Wolong, Sichuan, C China (30.5°N, 102.6°E)	late June 1990	3	2	–
suschkini	Listvyanka, SW Lake Baikal, Russia (51.6°N, 104.5°E)	June 1986	*c.* 5	–¶	1**

*Two additional DNA samples obtained from T. Price.

†Another tape recording, from Kedarnath, Uttaranchal, India (*c.* 30.44°N, 79.04°E), obtained from P. Singh.

‡One *thoracicus/kashmirensis/przevalskii* caught in south-east Nepal in early April 1983.

§Several more birds, probably *davidi*, observed on migration through Hebei and Jilin provinces, north-east China; several were heard singing and one was tape recorded, and one was caught and a DNA sample taken.

¶One DNA sample of *suschkini/davidi* from Mongolia obtained from Johan Ställberg.

**Tape recordings of another individual studied (Mild, 1987).

tarsus length, distal width, minimum depth; hallux length; tail length; central rectrix width; and width of white tip of longest undertail-coverts. Measurements of live birds (wing, tail, bill length) were taken in the same way as for museum specimens. All live birds except one were sexed as males, as they were heard singing just before (and often after) they were caught, and they showed a pronounced cloacal protuberance. The only bird assumed to be a female did not sing, lacked a cloacal protuberance and appeared to be paired with a singing bird that was caught at the same time. Univariate statistics were obtained and principal components analysis on the correlation matrix of untransformed variables was performed using Systat 8.0 (SPSS Inc., 1998). Sexes were segregated in analyses except for *kashmirensis*, for which very few sexed specimens are available.

In order to elucidate plumage distinctions, radiographs (X-rays) were used to allow ageing of specimens. Degree of skull pneumatization was judged by viewing the X-ray with a magnifying glass against a strong light. Birds with incomplete double-layering or cranial struts were considered young; in passerines, the skull is usually fully pneumatized in 3–6 months (Svensson, 1992).

Coloration of BMNH egg sets was directly compared in natural light between *thoracicus* (28 eggs in 11 clutches), *kashmirensis* [17 eggs in five clutches, excluding those labelled 'Kashmir', which are of questionable provenance (P. C. Rasmussen, P. Alström & U. Olsson, unpubl. data)] and *davidi/suschkini* (seven eggs in three clutches, all from 'Baikal'), as well as among all other mainland Asian *Bradypterus* taxa [Long-billed Bush Warbler *B. major*, Brown Bush Warbler *B. luteoventris* and Russet Bush Warbler *B. mandelli* (formerly *B. seebohmi*; see Dickinson *et al.*, 2000); eggs of the latter two species were not distinguished because earlier taxonomic confusion now prevents their separation].

VOCALIZATIONS

All tape recordings were made using a Sony WM-D6 cassette or DAT TCD-D3 recorder and a Telinga Pro parabolic reflector/microphone. Sonograms were made in Canary 1.2.4 (Mitchell *et al.*, 1995). We use the following terminology: element – a discrete, unbroken unit in a sonogram; note – a sound of one or more element; 'strophe' – a series of notes or, in the case of *davidi* and *suschkini*, a single note separated by distinct pauses. In the species under consideration, the pauses are generally < 1 s long, and accordingly the 'strophes' are less well separated than in most passerines, and hence the quotation marks around 'strophes'.

We carried out playback tests on 15 males in China. A speaker with a *c*. 15-m (in two cases 1.5 m) cable was placed in a male's territory. The playback was usually initiated by a variably long (a few seconds to 2 min) spell of the same taxon's song to arouse the bird and to ascertain that it was responsive. This was followed by a series of songs of different and the same taxa, each cut usually at least 2 min long; the different songs were separated by pauses lasting 30 s to 1 min. An example of a test on *davidi*: (1) *davidi* a few seconds, (2) *thoracicus* 4 min, (3) *davidi* 2 min, (4) *thoracicus* 4 min, (5) *davidi* 2 min, (6) *thoracicus* 4 min, (7) *davidi* 1 min. The response was scored on a four-point scale: no (0), faint (1), medium (2) and strong (3) response. Faint response involved no apparent aggression, seemingly just curiosity, and for most of the duration of the playback there was no reaction at all. Strong response involved strong aggression, the bird vigorously searching for the supposed intruder, generally remaining silent or only giving occasional short outbursts of song or alarm calls; sometimes the wings were lowered, slightly spread and quivering. Medium response meant that the bird showed some aggression, although this was not considered very pronounced. The tape recordings used during the playback test were: *davidi* from Heilongjiang, China; *thoracicus* from Sichuan, China; *B. tacsanowskius* from Hebei, China; *B. luteoventris* from Sichuan, China; and *B. m. mandelli* from Thailand (for descriptions and sonograms of the taxa not dealt with here, see Rasmussen & Anderton, 2005).

DNA EXTRACTION, SEQUENCING AND ANALYSIS

DNA extraction from blood or feathers, and sequencing of the cytochrome *b* gene were performed as described in Olsson *et al.* (2005). The sequences have been deposited in GenBank (Appendix 1). Molecular phylogenies were estimated by Bayesian inference using MrBayes 3.1 (Huelsenbeck & Ronquist, 2001, 2005; Ronquist & Huelsenbeck, 2003). The choice of model was determined based on the Akaike Information Criterion (AIC; Akaike, 1973) and a hierarchical likelihood ratio test (hLRT; Posada & Crandall, 1998), both calculated in MrModeltest 2.0 (Nylander, 2004). The best-fit model according to the AIC was a general time-reversible (GTR) model (Lanave *et al.*, 1984; Tavaré, 1986; Rodríguez *et al.*, 1990), with an estimated proportion of invariant sites (I; Gu, Fu & Li, 1995). However, the difference in weight between this model and the second best one, GTR with gamma distributed rate variation across sites (Γ; Yang, 1994), was marginal (0.4202 vs. 0.4179). The hLRT chose the GTR + Γ model. We therefore ran analyses under both these models. Default priors were used. Four Metropolis-coupled MCMC chains were run for 3×10^6 generations and sampled every 100 generations; the temperature was set to 0.1. Two

simultaneous, independent analyses starting from different random trees were run (by default); the samples from the stationary phases of these runs were pooled to obtain the final results.

Clade support for the unweighted data set was also assessed by parsimony bootstrapping in PAUP* 4.08b (Swofford, 2001), with branch-and-bound search, 1000 replicates. Pairwise sequence divergences were calculated in PAUP*; GTR + Γ distances were calculated using parameter estimate outputs from the Bayesian analyses.

RESULTS

PLUMAGE

Three main groups can be recognized based on a combination of qualitative plumage characters: the *davidi* group (including *davidi*, *suschkini* and the previously overlooked birds from central China that match *davidi*), the *thoracicus* group (including *thoracicus* and *przevalskii*) and *kashmirensis* (Table 2). Except for the unique 'buffy morph' of *kashmirensis*, the *thoracicus* group and *kashmirensis* are very similar, while the *davidi* group is slightly more divergent. As a result of intrataxon variation in all three groups (Table 2), < 10% of the museum specimens and individuals studied in the field were difficult to assign to one of these three groups based on plumage alone. Individuals with atypical plumage observed in the field in the breeding season were easily identified to group by song (see below). The existence of a buff-breasted morph among breeding adults is unique to *kashmirensis*; these individuals are so different from other *kashmirensis* that they have sometimes been misidentified as Brown Bush Warbler *B. luteoventris* (e.g. BMNH nos. 1876.2.12.844 and 1876.2.12.961, listed as *B. luteoventris* by Oates, 1889), or considered as a probable new taxon (judging by label annotations by W. Koelz on UMMZ specimens), or presumed to be young birds (e.g. Seebohm, 1881). That these buff-breasted birds are indeed a colour morph and not a separate species is shown by the sympatry with, and lack of differentiation in structure and song from, grey-breasted *kashmirensis*. The buff-breasted morph is fairly frequent, judging from the fact that seven (three at BMNH and four at UMMZ) of the 18 known museum specimens of *kashmirensis* from the breeding grounds are of this morph, as was one out of about ten birds observed in the field.

The taxon *przevalskii* is doubtfully separable from *thoracicus* on plumage, although northerly populations differ on average (Table 2). We have not detected any differences between *thoracicus* from the Himalayas and China, as series from Bhutan, Sikkim, southern and south-eastern Tibet, north-western Yunnan and Sichuan are indistinguishable. We have not examined any definite *suschkini*, and hence cannot evaluate the alleged minor differences from *davidi* (Table 2).

Most specimens of the *thoracicus* and *davidi* groups from the non-breeding season have weak breast spots or none (as noted by Oates, 1889 for *thoracicus*), and the former have much less grey on the head and underparts than most breeding birds. Accordingly, differences between the *thoracicus* and *davidi* groups are less pronounced than in breeding plumage. Based on skull pneumatization, first-winter birds show, on average, the least grey and most brown wash below, and nearly or entirely lack dark speckles on the breast.

BIOMETRICS

On measurements, the *thoracicus* group and *kashmirensis* are extremely similar to each other, while *davidi* is more divergent (Table 3). Overall, *davidi* is significantly smaller than the *thoracicus* group and *kashmirensis*. The wing shape of *davidi* is significantly more pointed, with a narrower inner wing, than is that of either the *thoracicus* group or *kashmirensis* (Table 3). In a principal components analysis (PCA), *davidi* is well separated from the other groups on PC-I (Fig. 2), which is a strong size axis (Table 4). There are no significant differences in size or proportions between *thoracicus* and *przevalskii*. No definite *suschkini* were available for mensural analyses.

Live members of the *thoracicus* group and *davidi* from central China also differ in measurements (Table 5). In our sample, there is no overlap between the two groups in tail length and tail/wing ratio, and a very marginal overlap in the length of the 1st primary, while the other measurements do not differ

☆ *davidi/suschkini*
□ *thoracicus/przewalskii*
○ *kashmirensis*
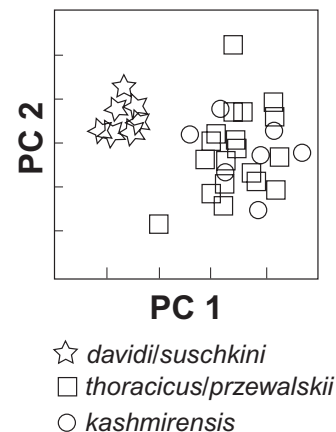
Figure 2. Principal components analysis of morphometric data for the members of the *Bradypterus thoracicus* complex. See Table 4 for summary statistics.

Table 2. Plumage characters of the taxa in the *Bradypterus thoracicus* complex in breeding plumage

	*thoracicus/przevalskii**	*davidi/suschkini†*	*kashmirensis*
Upperparts	Dark warm brown, slightly more rufescent on crown	Uniformly drab brown	Uniformly brown, slightly paler than in *thoracicus/przevalskii*
Supercilium	Grey or greyish-white, often white in front of and/or above eye‡	Buffy§	Grey or greyish-white, often white in front of and/or above eye 'Buffy morph': warm buffy
Ear-coverts, sides of neck, lower throat	Grey, contrasting with upperparts and flanks¶	Brown to greyish-brown, contrasting little or not at all with upperparts and flanks**	Grey, slightly paler than in *thoracicus/przevalskii* 'Buffy morph': warm buffy
Breast	Grey, contrasting with upperparts and flanks††	Brown to greyish-brown, contrasting little or not at all with upperparts and flanks‡‡	Grey, slightly paler than in *thoracicus/przevalskii* Buffy morph: warm buffy
Spots on lower throat/ breast	A few light and fine to many heavy blackish	A few light and fine to many heavy blackish	Brown, fine; sometimes moderately heavy dark grey Buffy morph: unspeckled or lightly speckled with dark brown
Flanks and bases to undertail-coverts	Dark, cold brown	Medium brown	Fulvous, slightly paler than in *thoracicus/ przevalskii*
Width of white tips to longest undertail-coverts	3.45 ± 0.82 mm ($N = 31$)	4.55 ± 1.31 mm ($N = 9$)	5.26 ± 0.81 mm ($N = 7$)

*przevalskii from northern part of range (e.g. Qinghai, Gansu) typically paler overall and more rufescent above than *thoracicus*, lacking contrastingly rufous crown; southerly populations assigned to *przevalskii* indistinguishable from *thoracicus*.

†*suschkini* said to differ by being slightly paler and more reddish-brown above than *davidi*, with a whiter, bolder supercilium and weaker speckles on breast (Dement'ev & Gladkov, 1968; Round & Loskot, 1995). We have not examined any definite *suschkini*.

‡Rarely, buffy-tinged throughout.

§Rarely, whitish in front of and above eye.

¶Rarely, brown ear-coverts and sides of neck.

**Rarely, ear-coverts and (lower) neck-sides greyish-tinged, though less pure in colour and less extensive than in typical individuals of the *thoracicus* group.

††Rarely, lower throat and central breast grey or brown-grey and sides of breast brown.

‡‡Rarely, centre of breast brownish-grey, though less pure in colour and less extensive than in typical individuals of the *thoracicus* group.

significantly. Central Chinese *davidi* appear larger than other populations of *davidi* and *suschkini* (cf. Tables 3 and 5).

EGGS

The eggs of all three examined taxa are distinct, those of *thoracicus* being most divergent. For *thoracicus*, all but two clutches of two eggs each are pinkish-buff with chestnut-brown speckles, fairly coarse in most. Many eggs of *thoracicus* are almost uniformly and densely speckled chestnut, while others have weaker but uniformly distributed speckles, and several have the speckles forming an almost solid band around the larger end. In contrast, the eggs of both *kashmirensis* and *davidi/suschkini* have a whiter background, with fine, dark brown rather than chestnut speckles. In some *kashmirensis* eggs the speckles are crisp and in others they are weak, but in all they are fairly evenly distributed. The *davidi* eggs differ slightly from *kashmirensis* in being slightly whiter with blacker, very fine spots; they vary in amount of spotting over the egg and, unlike *kashmirensis*, some have a dense ring

Table 3. Univariate statistics for untransformed measurements (in mm) of museum specimens of the *Bradypterus thoracicus* complex

		davidi suschkini	*thoracicus/przevalskii*	*kashmirensis*†
Culmen length from skull	M	13.70 ± 0.37 (5)[NS]	14.13 ± 0.58 (18)[NS]	14.23 ± 0.82 (7)[NS]
	F	13.65 ± 0.35 (2)	13.96 ± 0.83 (12)	
Wing length	M	52.90 ± 1.95 (5)***	55.80 ± 2.18 (20)[NS]	55.36 ± 1.91 (11)***
	F	52.75 ± 0.35 (2)	54.04 ± 1.48 (13)	
Primary 1 shortfall from wing tip	M	25.42 ± 1.46 (5)[NS]	24.65 ± 1.99 (20)[NS]	23.54 ± 2.32 (11)[NS]
	F	26.00 ± 1.98 (2)	22.06 ± 6.56 (12)	
Primary 2 shortfall from wing tip	M	7.30 ± 1.17 (5)**	8.31 ± 1.23 (20)[NS]	7.81 ± 1.17 (12)[NS]
	F	6.65 ± 0.92 (2)	8.42 ± 1.14 (13)	
Primary 3 shortfall from wing tip	M	0.50 ± 0.08 (4)**	1.31 ± 0.73 (20)[NS]	1.28 ± 0.89 (11)[NS]
	F	0.50 ± 0.08 (4)	1.54 ± 0.78 (13)	
Primary 4 shortfall from wing tip	M	0 ± 0 (5)[NS]	0.15 ± 0.26 (19)[NS]	0.25 ± 0.48 (12)[NS]
	F	0 ± 0 (2)	0.17 ± 0.34 (12)	
Primary 5 shortfall from wing tip	M	1.02 ± 0.26 (5)**	0.22 ± 0.50 (18)[NS]	0.51 ± 0.60 (10)[NS]
	F	1.00 ± 0 (2)	0.38 ± 0.49 (12)	
Primary 6 shortfall from wing tip	M	3.30 ± 0.43 (4)***	2.06 ± 0.78 (19)[NS]	2.30 ± 0.57 (10)***
	F	3.40 ± 0.14 (2)	1.90 ± 0.61 (13)	
Primary 7 shortfall from wing tip	M	4.92 ± 0.62 (4)***	3.56 ± 0.89 (16)[NS]	3.84 ± 0.41 (8)**
	F	4.95 ± 0.21 (2)	3.13 ± 0.89 (9)	
Primary 8 shortfall from wing tip	M	6.55 ± 0.59 (4)**	5.29 ± 1.07 (15)[NS]	5.44 ± 0.83 (7)[NS]
	F	6.20 ± 0.14 (2)	4.76 ± 0.98 (8)	
Primary 9 shortfall from wing tip	M	7.87 ± 0.72 (4)*	6.62 ± 1.19 (15)[NS]	6.60 ± 0.67 (8)[NS]
	F	7.25 ± 0.64 (2)	6.05 ± 0.79 (8)	
Primary 1 notch length	M	5.34 ± 0.34 (5)***	7.70 ± 0.98 (19)[NS]	7.51 ± 0.83 (10)***
	F	6.70 (1)	7.53 ± 0.99 (12)	
Primary 2 notch length	M	9.50 ± 0.33 (5)**	11.21 ± 0.97 (18)[NS]	10.70 ± 3.13 (12)[NS]
	F	9.40 (1)	11.60 ± 0.86 (13)	
Primary 1 length	M	12.18 ± 0.88 (5)***	15.87 ± 2.04 (19)[NS]	15.99 ± 1.55 (10)***
	F	12.77 ± 1.0 (3)	15.42 ± 1.35 (13)	
Primary 1 width	M	2.54 ± 0.24 (5)***	3.12 ± 0.32 (19)[NS]	3.34 ± 0.35 (10)***
	F	2.20 ± 0.14 (2)	3.26 ± 0.24 (13)	
Primary 2 width	M	4.72 ± 0.23 (5)**	5.15 ± 0.42 (19)[NS]	5.22 ± 0.57 (12)*
	F	4.80 ± 0.28 (2)	5.16 ± 0.39 (13)	
Tarsus length	M	18.60 ± 0.24 (5)***	20.58 ± 0.94 (19)[NS]	20.26 ± 1.05 (10)***
	F	18.30 ± 0.60 (3)	20.45 ± 0.89 (13)	
Tarsus distal width	M	2.32 ± 0.15 (5)***	2.53 ± 0.13 (19)[NS]	2.46 ± 0.12 (9)[NS]
	F	2.33 ± 0.06 (3)	2.56 ± 0.18 (13)	
Tarsus minimum depth	M	1.57 ± 0.15 (3)*	1.79 ± 0.29 (12)[NS]	1.78 ± 0.17 (9)*
	F	1.47 ± 0.15 (3)	1.67 ± 0.09 (11)	
Hallux length	M	5.90 ± 0.73 (5)*	6.76 ± 0.92 (11)[NS]	5.87 ± 0.54 (9)[NS]
	F	5.37 ± 0.06 (3)	6.26 ± 0.67 (11)	
Tail length	M	44.04 ± 1.50 (5)***	49.94 ± 2.76 (16)[NS]	48.17 ± 2.24 (9)**
	F	43.50 (1)	48.62 ± 1.72 (11)	
Central rectrix width	M	8.14 ± 0.97 (5)***	9.61 ± 0.61 (15)[NS]	8.98 ± 0.54 (9)[NS]
	F	8.60 (1)	9.45 ± 0.83 (11)	
Longest undertail-covert tip to rectrix 1 tip	M	16.43 ± 1.73 (3)***	22.72 ± 3.25 (12)[NS]	21.03 ± 2.31 (7)**
	F	15.60 (1)		20.97 ± 2.52 (9)
Longest undertail-covert tip to rectrix 6 tip	M	−4.95 ± 4.17 (2)*	−0.05 ± 4.80 (11)[NS]	−2.71 ± 2.63 (7)[NS]
	F	−3.50 ± 0.71 (2)		−0.23 ± 2.55 (7)

†Sexes pooled for *kashmirensis*.
No definite *suschkini* have been examined. For explanations of measurements, see Material and methods. Significance levels (Bonferroni adjusted) between groups, with sexes lumped (ANOVA): *$P \leq 0.05$, **≤ 0.01, ***≤ 0.001; values under *davidi/suschkini* for comparisons with *thoracicus/przevalskii*; values under *thoracicus/przevalskii* for comparisons with *kashmirensis*; and values under *kashmirensis* for comparisons with *davidi/suschkini*.
Abbreviations: M, male; F, female.

of dark brown spots around the larger end. The differences between the eggs of *kashmirensis* and *thoracicus* have been accurately described by Baker (1933).

Song

The songs of all three groups are highly distinctive (Fig. 3, Table 6), although there is considerably more similarity between the *thoracicus* group and *kashmirensis* than between any of these and the *davidi* group. In central China, *thoracicus* and *przevalskii* sing with a fast, monotonous, prolonged, rhythmic, mechanical reel of short clicking and more drawn-out metallic buzzing sounds, which could be transcribed as *tri-tri-tri-treez tri-tri-tri-treez tri-tri-tri-treez tri-tri-tri-treez tri-tri-tri-treez* . . . (Fig. 3A, B, Table 6). The individual variation is negligible in this context, and we cannot detect any consistent differences between *thoracicus* and *przevalskii*.

We do not know the song of *thoracicus* from the Himalayas with certainty. We have three recordings from the plains of Nepal and north-east India in the non-breeding season. These differ clearly from the songs of *thoracicus/przevalskii* from China and *kashmirensis* in the individual elements, syntax, and length of the strophes and pauses. However, they also differ between strophes of the same bird and between the three individuals, and probably represent developmental song.

The song of *kashmirensis* has the same clicking and buzzing quality as the song of *thoracicus/przevalskii*, but sounds markedly different, e.g. *tre-tre-tre-trip-treez-trip-treez*, *tre-tre-tre-trip-treez-trip-treez*, *tre-tre-tre-trip-treez-trip-treez*, . . . , and differs in several details (Fig. 3C, Table 6). The individual variation is slight and mainly concerns the number of 'introductory elements'.

The song of the *davidi* group is strikingly different: a dry, rasping, monotonous, drawn-out *brzzzzzz . . . . . . brzzzzzz . . . . . . brzzzzzz . . . . . . ,* which often continues for lengthy periods; each note increases in loudness towards the end, and is separated from the next one by a distinct, variably long pause (Fig. 3D–F, Table 6). The individual variation is slight, and we cannot detect any consistent differences between *davidi* from different regions, or between *davidi* and *suschkini*.

In playback experiments (Table 7), five of the six *przevalskii* that were exposed to playback of *davidi* did not respond at all, while they did respond strongly to song of *thoracicus*. The sixth bird (Jiuzhaigou, Sichuan on 18 June 1994) responded as vigorously to song of *davidi* as to *thoracicus*, save for a relatively mild response the first time *davidi* was played. Five of the seven *davidi* that were exposed to playback of *thoracicus* completely ignored this song, while they responded strongly to song of *davidi*. The other two *davidi* showed some interest in song of *thoracicus*, although no aggression was evident; in contrast, they responded aggressively to song of *davidi*. On Taibai Shan, Shaanxi, on 14 June 1995 a *przevalskii* and a *davidi* were brought in to the same bush, to

Table 4. Results of principal components analysis on the correlation matrix of untransformed variables of museum specimens of the *Bradypterus thoracicus* complex

	Factor loadings		
	1	2	3
Wing length	0.72	−0.38	0.13
Culmen length from skull	0.38	−0.33	−0.71
Tail length	0.52	−0.38	0.51
Tarsus length	0.74	0.11	0.05
Primary 2 shortfall from wing tip	0.39	−0.71	−0.21
Primary 1 length	0.75	0.47	0.04
Primary 1 notch length	0.83	0.21	0.21
Primary 1 distal width	0.56	0.48	−0.43
Eigenvalues	3.20	1.41	1.07
% variance explained	40.05	17.61	13.34

Table 5. Ranges of measurements (in mm) of live males of *thoracicus/przevalskii* and *davidi* from Sichuan, Qinghai and Shaanxi provinces, China. Abbreviations as in Table 2

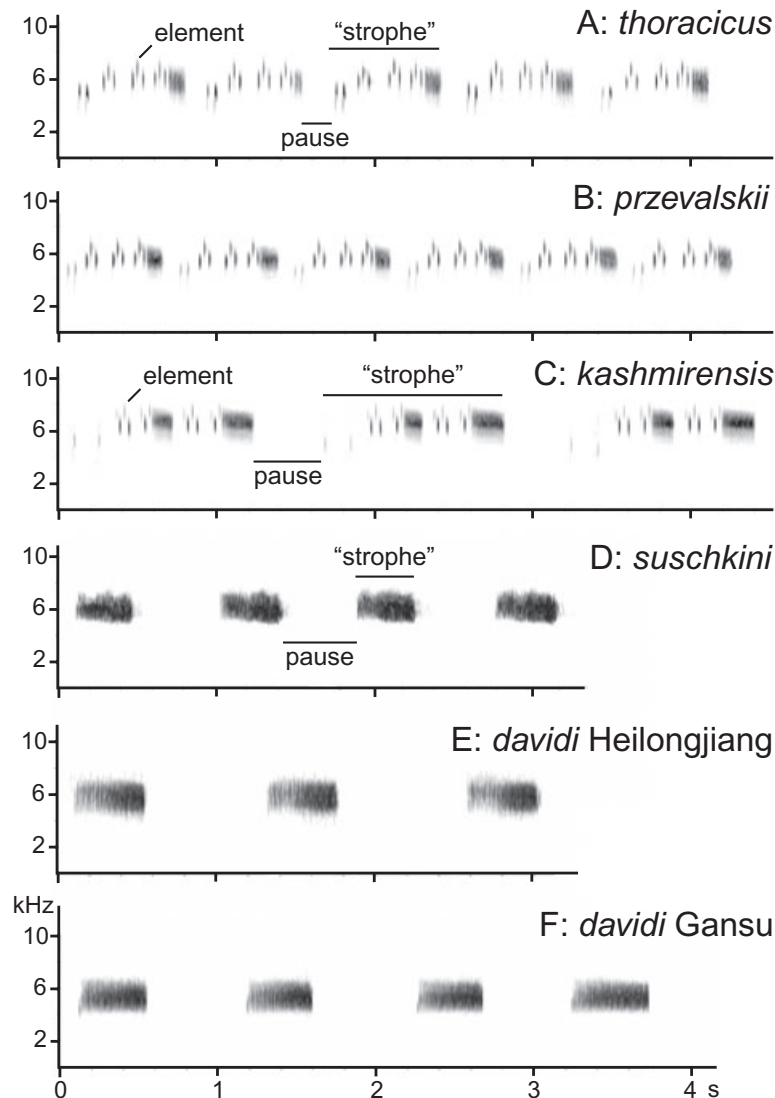|	*thoracicus/przevalskii*	*davidi* C China
Wing length	55.5–59.0 (57.7 ± 1.25; 6)	55.5–58.0 (56.9 ± 1.11; 4)
Tail length*	49.5–53.5 (50.9 ± 1.56; 5)	43.5–49.0 (46.8 ± 2.72; 4)
Tail/wing*	0.86–0.92 (0.88 ± 0.02; 5)	0.77–0.85 (0.82 ± 0.04; 4)
Culmen length from skull	13.1–14.8 (13.5 ± 0.65; 6)	13.3–14.4 (13.9 ± 0.46; 4)
Primary 1 > primary coverts*	6.5–9.0 (7.6 ± 1.07; 6)	5.0–6.5 (5.9 ± 0.63; 4)

Values in parentheses: (mean ± SD; *N*). Significance levels (two-sample *t*-test, separate variance): *$P \leq 0.05$.

Figure 3. Sonograms of songs: A, *thoracicus* Emei Shan, Sichuan, China, early May; B, *przevalskii* Mengda, Qinghai province, China, mid-June; C, *kashmirensis* Manali, Himachal Pradesh, India, late June; D, *suschkini* Listvyanka, Lake Baikal, Russia, June; E, *davidi* Huzong, Heilongjiang province, China, late June; F, *davidi* Jiuzhaigou, Gansu province, China, mid-June. All recordings by Per Alström.

within ≤ 0.5 m from each other, without showing any aggression toward each other, while responding strongly to playback of their own type of song.

DNA

The cytochrome *b* tree (Fig. 4) shows *thoracicus* and *przevalskii* to be sisters, with strong support, and *kashmirensis* to be sister to these two; the posterior probability for the latter relationship is moderate, while the bootstrap support is fairly high. The *davidi*-like birds from central China, and *davidi* and *davidi*/*suschkini* from further north form a polytomy.

The cytochrome *b* divergences among the three main clades, representing the *thoracicus* and *davidi* groups and *kashmirensis*, are 3.5–5.2% (uncorrected p distance) or 5.0–8.7% (corrected: GTR + Γ); the *thoracicus* group and *kashmirensis* are most similar in pairwise comparisons of the three main clades (Table 8). In contrast, the distances within the main clades are a maximum of 0.5%; the *davidi*/*suschkini* haplotype from Mongolia is most divergent, while the difference between *thoracicus* and *przevalskii* matches individual variation in the other taxa (Table 8).

Table 6. Characteristics of songs

	thoracicus/przevalskii	kashmirensis	davidi/suschkini
'Strophe' length (ms)	558–749 (626 ± 32; 60)	908–1444 (1170 ± 116; 53)	359–497 (423 ± 33; 70)*
Pause length (ms)	94–325 (170 ± 49; 60)	342–1833 (687 ± 332; 49)	413–1212 (645 ± 178; 70)
Buzz length (ms)†	76–118 (101 ± 9.3; 50)	105–220 (157 ± 40; 58)	359–497 (423 ± 33; 70)*
Frequency span buzz (Hz)†	1470–2511 2005 ± 248; 50	1344–2823 (2136 ± 331; 58)	1933–2782 (2395 ± 195; 70)
Mean frequency buzz (Hz)†	5412–5956 (5648 ± 135; 50)	5847–6698 (6287 ± 274; 58)	5208–6179 (5673 ± 269; 70)
Number of buzzes/'strophe'	1	2	1*
Number of short elements/ 'strophe'	2 'introductory elements' + 3 + 3 + 3	1–5 'introductory elements' + 4 + 3	0

Values in parentheses: (mean ± SD; N).

*In our terminology, the buzzes of *davidi/suschkini* are synonymous with 'strophes', but these notes are presumably not homologous with the 'strophes' of *thoracicus/przevalskii* and *kashmirensis*, but instead with the buzzes in the strophes of these taxa.

†Both buzzes in each strophe in *kashmirensis*; length of first buzz 105–143 ms (mean 118 ± 0.009), second buzz 164–220 ms (mean 195 ± 0.01).

Table 7. Results from playback tests

	Sources				
Targets	thoracicus	davidi	tacsanowskius	luteoventris	mandelli
przevalskii Huzu Bei Shan	3 (1; 4)	0 (1; 10)	–	–	–
przevalskii Mengda	3 (2; 7)	0 (2; 8)	–	–	–
przevalskii Laoye Shan	3 (1; 4)	0 (1; 5)	–	–	0 (1; 4)
przevalskii Taibai Shan	3 (1; 4)	0 (1; 6)	–	–	–
przevalskii Jiuzhaigou	3 (1; 4)	2 (1; 14*)	0 (1; 4)	0 (1; 4)	0 (1; 4)
davidi Huzong	0 (2; 4)	3 (2; 6)	–	–	–
davidi Taibai Shan	0 (4; 36)	3 (4; 19)	–	–	0 (1; 2)
davidi Jiuzhaigou	0 (1; 14)	3 (1; 3.5)	–	–	–
davidi Wolong	1 (1; 8)	3 (1; 4)	–	1 (1; 2)	–

Numbers refer to strength of response [graded on a four-point scale: no (0), faint (1), medium (2) and strong (3) response], and, in parentheses, number of individuals tested; total duration of playback (minutes).

*The two final minutes were played 1.5 h after the first session (no other taxon was played then).

Table 8. Pairwise genetic distances among and within taxa

Pairwise comparisons	Uncorrected p (%)	GTR + Γ (%)
thoracicus/przevalskii (N = 3) vs. *kashmirensis* (N = 2)	3.5–3.7	5.0–5.5
thoracicus/przevalskii (N = 3) vs. *davidi* and *davidi/suschkini* (N = 5)	4.1–4.4	6.1–6.8
kashmirensis (N = 2) vs. *davidi* and *davidi/suschkini* (N = 5)	4.7–5.2	7.4–8.7
thoracicus (N = 2) vs. *przevalskii* (N = 1)	0.2	0.2
davidi Sichuan and Hebei (N = 4) vs. *davidi/suschkini* Mongolia (N = 1)	0.4–0.5	0.4–0.5
davidi Sichuan (N = 2) vs. *davidi* Hebei (N = 2)	0.2–0.3	0.2–0.3
thoracicus vs. *thoracicus* (N = 2)	0	0
kashmirensis vs. *kashmirensis* (N = 2)	0.2	0.2
davidi Sichuan vs. *davidi* Sichuan (N = 2)	0	0
davidi Hebei vs. *davidi* Hebei (N = 2)	0.1	0.1

Figure 4. Tree for all haplotypes, estimated by Bayesian analysis of cytochrome *b* (1073 bp) under the GTR + Γ model. Posterior probabilities (≥ 50%; 50 000 trees) are indicated above the nodes and parsimony bootstrap values (≥ 50%; 1000 replicates) below the nodes.

SYMPATRY AND HABITAT/ALTITUDINAL DISTRIBUTION

We have observed the *thoracicus* group and *davidi* in sympatry in the breeding season at three localities (Fig. 1). T. E. Ortvad and J. S. Hansen (in litt.) have found them sympatrically at two of these sites, as well as at two additional ones (Emei Shan, Fig. 1; Wawu Shan, Sichuan, *c*. 29.4°N, 103.0°E).

The *thoracicus* group has been found at 2200–3700 m a.s.l. and *davidi* at 1700–3100 m a.s.l. Although there is much altitudinal overlap between the two groups, where they occur sympatrically, they are largely segregated altitudinally (Fig. 5). Partly as a result of the differences in altitude, the two groups were mainly found in different habitats. In central China, *thoracicus* and *przevalskii* were found among herbs and low bushes and in thickets of low bamboo at or just above the tree line, or in similar habitat in forest glades down to several hundred metres below the tree line. In the same region, *davidi* was found among lush herbs and bushes in glades inside deciduous or mixed forest, generally well below the tree line, i.e. in much the same habitat as that in which we have observed *davidi* and *suschkini* in north-east China and Siberia, respectively.

The taxon *kashmirensis* occurs in similar habitat as *thoracicus/przevalskii*. At Manali, Himachal Pradesh, north-west India, we observed *kashmirensis* in herbs and low bushes from just below to above the tree line, at 3200–3600 m, and Price *et al*. (2003) reported it from the same place at 3100–3730 m. At Kedarnath, Uttaranchal, north-west India (*c*. 30.4°N, 79.0°E), R. Raza (in litt.) has found it 'mainly in moist tall herbaceous alpine vegetation, more than two feet in height, at places also dominated by tussock grass *Danthonia cashmeriana*', mainly at 3350–3920 m, but also down to 3100 m, below the tree line, in open herbaceous patches.

Figure 5. Altitudinal distributions of *thoracicus/przevalskii* and *davidi* at three localities in central China where these two groups have been found in sympatry. Includes observations by T. E. Ortvad and J. S. Hansen (in litt.).

DISCUSSION

THE USE OF MULTIPLE CRITERIA IN SPECIES AND SUBSPECIES DELIMITATION

Helbig *et al*. (2002) advocated basing species criteria on multiple, functionally independent, characters, and suggested that for allopatric or parapatric taxa to qualify as species they should be at least as different in these respects as related species coexisting in sym-

patry. Zink (2004) argued that 'Only taxa defined by the congruence of multiple morphological or molecular characters should be recognized at some rank'. We agree that this is a good guideline, which we follow in the delimitation of the taxa in the *B. thoracicus* complex (except for the data-deficient taxon *suschkini*; see below). However, we warn that its stringent application could lead to the rejection of (1) some anciently diverged but still morphologically similar taxa ('cryptic species'); or (2) some recently evolved distinctive taxa with few, albeit fixed, morphological differences but as yet incompletely sorted haplotypes. For example, several *Motacilla* (wagtail) taxa that qualify as species under the 'phylogenetic' species concept *sensu* Cracraft (1983, 1989) differ in essentially one morphological character and are inseparable in other respects, including the genetic markers studied to date (review in Alström & Mild, 2003). Alström & Mild (2003: 30–35) argued that least-inclusive taxa that are believed to have diverged relatively recently be classified as subspecies of the same species. Evidence of recent divergence would be a combination of slight differentiation in morphology (e.g. only a few plumage characters), vocalizations, behaviours and molecular markers in comparison with other closely related taxa, and allopatric/parapatric distributions (often joined by hybrid zones). This is subjective but, as remarked by Lidén (1990), an historical (phylogenetic) 'continuum can only be arbitrarily divided'.

In the *B. thoracicus* complex, data from a wide range of criteria are congruent in the recognition of three main groups, representing the *thoracicus* group, the *davidi* group and *kashmirensis*. The *davidi* group is the most divergent one, and differs from the others in all six variables studied. In contrast, the *thoracicus* group and *kashmirensis* are weakly separable by plumage, except for the 'buffy morph' of the latter, and have similar structure and habitat requirements. An assessment based exclusively on morphology and requiring diagnostic qualitative or quantitative differences might have synonymized *kashmirensis* with the *thoracicus* group (unless the presence of a distinct colour morph in *kashmirensis* would have been considered sufficient to justify recognition of *kashmirensis*) – despite the marked oological, vocal and mitochondrial differences between them. The parapatric *thoracicus–przevalskii* differ only in one of the five variables for which we have data, namely plumage, and these differences are not diagnostic. This probably applies also to *davidi* and *suschkini*, although we have insufficient data on the latter. Thus, the use of multiple criteria has greatly improved the assessment of the taxonomic status of the taxa in the *B. thoracicus* complex.

SPECIES LIMITS IN SYMPATRIC TAXA: *THORACICUS/ PRZEVALSKII* VS. *DAVIDI*

Assessment of taxonomic rank is unproblematic in cases where taxa are sympatric and reproductively isolated from each other (however, see Zink, 2002). In the case of the *thoracicus* and *davidi* groups, the congruent differences in plumage, biometrics, eggs, song, cytochrome *b* and habitat/altitudinal distribution, and results from playback experiments, strongly support the proposal of Round & Loskot (1995) that these two groups be considered separate species. In the area of sympatry in central China, the strikingly different songs probably act as a reproductive isolating barrier. Our playback tests corroborate this, especially the simultaneous test on *przevalskii* and *davidi* on Taibai Shan on 14 June 1995. The single *przevalskii* in Jiuzhaigou that responded strongly to playback of *davidi* is an exception. However, several species have been reported to respond to playback of other closely related sympatric species (e.g. Emlen, Rising & Thompson, 1975; Payne & Groschupf, 1984; Catchpole & Leisler, 1986; Prescott, 1987; Alatalo *et al.*, 1990), or even to distantly related sympatric species that occupy similar niches (Reed, 1982); in both these cases, interspecific territorialism can be assumed to be the cause of the response. Also, some birds may respond to playback of similarly sounding allopatric species that are not closely related (Schottler, 1995; P. Alström & U. Olsson, pers. observ.). Thus, a positive response to playback is of little taxonomic value, while a strong response to playback of own song combined with a lack of response to the song of closely related taxa is of taxonomic importance (as stressed by Alström & Olsson, 1992; Alström, Olsson & Colston, 1997). The partial segregation in habitat and altitude should also contribute to reduce gene flow between *thoracicus/przevalskii* and *davidi*.

SPECIES LIMITS IN GEOGRAPHICALLY SEPARATED TAXA: *THORACICUS/PRZEVALSKII* VS. *KASHMIRENSIS*

For taxa with allopatric distributions, species limits often differ under different species definitions, as well as among proponents of the same species concept. This is equally true for the delimitation of least-inclusive taxa, and is a necessary consequence of a gradual evolutionary process. Under a 'morphological' or 'phylogenetic' species definition (e.g. Rosen, 1978, 1979; Nelson & Platnick, 1981; Cracraft, 1983, 1989; Donoghue, 1985), *kashmirensis* is a distinct species, as it is diagnosably different in multiple, unlinked traits from the other taxa in the *B. thoracicus* complex. Under the 'biological' species definition (Mayr, 1942, 1963), the taxonomic status of *kashmirensis* is debatable. Although *kashmirensis* is poorly

differentiated from the *thoracicus* group in several aspects, the songs of *kashmirensis* and the *thoracicus* group sound so different, at least to the human ear, that they seem likely to act as a premating barrier if these taxa were to meet. Moreover, their cytochrome *b* divergence approaches that between the sympatric *thoracicus* group and *davidi*, and exceeds that among other Old World warbler taxa that are usually treated as conspecific (e.g. Helbig *et al.*, 1996; Drovetski *et al.*, 2004; Martens *et al.*, 2004; Olsson, Alström & Sundberg, 2004; Olsson *et al.*, 2005), indicating long-standing separation (but see Irwin, 2002). In other words, also under the 'biological' species concept, *kashmirensis* is appropriately considered a distinct species.

Species limits in parapatric taxa: *thoracicus* vs. *przevalskii* and *davidi* vs. *suschkini*

The taxa *thoracicus* and *przevalskii* differ only in plumage colours, and the differences are very slight. The variation appears to be clinal and does not fit racial boundaries as currently defined; indeed, different sources describe and/or map the range of *przevalskii* very differently (e.g. Dement'ev & Gladkov, 1968; Etchécopar & Hüe, 1983; Cheng, 1987). Although specimens from the northern part of the range of *przevalskii* are distinctly paler overall and brighter rufous above than *thoracicus*, there appears to be a continuum in these characters over the broad range of the *thoracicus* group in China, and in our view *przevalskii* should therefore be synonymized with *thoracicus*. It should, however, be stressed that the assumption of a close relationship between *thoracicus* from the Himalayas and China is based exclusively on morphology.

Based on the close similarity between *suschkini* and *davidi* in all studied aspects, we consider these to be conspecific. As the only known difference between them, in plumage, appears to be very marginal, *suschkini* is perhaps best synonymized with *davidi*. However, without further study we cannot evaluate the validity of *suschkini*. The genetic distance between *davidi* / *suschkini* from Mongolia and *davidi* from north-east and central China suggests that the Mongolian sample, which was on migration, might represent *suschkini*, and that there may be a slight genetic differentiation between the two taxa.

The *davidi* from central China have longer and more rounded wings (shorter second and third primaries) than *davidi* from Russia, and are actually closer to the *thoracicus* group in these respects. The difference in wing length is too large to be explained by shrinkage of museum specimens (the birds from central China were measured in the field, unlike those from Siberia and north-eastern China), as

wings shrink only 1–3% in specimens (Knox, 1980; Engelmoer *et al.*, 1983). The difference in wing formula between birds from central China and Siberia/north-east China probably reflects the fact that the more northerly breeding populations migrate further than the more southerly nesting ones (Fig. 1); among warblers in general, long-distance migrants have more pointed wings than short-distance migrants (e.g. Ticehurst, 1938; Cramp, 1992; Marchetti, Price & Richman, 1995).

Taxonomic recommendations

We propose that *Bradypterus thoracicus s.l.* should be treated as three separate species: *B. thoracicus* (Blyth, 1845), monotypic; *B. kashmirensis* (Sushkin, 1925), monotypic; and *Bradypterus davidi*, with subspecies *davidi* (La Touche, 1923) and *suschkini* (Stegmann, 1929). The validity of *suschkini* requires further study.

We suggest the following common names: for *B. thoracicus*, Spotted Bush Warbler; for *B. davidi*, Baikal Bush Warbler (already used in Gill & Wright, 2006; in slightly different form, as Baikal Bush-warbler, in Rasmussen & Anderton, 2005); and for *B. kashmirensis*, West Himalayan Bush Warbler.

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APPENDIX 1

Samples used for the molecular study and GenBank accession numbers. ZMUC = Zoological Museum, University of Copenhagen, Denmark; NRM = Swedish Museum of Natural History, Stockholm. b = breeding, m = migrant

Taxon	Locality	Status	Museum no.	GenBank no.	Documentation
B. castaneus castaneus	Sulawesi, Indonesia	b	NRM 20066006	DQ367925	Photo, sound recording
B. tacsanowskius	Hebei, China	m	NRM 20046783	DQ008474	–
thoracicus Sichuan 1	Wolong, Sichuan, China	b	ZMUC 117765	DQ367929	Photo, sound recording
thoracicus Sichuan 2	Emei Shan, Sichuan, China	b	NRM 20056582	DQ367930	Photo, sound recording
'*przevalskii*'	Laoye Shan, NE Qinghai, NC China	b	NRM 20056583	DQ367928	Photo, sound recording
kashmirensis 1	Manali, Himachal Pradesh, India	b	NRM 20056593	DQ367926	–
kashmirensis 2	Manali, Himachal Pradesh, India	b	NRM 20056594	DQ367927	–
davidi Hebei 1	Beidaihe, Hebei, China	m	NRM 20056595	DQ367931	Photo
davidi Hebei 2	Beidaihe, Hebei, China	m	NRM 20056596	DQ367932	–
davidi Sichuan1	Wolong, Sichuan, China	b	ZMUC 117767	DQ367933	Photo
davidi Sichuan2	Wolong, Sichuan, China	b	ZMUC 117768	DQ367934	Photo
davidi/suschkini	C Mongolia (*c.* 44.1°N, 105.6°E)	m	NRM 20056597	DQ367935	Photo