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Integrative taxonomy of the Russet Bush Warbler *Locustella mandelli* complex reveals a new species from central China

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Abstract

Background: The Russet Bush Warbler *Locustella* (previously *Bradypterus*) *mandelli* complex occurs in mountains in the eastern Himalayas, southern China, Vietnam, the Philippines, and Indonesia. The taxonomy has been debated, with one (*L. seebohmi*) to four (*L. seebohmi*, *L. mandelli*, *L. montis* and *L. timorensis*) species having been recognised.

Methods: We used an integrative approach, incorporating analyses of morphology, vocalizations and a molecular marker, to re-evaluate species limits in the *L. mandelli* complex.

Results: We found that central Chinese *L. mandelli* differed from those from India through northern Southeast Asia to southeast China in plumage, morphometrics and song. All were easily classified by song, and (wing + culmen)/tail ratio overlapped only marginally. Both groups were reciprocally monophyletic in a mitochondrial cytochrome *b* (cyt*b*) gene tree, with a mean divergence of 1.0 ± 0.2%. They were sympatric and mostly altitudinally segregated in the breeding season in southern Sichuan province. We found that the Mt Victoria (western Myanmar) population differed vocally from other *L. mandelli*, but no specimens are available. Taiwan Bush Warbler *L. alishanensis* was sister to the *L. mandelli* complex, with the most divergent song. Plumage, vocal and cyt*b* evidence supported the distinctness of the south Vietnamese *L. mandelli idonea*. The Timor Bush Warbler *L. timorensis*, Javan Bush Warbler *L. montis* and Benguet Bush Warbler *L. seebohmi* differed distinctly in plumage, but among-population song variation in *L. montis* exceeded the differences between some populations of these taxa, and mean pairwise cyt*b* divergences were only 0.5–0.9%. We also found that some *L. montis* populations differed morphologically.

Conclusions: We conclude that the central Chinese population of Russet Bush Warbler represents a new species, which we describe herein, breeding at mid elevations in Sichuan, Shaanxi, Hubei, Hunan and Guizhou provinces. The taxonomic status of the other allopatric populations is less clear. However, as they differ to a degree comparable with that of the sympatric *L. mandelli* and the new species, we elevate *L. idonea* to species status, and retain *L. seebohmi* and *L. montis* as separate species, the latter with *timorensis* as a subspecies. Further research should focus on different populations of *L. montis* and the Mt Victoria population of *L. mandelli*.

Keywords: *Bradypterus*, Cryptic species, *Locustella seebohmi*, *Locustella mandelli*, *Locustella montis*, *Locustella timorensis*, *Locustella alishanensis*, *Locustella idonea*, Integrative taxonomy

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Background

Bush warblers in the genera *Locustella* and *Bradypterus* are renowned for being cryptically coloured and difficult to identify except by song (Bairlein et al. 2006; Kennerley and Pearson 2010). These genera occur mainly in scrubby, grassy or reedy habitats at varied elevations, and are difficult to see except sometimes when singing (Bairlein et al. 2006; Kennerley and Pearson 2010). A recent comprehensive molecular phylogeny (Alström et al. 2011) revealed that *Bradypterus* is restricted to Africa, whereas all Asian species studied traditionally placed in that genus should be classified as *Locustella*. In addition, Alström et al. (2011) confirmed that the Marsh Grassbird *L. pryeri*, long placed in *Megalurus*, belongs in *Locustella*, as suggested by both morphology (Morioka and Shigeta 1993) and mitochondrial DNA (Drovetski et al. 2004). Further, African *Bradypterus sensu stricto* are evidently more closely related to the Brown Emutail *B. brunneus* of Madagascar (previously in genus *Dromaeocercus*), African Fan-tailed Grassbird *Schoenicola brevirostris* and the genus *Megalurus* (including Australian *Eremiornis* and *Cincloramphus* that were proposed as synonyms of *Megalurus* by Alström et al. 2011) than to Eurasian *Locustella*. For a review of recent advances in the systematics and taxonomy of these genera, see Alström et al. (2013).

In addition, species level taxonomy has been much confused and debated within *Locustella* and *Bradypterus*, and it has been suggested that several taxa previously regarded as subspecies of polytypic species are better treated as separate species (e.g. Dickinson et al. 2000; Drovetski et al. 2004; Alström et al. 2008, 2011). The Russet Bush Warbler *Locustella mandelli*, which occurs in mountains from Sikkim, eastern Himalayas to western Myanmar, northwestern Thailand, northern Laos, northern Vietnam, southeast and central China, with a disjunct population in southern Vietnam (Figure 1) has a long history of taxonomic confusion. Within the South Asian region it was even erroneously conflated with the superficially similar Brown Bush Warbler *Locustella luteoventris* for many years (Seebohm 1881, Ali and Ripley 1973). However, outside the South Asian region Russet Bush Warbler was generally recognized as a separate species, under the name *Bradypterus seebohmi* (e.g. Watson et al. 1986; Sibley and Monroe 1990), with subspecies *seebohmi* (Luzon, Philippines), *melanorhynchus* (southeast China, Taiwan), *idoneus* (southeast Tibet, northern Thailand, southern Vietnam), *montis* (Java) and *timorensis* (Timor). Other authorities (e.g., Delacour 1943, 1952; Deignan 1963) differed in subspecific and distributional details. Dickinson et al. (2000) revised the Russet Bush Warbler complex based on morphology and vocalizations, showing that the name *mandelli* has priority over *seebohmi* and should be used for the South Asian and Thai populations, and probably also for those from Laos and northern Vietnam, and restricting *idoneus* to southern Vietnam. They tentatively recommended recognition of four species: Benguet Bush Warbler *B. seebohmi sensu stricto* (monotypic; Luzon, Philippines), Timor Bush Warbler *B. timorensis* (monotypic; Timor), Javan Bush Warbler *B. montis* (monotypic; Java, Bali) and Russet Bush Warbler *B. mandelli sensu stricto* (with subspecies *mandelli*, *melanorhynchus* and *idoneus*; continental Asia). The Taiwanese population that had previously been considered either Russet Bush Warbler of the subspecies *melanorhynchus* or *B. luteoventris*, but which has a strikingly different song, was described as a new species, Taiwan Bush Warbler *Locustella* (originally *Bradypterus*) *alishanensis* (Rasmussen et al. 2000). Alström et al. (2011) analysed mitochondrial cytochrome *b* from a few individuals of *L. mandelli* and *L. montis*, and suggested, based on the slight divergences, that their status as separate species should be re-evaluated. *Locustella timorensis*, then only known from two 1932 specimens from Mt. Mutis, Timor (Dickinson et al. 2000), was recently rediscovered, along with a possibly undescribed taxon from nearby Alor (Trainor et al. 2012; Verbelen and Trainor 2012).

In 1987, P.A. and U.O. noticed that the song of *Locustella mandelli* in Sichuan province, China differed markedly from *L. mandelli* songs in northwestern Thailand. This was later noted by Dickinson et al. (2000), and Xia et al. (2011) reported the discovery of *L. mandelli* in Guizhou province with similar song to Sichuan birds; however, the implications of these song differences were not considered further by these authors. Since then, we have been collecting data on this complex in the field, mainly in China, and in museums and the lab. We here report the results from these studies, based on morphology, vocalizations, mitochondrial DNA and geographical distributions, and revise the taxonomy of the *L. mandelli* complex.

Methods

Study group, taxonomy and nomenclature

We analysed all valid members of the *Locustella mandelli* complex (*L. m. mandelli*, *L. m. melanorhyncha*, *L. m. idonea*, *L. seebohmi*, *L. montis*, *L. timorensis*), as well as *L. alishanensis*, sister to *L. mandelli* and *L. montis* (Alström et al. 2011) (the latter study included only *L. mandelli*, *L. montis*, and *L. alishanensis*). Taxonomy and distribution of subspecies herein follow Dickinson (2003), and English names follow Gill and Donsker (2014). Henceforth in this text, *Locustella* (or *L.*) *mandelli* and other names that include generic names refer to species, whereas *mandelli* and other names without generic names represent the least-inclusive taxon, i.e. monotypic species or subspecies of polytypic species. The endings of the following names were changed to agree in gender with the genus name when the taxa were moved from *Bradypterus* to *Locustella*:

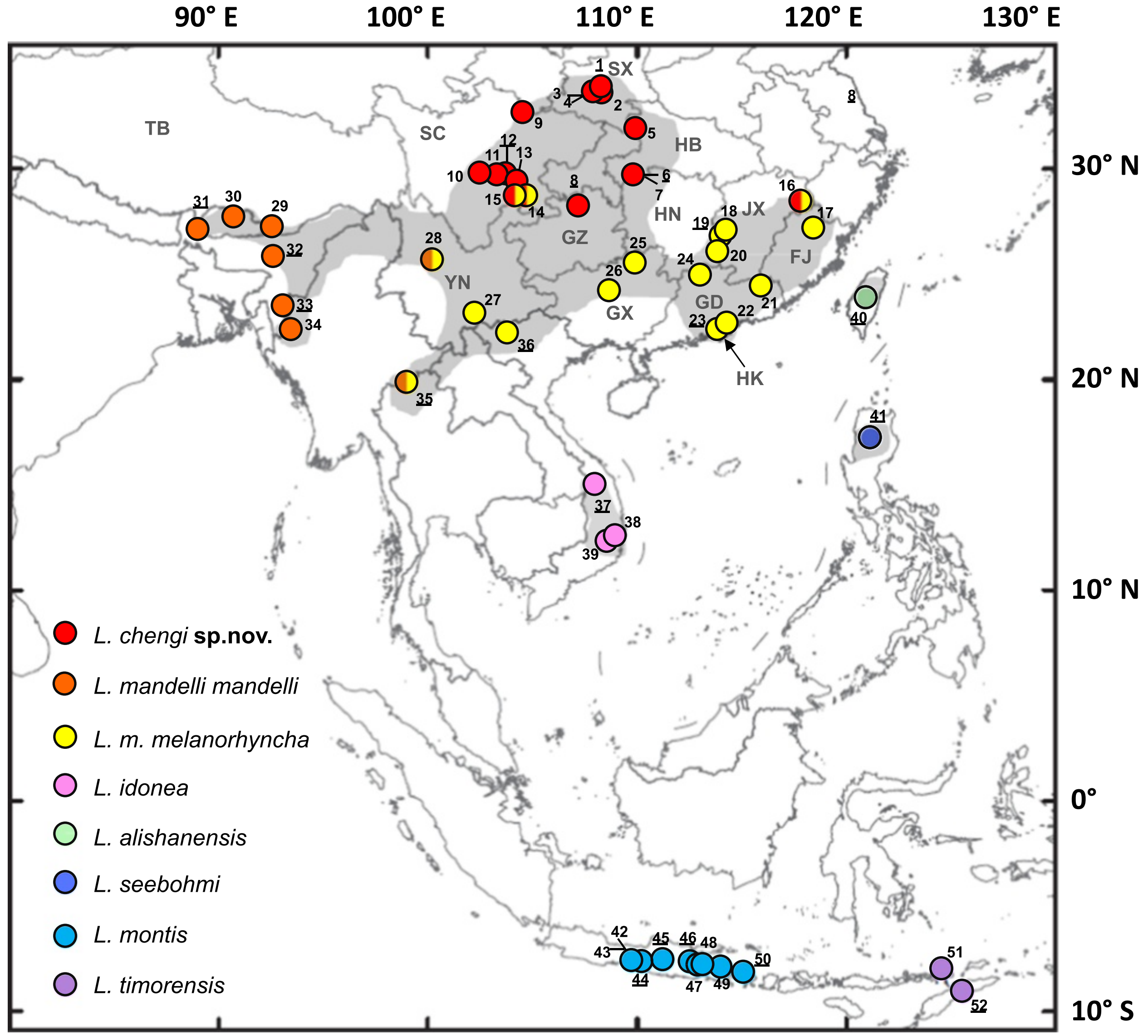

Figure 1 Map showing the distribution of members of the *Locustella mandelli* complex, with localities from which we have sound recordings and/or DNA samples (latter underscored; details in Additional file 1: Table S1). The bicoloured red + yellow circles are places where both *L. chengi* sp. nov. and *L. mandelli* have been found in sympatry; bicoloured orange and yellow circles are places where the subspecific status is uncertain. Chinese provinces: FJ – Fujian, GD – Guangdong, GX – Guangxi, GZ – Guizhou, HB – Hubei, HK – Hong Kong, HN – Hunan, JX – Jiangxi, SC – Sichuan, SX – Shaanxi, TB – Tibet, YN – Yunnan.

melanorhynchus to *melanorhyncha* and *idoneus* to *idonea*. For clarity, we refer to the new species as Sichuan Bush Warbler because it is widespread in Sichuan and this is where we first observed it.

Morphology

Almost all then-known specimens of the *Locustella mandelli* complex were studied and measured by P.C.R. for Dickinson et al. (2000) and Rasmussen et al. (2000), and are listed with registration numbers in Dickinson et al. (2000). Many specimens, including all key taxa, were re-examined and re-measured by P.C.R. in 2013–2014 for the present study at AMNH, BMNH, FMNH, MNHN, MZB, NNM and NMNH (full museum names given in Acknowledgements), with the addition of a newly collected specimen of *L. mandelli idonea* (KUMNH 122801), two previously misidentified *L. mandelli* (FMNH 306050, 306051: Sikkim), and specimens from KIZ (not previously examined), IOZ and BNU (most of which were recently collected). All measurements of museum specimens were taken by P.C.R.; those of live birds (treated separately) were taken by P.A. and P.J.L.; for comparison, P.A.'s and P.J.L.'s measurements of *L. mandelli* are also included separately, except for 2014 live birds for which P.A. took measurements with instruction on methods from P.C.R.

Measurements (in mm, using digital calipers) used in this study include: culmen from skull; culmen from feathers; bill height (depth) and width at distal edge of nares; wing length (flattened); shortfalls of primaries 1–5 (numbered ascendantly, for consistency with previous studies on this group: Dickinson et al. 2000; Rasmussen et al. 2000) in relation to the wing tip; lengths of primaries 1 and 2 from the distal edge of the primary coverts; tarsus length; tarsus proximal depth, minimum width and depth, and distal width; length of middle toe claw and hind claw from distal edge of scute; tail length (with calipers inserted between central pair of rectrices); maximum width of central rectrices; longest undertail-covert length from pygostyle; shortfall of longest undertail-covert to tail tip; and maximum width of pale undertail-covert tips. A few ratios between measurements were calculated; "(wing + culmen)/tail" refers to wing length plus culmen length (to skull) divided by tail length.

Thirteen external plumage and soft-part colours were scored by P.C.R. on skin specimens using a 10-point scale for each character, as follows: lower mandible colour (1 = all pale–10 = all black); upperparts colour (1 = cold brown–10 = very warm brown); supercilium prominence (1 = none–10 = strong); throat ground colour (1 = white–10 = solid dark); throat speckling (1 = none–10 = heavy); breast ground colour (1 = brown–10 = solid grey); breast speckling (1 = none–10 = heavy); upper flank markings (1 = none–10 heavy); flank colour (1 = cold brown–10 = rich russet); undertail-coverts ground colour (1 = medium brown–10 = dark brown); undertail-coverts pale tip contrast (1 = none–10 = strongly contrasting); undertail-coverts pale tip maximum breadth (1 = none–10 = broad); leg colour (1 = all pale–10 = all dark).

Univariate and multivariate statistics were analysed in MYSTAT v. 12.02.00 (SYSTAT Software). For tests of significance between univariate measurements and ratios of taxa for which we had at least seven individuals, two-sample *t*-tests were done, with Bonferroni-adjusted *p*-values. Due to small sample sizes and the preponderance of unsexed and questionably sexed specimens, sexes were pooled. Bonferroni-adjusted significant differences (pooled variances) are from two-sample *t*-tests between *L. m. mandelli* and *L. m. melanorhyncha* (*sensu stricto*; including Laos and Tonkin birds), Sichuan Bush Warbler, and *L. montis*. Plumage scores were tested for significance using Kruskal-Wallis two-way AOVs, but because many specimens at different museums could not be directly compared, only highly significant plumage differences were considered important. PCAs were done in MYSTAT using covariance matrices. For one PCA on morphometrics, in order to compare more directly with the Sichuan Bush Warbler (all of which were males), only males and unsexed specimens (assuming most unsexed birds are likely to be males, given the difficulty of collecting females) were included. Also, one of the three *idonea* specimens is missing its bill, so a PCA of external measurements excluded bill measurements in order to maximise the number of specimens of this taxon that could be included.

Song

We obtained sound recordings of songs of all taxa. In total, we obtained 166 recordings of the *Locustella mandelli* complex (excluding *L. alishanensis*) from across its range, of which 159 were analysed (Figure 1, Additional file 1: Table S1). Sonograms were created in Raven Pro 1.4 (Bioacoustics Research Program 2011). Before analysis, the sampling frequency was set to 48 kHz and sampling depth to 24 bits (however, it was not always possible to change sampling depth). We measured duration (s), maximum frequency (maxfreq), minimum frequency (minfreq), mid-frequency (the frequency that divides the selection into two frequency intervals of equal energy) and bandwidth 90% for the lower-amplitude (grey in sonogram) initial part of a note (lowamp), and the same for the higher-amplitude (solid black part in a sonogram) terminal part (highamp) of the note in a "strophe" (Figure 2) (bandwidth 90% is the frequency range that divides the selection into two frequency intervals containing 5% and 95% of the energy; Charif et al. 2010). Five "strophes" per individual were measured (or the maximum number of strophes in recordings of fewer than five strophes). For *mandelli/melanorhyncha* and Sichuan Bush Warbler, which have a secondary element in addition to the main (principal) note (Figure 2), we took the same measurements for the secondary note, as well as the total duration of the "strophe". The mean of the five (or fewer) recordings for each individual were used in the analyses. A Discriminant Function Analysis (DFA) of the song variables was carried out in SPSS Statistics version 20 (IBM Corp.); *mandelli* and Sichuan Bush Warbler were analysed, both together with all other taxa based on 11 variables and separately from the others, with seven additional variables.

DNA

DNA was extracted using QIA Quick DNEasy Kit (Qiagen, Inc), according to the manufacturer's instructions, but with 30 μl DTT added to the initial incubation step for extraction from feathers and toepads. We sequenced the mitochondrial cytochrome *b* (cyt*b*) gene for all samples. Amplification and sequencing of the fresh samples followed the protocols described in Olsson et al. (2005). Toepads were sequenced with specifically designed primers amplifying short (95–315 bp, median 180 bp), partly overlapping fragments. All sequences have been submitted to GenBank (Additional file 1: Table S1).

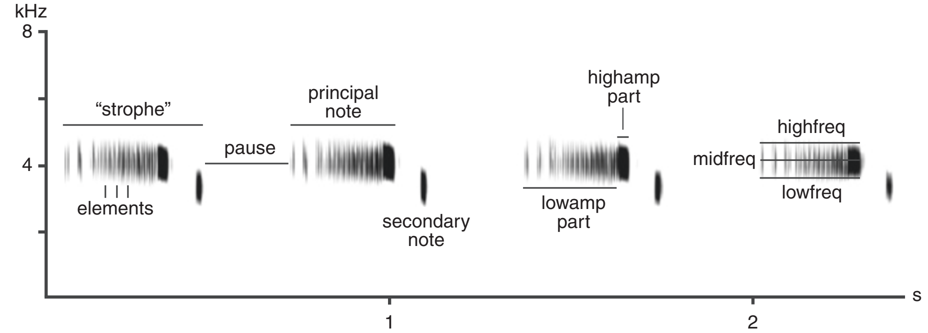

Figure 2 Sonogram terminology. Part of continuous song (four strophes) of Locustella mandelli mandelli Mt Victoria, Myanmar, 1700/1800 m, mid-April 2000 (AV 19008) (Per Alström).

Sequences were aligned and checked using Geneious 7.0.6 (Biomatters Ltd.). The HKY model (Hasegawa et al. 1985) was the best-fit model for the phylogenetic analysis according to the Bayesian Information Criterion (BIC) calculated in jModeltest 0.1.1 (Posada 2008a, b). The analyses were run in MrBayes 3.2 (Huelsenbeck and Ronquist 2001) assuming rate variation across sites according to a discrete gamma distribution with four rate categories (Γ; Yang 1994) or with an estimated proportion of invariant sites (I; Gu et al. 1995), as these had very similar BIC values. The analyses were also run using the "mixed" command to sample across the GTR model space in the Bayesian MCMC (Huelsenbeck et al. 2004) + Γ, as well as partitioned by codon, using rate multipliers to allow different rates for different partitions (Ronquist and Huelsenbeck 2003; Nylander et al. 2004), with the HKY model plus an estimated proportion of invariant sites (I; Gu et al. 1995) for the first position and the HKY model for the second and third positions. Default priors were used. Four Metropolis-coupled MCMC chains with incremental heating temperature 0.1 were run for 5×10^6 generations and sampled every 1000 generations. Convergence to the stationary distribution of the single chains was inspected in Tracer 1.5.0 (Rambaut and Drummond 2009) using a minimum threshold for the effective sample size. The joint likelihood and other parameter values reported large effective sample sizes (>1000). Good mixing of the MCMC and reproducibility was established by multiple runs from independent starting points. Topological convergence was examined by eye and by the average standard deviation of split frequencies (<0.005). The first 25% of generations were discarded as "burn-in", well after stationarity of chain likelihood values had been established, and the posterior probabilities were calculated from the remaining samples (pooled from the two simultaneous runs).

The data were also analysed in BEAST version 1.8.1 (Drummond and Rambaut 2007, 2014). Xml files were generated in BEAUti version 1.8.1 (Rambaut et al. 2014). Analyses were run under the general time-reversible (GTR) model (Lanave et al. 1984; Tavaré 1986; Rodríguez et al. 1990) + Γ model (cf. Weir and Schluter 2008), using an uncorrelated lognormal relaxed clock model (Drummond et al. 2006) with the mean rate of 2.1%/MY (Weir and Schluter 2008) and either a "birth-death incomplete sampling" species tree prior or a coalescent constant size population prior. Other priors were used with default values. 50×10^6 generations were run, sampled every 1000 generations. Every analysis was run twice. The MCMC output was analysed in Tracer version 1.5.0 (Rambaut and Drummond 2009) to evaluate whether valid estimates of the posterior distribution of the parameters had been obtained. The first 25% of the generations were discarded as "burn-in", well after stationarity of chain likelihood values had been established. Trees were summarized using TreeAnnotator version 1.8.1 (Rambaut and Drummond 2014), choosing "Maximum clade credibility tree" and "Mean heights", and displayed in FigTree version 1.4.0 Rambaut (2012).

Maximum likelihood bootstrapping (MLBS) was also performed. 1000 replicates were run with RAxML-HPC2 8.0.24 (Stamatakis 2006; Stamatakis et al. 2008) on the Cipres portal (Miller et al. 2010). The data were unpartitioned, and as per default GTRCAT was used for the bootstrapping phase, and GTRGAMMA for the final tree inference.

Pairwise cyt*b* distances were calculated in MEGA 6.06 (Tamura et al. 2013), both uncorrected p and maximum Composite Likelihood + Γ.

Results

Morphology

The rather slight differences among the taxa in the *Locustella mandelli* complex have been detailed elsewhere (see e.g. Dickinson et al. 2000; Rasmussen et al. 2000), but Sichuan Bush Warbler was conflated therein with *L. mandelli melanorhyncha*. The following therefore adds to and amends Dickinson et al. (2000).

Locustella mandelli melanorhyncha

The taxon treated in Dickinson et al. (2000) as *melanorhyncha* and as confined to SE China differs from *mandelli* only in its slightly smaller size. However, this is only the case when birds from eastern Southeast Asia are included with SE Chinese birds (Figures 3 to 4). We therefore (as explained in the Discussion) provisionally treat *L. m. melanorhyncha* as occurring from at least N Laos through N Vietnam and SE China, and we cannot determine to which of these taxa Sichuan birds belong so we refer to them as *mandelli*/*melanorhyncha*.

Sichuan Bush Warbler

The Sichuan Bush Warbler is most similar to *L. m. mandelli*/*melanorhyncha*, to which specimens have long been ascribed. Compared to these, Sichuan Bush Warbler is typically greyer (less russet) above and on the breast-sides and flanks (Figures 5 to 6); however, this difference does not always hold (e.g., of one *mandelli/melanorhyncha* and one Sichuan Bush Warbler caught together on Laojun Shan, Pingshan county, Sichuan on 27 May 2014, the latter was marginally more russet above). Of all characters for which plumage scoring was done, only upperpart color was highly significantly different between *mandelli* and the Sichuan Bush Warbler (Table 1). In a PCA of plumage scores (Figure 7), Sichuan Bush Warbler clustered together in morphospace with many *mandelli/melanorhyncha*, the similarities in most characters obscuring the typical difference in upperparts color in this analysis.

In univariate measurements from skin specimens (Table 1), Sichuan Bush Warbler has significantly longer culmen than *melanorhyncha* (but not *mandelli*), and its wing is significantly longer than in *mandelli* and especially *melanorhyncha*. The shortfall of P1 is significantly greater in Sichuan Bush Warbler than in *melanorhyncha*, and P2 length and primary projection average greater in Sichuan Bush Warbler than in *mandelli*/*melanorhyncha*, although these measures are likely correlated with wing length. The tail of Sichuan Bush Warbler is significantly shorter than in *mandelli*/*melanorhyncha*, and has little overlap with *mandelli*, but greater overlap with *melanorhyncha*. The central rectrices of Sichuan Bush Warbler are significantly narrower than in *mandelli*, but not than in *melanorhyncha*, likely due to small sample sizes. The distance between the longest undertail-coverts and the tail tip is significantly shorter in Sichuan Bush Warbler than in *mandelli*/*melanorhyncha*, although this character is likely correlated with the short tail of Sichuan Bush Warbler. The wing/tail ratio of Sichuan Bush Warbler is significantly greater than in *mandelli*/*melanorhyncha*. (Wing + culmen)/tail ratios (Figure 8, Table 1) are highly significantly different between Sichuan Bush Warbler and *mandelli*/*melanorhyncha* and discriminate them fairly well, but with some overlap between Sichuan Bush Warbler and *mandelli*.

For univariate comparisons between *L. m. mandelli* and *L. m. melanorhyncha*, only culmen and wing length were significantly different between the two taxa, being shorter in *melanorhyncha* (Table 1).

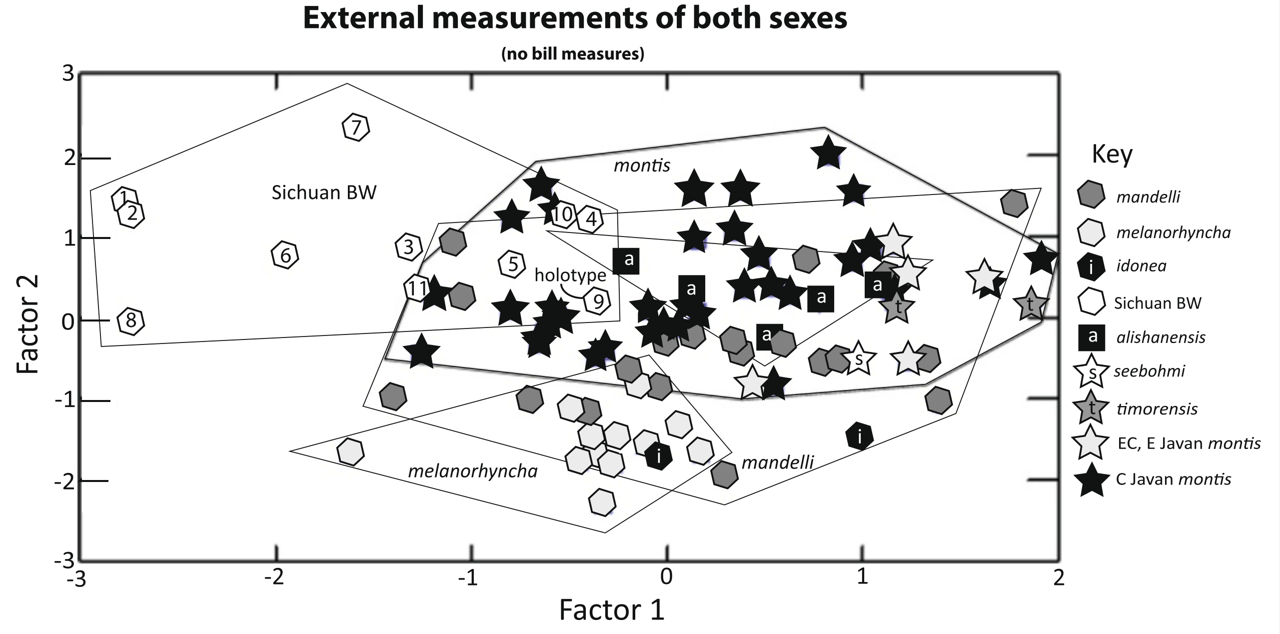

Figure 3 Principal components analysis of external measurements (not including bill measurements, to maximize inclusion of specimens) of both sexes of all recognized taxa of the *Locustella mandelli* complex and *L. alishanensis.* Sichuan BW = Sichuan Bush Warbler. Numbers within white polygons refer to specimens listed in Table 4.

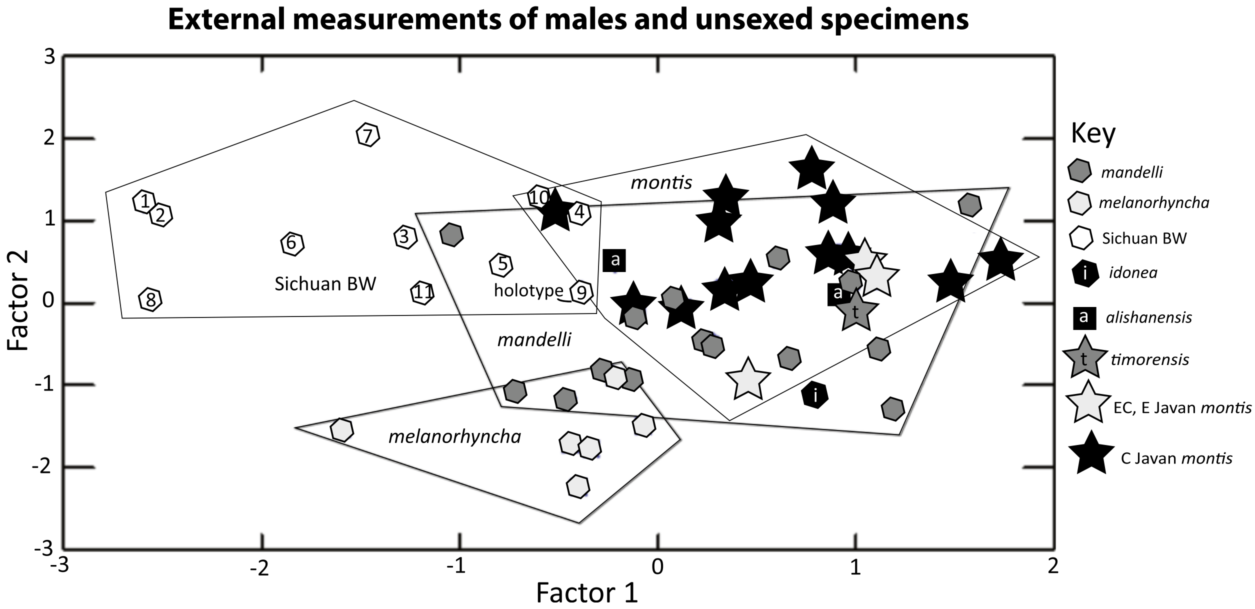

Figure 4 Principal components analysis of external measurements of males and unsexed individuals only of all recognized taxa of the *Locustella mandelli* complex and *L. alishanensis*.

In a PCA of external measurements (excluding bill) of both sexes (Figure 3), about half (5 of 11) of the specimens of Sichuan Bush Warbler form a distinct cluster on Factor 1 (which is influenced most heavily by tail length; Additional file 2: Table S2), although four Sichuan Bush Warblers (including the holotype) overlap with, and two others are very close to, *L. m. mandelli* on Factor 1. On this same PCA, all Sichuan Bush Warblers are well-separated from *melanorhyncha* on Factor 2, which most strongly reflects a contrast between wing and primary lengths vs. tail length (Additional file 2: Table S2). In a PCA of external measurements of only males and unsexed specimens (most of which are likely to be males given their greater likelihood of detection and collection; Figure 4), Sichuan Bush Warblers overlap in morphospace with just one *mandelli* (an unsexed individual). In fact, all *mandelli* that overlap the Sichuan Bush Warbler on PC1 scores (in which tail length is much the most important) are unsexed, and therefore may well be females. A PCA in which only *mandelli*, *melanorhyncha*, and the Sichuan Bush Warbler are included (not figured here) did not differ materially from that in which all taxa are included, either in relative separation of these taxa or in relative contributions of the variables.

Locustella mandelli idonea

We examined the three known specimens of *L. m. idonea* (USNM 359220, BMNH 1919.12.20.376: both Da Lat, Annam, southern Vietnam; and KUMNH 122801: Vietnam; Kom Tum Province; Ngoc Linh Nature Reserve, 1750 m; m, testes 3×1; in molt). As one (the BMNH specimen) has an unmeasurable bill, and another (the KUMNH specimen) is in tail molt, only one *idonea* specimen can be fully measured. Compared to the other taxa, *idonea* has a fairly short wing and fairly long tail, hence a low wing/tail ratio, and short primary projection (Table 1). All *idonea* specimens differ from *L. m. mandelli* in their colder upperpart colour, whiter, more prominent supercilium, clean white throat and belly, and weak pale brownish or very pale grey breast with at most a few distinct round dark speckles on the upper breast. On a PCA of plumage scores (Figure 7), this taxon occupies mostly unique morphospace, reflecting the strong supercilia and drab upperparts. Two photos of *idonea* (http://orientalbirdimages.org/) show a bird very similar in plumage to the specimens.

Locustella seebohmi

Only a single specimen of *L. seebohmi* (AMNH 592174) is known. It is similar to some *L. m. mandelli/melanorhyncha* and the Sichuan Bush Warbler, with which it clusters on a PCA of plumage scores (Figure 7). However, the *L. seebohmi* specimen has very drab brown (not russet-tinged) flanks, and is relatively large (especially for a female). It differs from adult *L. montis* in its strong white supercilium broadly reaching the bill and ending over the eye, in being greyer below, and in lacking upper flanks streaking. Most individuals of a series putatively identified as this taxon were earlier reidentified as Luzon Bush Warbler *Cettia seebohmi* (Dickinson et al. 2000),

Figure 5 ***Locustella chengi*** **sp. nov., adult male (sexed by song and later in hand by prominent cloacal protuberance and lack of brood patch), Laojun Shan, Sichuan, China, 1350 m, 27 May 2014 (IOZ19663; same individual as in Figures 6a and 11a).** (Bo Dai)

but it was unknown whether this was also true for a specimen exchanged to IOZ as *L. seebohmi* (the former USNM 208499, now IOZ 59981). We have examined this specimen and it is indeed *C. seebohmi*, not *L. seebohmi*.

Locustella montis

Javan *L. montis* is the most distinctive taxon in plumage (Figure 7). It is the largest taxon, especially in bill and feet (Figures 3 to 4, Table 1), with long, broad, round-tipped tail; it is dark and richly colored above, with dark warm brown flanks, and very dark brown, broad, prominently pale-tipped undertail-coverts. It is very dark-crowned with a narrow, poorly marked supercilium and eyestripe, and dark grey auriculars. Adult male (and most adult female) specimens of *L. montis* are distinctively heavily marked below. Presumed first-winter birds and some females lack streaking and are very similar to *L. mandelli* and *L. seebohmi*.

Of the 30 adult *L. montis* at NNM from Sikatok, Bagelen (Mt Sundoro, approximately 7°18'S, 110°00'E, a minor correction from coordinates given in Dickinson et al. 2000), C Java, most have distinctly whitish breasts. However, most others from mountains to the east (Mt Lawu, EC Java and Mt Arjuno, E Java) show strongly grey breasts. Also, EC and E Javan birds are mostly longer-tailed than C Javan birds (tail length EC, E Java: mean = 62.5 mm, SD = 1.51, $n = 7$; Mt Sundoro/Sumbing: mean = 58.7 mm, SD = 3.26, $n = 34$), so there seems to be undescribed taxonomic variation within Java.

There are no *Locustella* specimens from Bali. However, a detailed plumage description of a Bali bird (in Dickinson et al. 2000) does not obviously differ from *L. montis*.

Locustella timorensis

The only specimens of *L. timorensis* are two March 1932 birds from Mt Mutis, Timor (AMNH 308007, 345901). The two *L. timorensis* specimens have relatively long tarsi, and their tails are long and narrow (Table 1). They differ from others of the complex (less so from *L. alishanensis*; see below) in their paler, brighter upperparts, their inconspicuous, narrow pale tips to paler brown undertail-coverts, and their long, narrow rectrices with relatively pointed tips. The labels of both *L. timorensis* specimens have gonad drawings that show they are breeding adults, so their tail shape is not due to immaturity.

No specimens exist from the taxon recently discovered on Alor (Trainor et al. 2012; Verbelen and Trainor 2012), but there are a few photographs of birds from there (http://orientalbirdimages.org). Of these, at least one shows more grey on the breast and a less obvious pale supercilium than the Timor specimens. However, *timorensis* plumage is probably more variable than known, and Alor birds might differ taxonomically from *timorensis*.

Locustella alishanensis

Locustella alishanensis is diagnosable morphologically on a combination of subtle structural and plumage characteristics (Rasmussen et al. 2000, modified by reference to recent photos): relatively slim bill; rather long wing; rather long tarsi and large feet; drab, rather pale brown upperparts; fairly prominent pale supercilium above dark lores; small pale throat patch; pale brownish-grey to mid-grey breast; speckling (if present) restricted mainly to lower throat; brownish auriculars; and nearly uniform dull brown undertail-coverts. It is superficially most similar to *L. timorensis*, but has darker browner auriculars, weaker supercilium, and finer bill. However, *L. alishanensis* does not occupy unique morphospace in PCAs in this study (Figures 3 to 4, 7).

Song

The songs of all taxa except *L. alishanensis* are basically rather similar, and in all there is at least some individual variation that can be observed in sonograms, and often readily heard (Figures 9, 10, 11). We have no evidence that

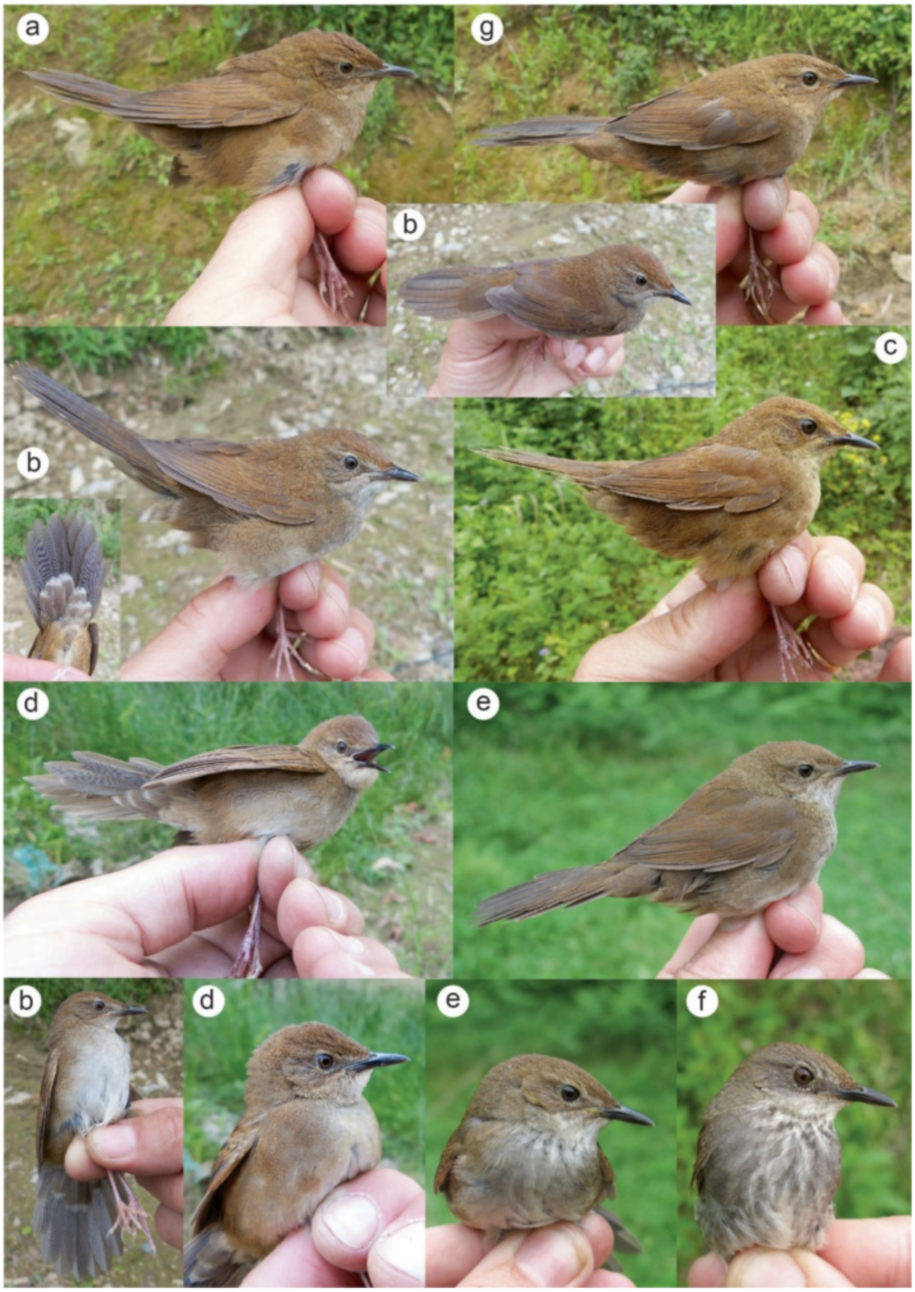

Figure 6 ***Locustella chengi*** **sp. nov. (a–f) and** ***L. mandelli mandelli/melanorhyncha*** **(g), all adults, identified as males by song (and prominent cloacal protuberance and lack of brood patch in a–d and g, not checked in e–f). a**: Laojun Shan, Sichuan, China, 1350 m, 27 May 2014 (IOZ19663; same individual as in Figures 5 and 10a) (Per Alström); **b**: Longcangguo, Sichuan, China, 1785 m, 27 May 2013 (IOZ19662; same individual as in Figures 5 and 10b) (Per Alström); **c**: Laojun Shan, Sichuan, China, 1040 m, 27 May 2014 (IOZ19665; same individual as in Figure 10d) (Per Alström); **d**: Longcangguo, Sichuan, China, 1810 m, 26 May 2013 (IOZ19661); **e**: Badagong Shan, 1615 m, 5 June 2010 (same individual as IOZ19989 in Figure 14) (Paul J. Leader); **f**: an individual with exceptionally strongly marked throat/breast, Badagong Shan, 1500 m, 6 June 2010 (same individual as IOZ 19991 in Figure 14) (Paul J. Leader); **g**: Laojun Shan, Sichuan, China, 1350 m, 27 May 2014 (IOZ19664; same individual as in Figures 10d and 14) (Per Alström).

a single male can sing more than a single type. The song of *L. m. mandelli*/*melanorhyncha* from the Himalayas, Myanmar, Thailand, northern Vietnam and south China (Yunnan, Guangxi, Guangdong, Hong Kong, Jiangxi, Fujian, southeast Hunan and south Sichuan; Figures 9, 10, Table 2, Additional file 3: Table S3), consists of "strophes" made up of a high-pitched, drawn-out, rasping principal note that progressively increases in loudness (amplitude), and is

Table 1 Univariate measurements of morphometrics of the *Locustella mandelli* complex and *L. alishanensis*

	Taxon								**Significance levels**				
Variable	***Mandelli***	***Melanorhyncha***	**Sichuan BW**	***Idonea***	***Alishanensis***	***Seebohmi***	***Timorensis***	***Montis***	***Mandelli vs. melanorhyncha***	***Mandelli vs.* Sichuan BW**	***Melanorhyncha vs.* Sichuan BW**	***Mandelli + melanorhyncha vs. montis***	**Sichuan BW *vs. montis***
Culmen l from skull	14.40 ± 0.43 (13.6–15.2; 30)	13.60 ± 0.43 (12.7–14.1; 16)	15.14 ± 0.66 (14.1–16.2; 10)	14.10 ± 1.13 (13.3–14.9; 2)	14.38 ± 0.52 (13.6–15.1; 6)	14.2	14.60 ± 0.28 (14.4–14.8; 2)	15.21 ± 0.79 (13.1–16.9; 39)	***		***	***	
Culmen length from skull (P.A./P.J.L.)		13.3(12.7–14; 5)	14.7(13.5–15.6; 13)										
Culmen length from feathers	10.74 ± 0.41 (9.9–11.6; 30)	10.14 ± 0.43 (9.3–10.8; 16)	11.09 ± 0.63 (10.3–12.2; 11)	10.45 ± 0.92 (9.8–11.1; 2)	10.05 ± 0.52 (9.1–10.6; 6)	11.0	10.75 ± 0.07 (10.7–10.8; 2)	11.26 ± 0.69 (10.0–12.9; 40)	**		*	***	
Bill depth from distal nostrils	3.07 ± 0.16 (2.7–3.4; 32)	3.04 ± 0.13 (2.7–3.2; 18)	3.14 ± 0.20 (2.8–3.5; 12)	3.10 ± 0.14 (3.0–3.2; 2)	2.95 ± 0.19 (2.7–3.2; 6)	3.2	3.20 ± 0.0 (3.2; 2)	3.31 ± 0.21 (2.9–3.6; 38)				***	
Bill depth from distal nostrils (P.A./P.J.L.)		3.0(3.0; 3)	3.1(2.8–3.3; 7)										
Bill width from distal nostrils	2.76 ± 0.18 (2.4–3.2; 33)	2.67 ± 0.22 (2.3–3.0; 18)	2.95 ± 0.22 (2.6–3.4; 11)	2.9 ± 0.0(3)	2.53 ± 0.14 (2.3–2.7; 6)	2.9	2.65 ± 0.35 (2.4–2.9; 2)	2.93 ± 0.21 (2.4–3.5; 41)				***	
Bill width from distal nostrils (P.A./P.J.L.)		3.0(2.9–3.1; 2)											
Wing length (flattened)	52.54 ± 2.36 (49.0–57.0; 33)	50.30 ± 1.07 (48.0–52.0; 17)	55.23 ± 1.31 (53.0–58.0; 11)	51.33 ± 1.16 (50.0–52.0; 3)	54.75 ± 1.54 (53.0–57.5; 6)	52.0	53.50 ± 0.71 (53.0–54.0; 2)	53.81 ± 1.82 (49.5–57.0; 42)	***	**	***	***	
Wing length (P.A./P.J.L.)		51.5(49–55; 5)	56.07 (53.0–57.5; 13)										
P1 shortfall	23.63 ± 1.63 (20.7–28.4; 30)	22.36 ± 1.12 (21.0–25.1; 18)	25.06 ± 1.61 (22.8–27.9; 11)	22.67 ± 1.17 (21.8–24.0; 3)	24.45 ± 1.19 (22.8–26.0; 6)	24.3	24.95 ± 0.50 (24.6–25.3; 2)	24.33 ± 1.59 (20.0–28.0; 41)			**	*	
P2 shortfall	8.97 ± 1.11 (7.0–10.9; 29)	9.02 ± 1.11 (6.5–11.3; 18)	8.97 ± 1.90 (6.0–13.7; 11)	8.90 ± 1.01 (8.0–10.0; 3)	9.63 ± 0.44 (9.1–10.3; 6)	9.5	10.65 ± 1.49 (9.6–11.7; 2)	10.58 ± 1.19 (8.0–13.2; 41)				***	
P3 shortfall	2.11 ± 0.84 (0–3.6; 28)	2.14 ± 0.55 (1.0–3.1; 18)	1.60 ± 0.37 (1.0–2.0; 9)	1.27 ± 1.10 (0–2.0; 3)	2.55 ± 0.75 (1.6–3.3; 6)	2.5	1.75 ± 1.06 (1.0–2.5; 2)	2.61 ± 0.80 (1.0–4.0; 41)					***
P4 shortfall	0.49 ± 0.60 (0–1.7; 29)	0.37 ± 0.44 (0–1.0; 18)	0.00 ± 0.00 (0; 9)	0.17 ± 0.29 (0–0.5; 3)	1.05 ± 0.84 (0–1.8; 6)	1.0	0.35 ± 0.21 (0.20–0.50; 2)	0.46 ± 0.59 (0–2.0; 40)					
P5 shortfall	0.03 ± 0.19 (0–1.0; 29)	0.08 ± 0.26 (0–1.0; 18)	0.11 ± 0.22 (0–0.5; 9)	0 ± 0(3)	0.18 ± 0.30 (0–0.7; 6)	0	0 ± 0(2)	0 ± 0(40)					
P1 length	14.16 ± 1.30 (11.3–16.1; 30)	14.38 ± 1.09 (13.1–16.4; 18)	15.76 ± 1.67 (12.9–19.0; 11)	14.10 ± 0.17 (14.0–14.3; 3)	14.47 ± 1.53 (12.4–16.8; 6)	13.4	13.90 ± 1.27 (13.0–14.8; 2)	15.20 ± 1.20 (14.0–16.4; 3)					
P2 length	28.31 ± 1.52 (25.9–32.2; 27)	27.35 ± 1.72 (24.4–29.9; 16)	31.88 ± 2.47 (29.0–37.1; 9)	27.90 ± 0.95 (26.9–28.8; 3)	28.63 ± 1.41 (26.7–30.8; 6)	27.8	27.90 ± 0.99 (27.2–28.6; 2)	30.10 ± 0.36 (29.7–30.4; 3)			**	***	
Primary projection	6.88 ± 0.96 (4.9–8.9; 27)	6.58 ± 1.36 (4.1–8.2; 12)	8.10 ± 1.58 (5.3–10.2; 9)	4.95 ± 0.07 (4.9–5.0; 2)	5.42 ± 0.71 (4.4–6.0; 4)	5.9	5.90 ± 1.27 (5.0–6.8; 2)	6.90 ± 1.81 (5.0–8.6; 3)					
Tarsus length	19.00 ± 0.96 (16.7–21.3; 34)	18.63 ± 0.77 (17.0–20.1; 18)	18.30 ± 0.77 (16.8–19.8; 11)	18.75 ± 0.65 (18.1–19.4; 3)	19.53 ± 0.72 (18.4–20.6; 6)	19.7	19.50 ± 0.14 (19.4–19.6; 2)	20.72 ± 0.67 (19.2–22.5; 41)				***	***
Tarsus length (P.A./P.J.L.)		17.3(16.6–17.7; 3)	18.3 (17.5–19.4; 13)										

Table 1 Univariate measurements of morphometrics of the *Locustella mandelli* complex and *L. alishanensis* *(Continued)*

Tarsus proximal depth	2.38 ± 0.21 (1.8–2.7; 33)	2.28 ± 0.22 (1.7–2.5; 16)	2.43 ± 0.14 (2.2–2.7; 9)	2.33 ± 0.23 (2.2–2.6; 3)	2.58 ± 0.23 (2.4–3.0; 6)	2.6	2.70 ± 0.0(2)	2.86 ± 0.17 (2.6–3.3; 40)				***	***
Tarsus distal width	2.56 ± 0.15 (2.3–3.0; 32)	2.48 ± 0.15 (2.2–2.7; 17)	2.54 ± 0.07 (2.5–2.6; 9)	2.53 ± 0.32 (2.3–2.9; 3)	2.75 ± 0.15 (2.5–2.9; 6)	2.7	2.85 ± 0.07 (2.8–2.9; 2)	2.91 ± 0.12 (2.6–3.2; 41)				***	***
Tarsus minimum width	1.10 ± 0.08 (1.0–1.3; 31)	1.04 ± 0.07 (0.9–1.2; 15)	1.08 ± 0.07 (1.0–1.2; 9)	1.13 ± 0.58 (1.10–1.20; 3)	1.08 ± 0.08 (1.0–1.2; 6)	1.4	1.20 ± 0.0 (1.2; 2)	1.12 ± 0.07 (1.0–1.2; 41)					
Tarsus minimum depth	1.76 ± 0.16 (1.4–2.1; 30)	1.67 ± 0.12 (1.4–1.8; 15)	1.81 ± 0.13 (1.6–2.0; 9)	1.83 ± 0.12 (1.7–1.9; 3)	1.82 ± 0.15 (1.7–2.0; 6)	1.9	1.80 ± 0.14 (1.7–1.9; 2)	1.90 ± 0.13 (1.7–2.1; 41)				***	
Middle claw length	3.90 ± 0.32 (3.1–4.7; 32)	3.76 ± 0.29 (3.0–4.2; 17)	4.01 ± 0.19 (3.7–4.3; 9)	4.30 ± 0.40 (3.9–4.7; 3)	4.15 ± 0.16 (3.9–4.4; 6)	4.6	4.05 ± 0.07 (4.0–4.1; 2)	4.27 ± 0.26 (3.6–4.7; 38)				***	
Hindclaw length	6.22 ± 0.40 (5.4–6.9; 31)	5.88 ± 0.37 (5.2–6.6; 14)	6.09 ± 0.25 (5.8–6.5; 11)	5.73 ± 0.70 (5.0–6.4; 3)	6.65 ± 0.22 (6.3–6.9; 6)	6.4	6.45 ± 0.64 (6.0–6.9; 2)	6.42 ± 0.39 (5.4–7.2; 41)				*	
Hindclaw length (P.A./P.J.L.)		5.6(5.3–6.0; 6)	6.0(5.5–6.4; 9)										
Tail length	59.13 ± 3.16 (52.8–65.2; 29)	57.01 ± 1.88 (52.1–59.7; 16)	52.06 ± 3.90 (46.7–56.9; 11)	60.10 ± 2.83 (58.1–62.1; 2)	60.06 ± 2.08 (57.3–62.5; 5)	62.1	64.3 ± 2.0 (62.9–65.7; 2)	59.36 ± 3.36 (53.2–65.9; 41)		**	*		***
Tail length (P.A./P.J.L.)		59.8(57–67; 5)	55.9(52–58; 11)										
Central rectrix width	10.45 ± 0.86 (8.0–12.0; 28)	10.28 ± 0.79 (8.8–11.7; 16)	9.22 ± 0.80 (8.1–10.5; 9)	10.13 ± 1.17 (8.8–11.0; 3)	10.88 ± 0.84 (9.7–11.6; 5)	13.1	10.45 ± 0.07 (10.4–10.5; 2)	12.38 ± 0.88 (11.0–14.0; 40)		*		***	***
Undertail coverts length from pygostyle	31.15 ± 5.00 (21.0–38.5; 26)	27.21 ± 3.85 (21.4–33.5; 16)	28.66 ± 2.93 (24.6–33.2; 8)	28.65 ± 3.61 (26.1–31.2; 3)	28.53 ± 2.41 (24.0–30.3; 6)	31.6	28.40 ± 2.12 (26.9–29.9; 2)	26.58 ± 3.62 (18.0–32.0; 37)			*	*	
Undertail coverts to tail tip	31.28 ± 5.29 (21.0–38.5; 23)	32.32 ± 3.80 (24.0–43.0; 17)	25.51 ± 2.86 (19.7–28.2; 10)	33.4 ± 3.68 (30.8–36.0; 2)	35.16 ± 4.58 (31.6–42.4; 5)	32.8	37.90 ± 4.53 (34.7–41.1; 2)	34.70 ± 3.73 (28.0–42.0; 38)		**	***		***
Maximum pale tip width	3.00 ± 0.74 (1.8–4.6; 30)	2.69 ± 0.41 (2.1–3.7; 13)	3.44 ± 1.23 (2.1–5.6; 10)	2.67 ± 0.68 (1.9–3.2; 3)	2.92 ± 0.34 (2.5–3.5; 6)	3.1	2.20 ± 0.28 (2.0–2.4; 2)	2.40 ± 0.52 (1.4–3.5; 35)				*	
Wing/tail ratio	0.91 ± 0.08 (0.78–1.09; 28)	0.88 ± 0.04 (0.84–0.97; 17)	1.06 ± 0.08 (0.97–1.18; 11)	0.85 ± 0.02 (0.84–0.86; 2)	0.90 ± 0.04 (0.86–0.96; 5)	0.84	0.83 ± 0.04 (0.81–0.86; 2)	0.91 ± 0.05 (0.82–1.03; 41)		***	***		***
Culmen/tail ratio	0.24 ± 0.01 (0.22–0.27; 23)	0.24 ± 0.01 (0.23–0.28; 15)	0.29 ± 0.02 (0.26–0.32; 10)	0.21 (1)	0.24 ± 0.01 (0.22–0.25; 5)	0.23	0.23 ± 0.01 (0.22–0.24; 2)	0.26 ± 0.02 (0.22–0.30; 38)		***	***	**	**
Tail l/c rectrix w ratio	5.64 ± 0.29 (5.12–6.19; 26)	5.50 ± 0.28 (5.05–5.95; 16)	5.60 ± 0.46 (5.07–6.62; 9)	5.56 ± 0.12 (5.48–5.65; 2)	5.54 ± 0.38 (5.06–5.96; 5)	4.74	6.15 ± 0.15 (6.05–6.26; 2)	4.83 ± 0.41 (3.81–5.88; 40)				***	*
(Wing + culmen)/tail	1.13 ± 0.07 (1.00–1.33; 23)	1.13 ± 0.05 (1.08–1.23; 15)	1.34 ± 0.08 (1.23–1.48; 10)	1.05 (1)	1.14 ± 0.05 (1.10–1.21; 5)	1.07	1.06 ± 0.05 (1.03–1.09; 2)	1.17 ± 0.06 (1.06–1.33; 38)		***	***		
Lower mandible color	5.5 ± 2.3 (2–10; 26)	6.8 ± 2.3 (2–10; 11)	7.8 ± 1.6 (5–9; 8)	5.3 ± 2.5 (3–8; 3)	5.0 ± 1.8 (3–7; 4)	2	3.5 ± 0.7 (3–4; 2)	5.4 ± 1.8 (1–8; 41)		*			**
Upperparts color	8.0 ± 1.3 (3–9; 27)	7.9 ± 1.0 (6–9; 12)	3.9 ± 2.9 (1–10; 8)	2.3 ± 2.3 (1–5; 3)	4.8 ± 0.5 (4–5; 4)	6	5 ± 0.0(2)	8.9 ± 0.3 (8–9; 42)		**	**	***	***
Supercilium prominence	5.0 ± 1.0 (3–7; 26)	3.8 ± 1.1 (3–6; 12)	3.5 ± 0.8 (3–5; 6)	8.7 ± 0.6 (8–9; 3)	3.3 ± 0.5 (3–4; 4)	7	4.5 ± 0.7 (4–5; 2)	2.8 ± 0.8 (1–5; 42)	**	*		***	
Throat ground color	2.8 ± 0.8 (1–4; 27)	3.1 ± 0.7 (2–4; 12)	3.0 ± 0.8 (2–4; 7)	1 ± 0.0(3)	2.3 ± 0.5 (2–3; 4)	2	2.5 ± 0.7 (2–3; 2)	2.8 ± 1.4 (1–8; 42)					

Table 1 Univariate measurements of morphometrics of the *Locustella mandelli* complex and *L. alishanensis* *(Continued)*

Throat speckles	2.8 ± 1.5 (1–9; 27)	2.3 ± 2.5 (1–9; 12)	3.0 ± 0.9 (2–4; 8)	2.7 ± 1.2 (2–4; 3)	3.8 ± 2.5 (1–7; 4)	3	4.0 ± 1.4 (3–5; 2)	5.9 ± 2.2 (2–9; 42)		**	***	***
Breast ground color	4.2 ± 2.6 (1–9; 27)	2.4 ± 2.5 (1–9; 12)	5.9 ± 1.8 (4–9; 8)	7.3 ± 3.6 (4–10; 3)	3 ± 0.0(4)	3	4.5 ± 2.1 (3–6; 2)	3.4 ± 2.2 (1–9; 42)	*	**		**
Breast speckling	2.7 ± 1.5 (1–6; 27)	1.7 ± 1.0 (0–4; 12)	3.4 ± 1.2 (2–5; 8)	2.3 ± 0.6 (2–3; 3)	1.8 ± 0.5 (1–2; 4)	3	4.5 ± 2.2 (3–6; 2)	7.0 ± 2.1 (2–9; 42)	*	**	***	***
Upper flank markings	1 ± 0(23)	1.3 ± 0.50 (1–2; 4)	1.0 ± 0(8)	1 ± 0.0(3)	1 ± 0.0(4)	1	1 ± 0.0(2)	4.9 ± 1.8 (1–8; 39)			***	***
Flank color	4.1 ± 1.9 (2–8; 27)	4.7 ± 1.5 (2–6; 12)	4.0 ± 2.4 (2–9; 8)	2.3 ± 0.6 (2–3; 3)	2.5 ± 0.6 (2–3; 4)	2	2.5 ± 0.7 (2–3; 2)	5.6 ± 1.8 (2–9; 42)			**	*
Undertail coverts color	4.5 ± 1.5 (2–8; 26)	5.5 ± 1.7 (2–8; 12)	4.0 ± 2.4 (1–7; 7)	1.7 ± 0.6 (1–2; 3)	1.8 ± 0.5 (1–2; 4)	5	2.5 ± 0.7 (2–3; 2)	8.4 ± 1.0 (5–9; 39)	*		***	***
Undertail covert tip contrast	5.4 ± 1.0 (4–7; 25)	5.8 ± 1.0 (4–7; 12)	6.1 ± 1.1 (5–8; 7)	5.0 ± 1.7 (3–10; 3)	4.0 ± 0.8 (3–5; 4)	7	4.0 ± 1.4 (3–5; 2)	6.4 ± 1.8 (2–8; 38)			***	
Undertail covert tip breadth	6.4 ± 0.9 (5–8; 25)	6.1 ± 1.3 (5.0–9.0; 12)	6.9 ± 1.6 (5–9; 7)	6.7 ± 3.5 (3–10; 3)	7.5 ± 1.3 (6–9; 4)	7	3 ± 0.0(2)	5.4 ± 1.9 (2–8; 38)				
Leg color	2.2 ± 1.2 (1–6; 26)	3.8 ± 2.0 (1–7; 12)	2.6 ± 1.1 (1–4; 7)	1.7 ± 0.6 (1–2; 3)	1.8 ± 1.0 (1–3; 4)	3	1 ± 0.0(2)	5.5 ± 1.7 (2–9; 40)	*		***	***

L = length, w = width, d = depth. All measurements in mm. Primaries numbered ascendantly. Sexes are pooled. Bonferroni-adjusted significant differences (pooled variances) are from two-sample *t*-tests between *L. m. mandelli* and *L. m. melanorhyncha* (* = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$); no statistical tests were done for samples with $n < 7$.

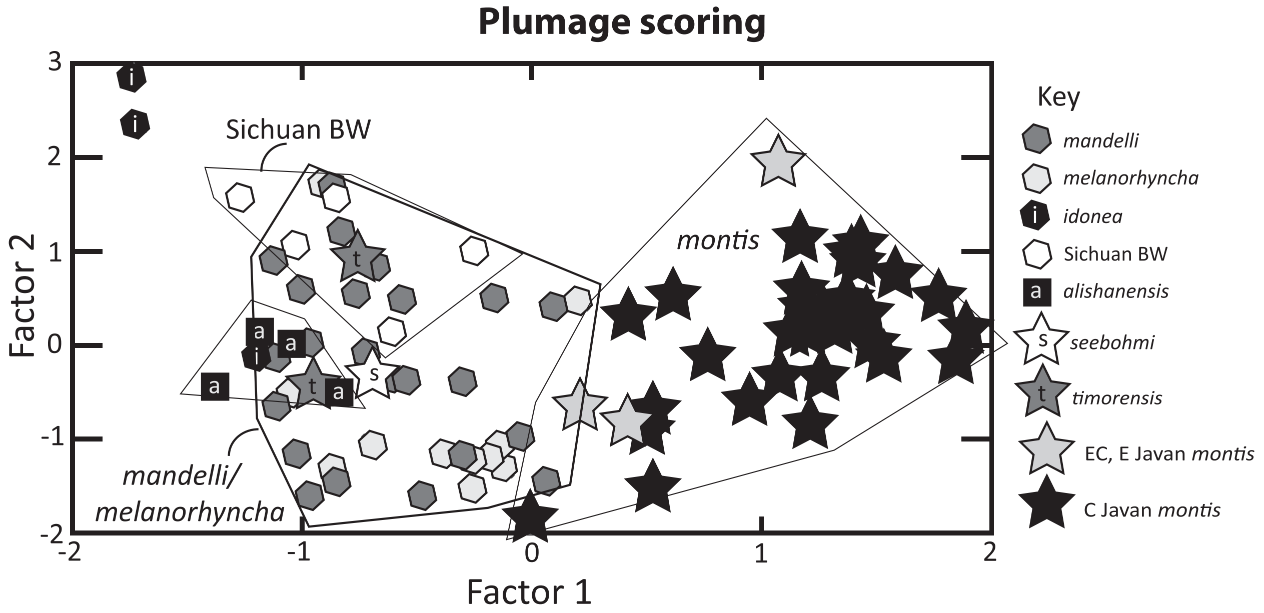

Figure 7 Principal components analysis of plumage scores for all recognized taxa of the *Locustella mandelli* complex and *L. alishanensis.*

immediately followed by a short clicking slightly lower-pitched secondary note. The "strophes" are repeated at varying rate, depending on level of excitement, but during continuous song the pauses between the "strophes" are usually constant in length, around a quarter of a second, and the song may continue for prolonged periods without interruption (Figures 2, 9 to 10). The song can be transcribed as *trrreee-it… trrreee-it… trrreee-it….* The overall pitch varies among different individuals (see below), and this is often clearly audible. Males with different pitch are often found at the same locality (e.g. Figure 10j-l, q-r, t-u). There is also some minor individual variation in details of, in particular, the ending of the principal note and in the pitch of the secondary note in relation to the principal one. No consistent geographical variation is apparent, except that birds from Mt Victoria in W Myanmar (Figures 2, 10z) have on average more pronounced highamp part of the principal note and more hesitant beginning of the same and longer

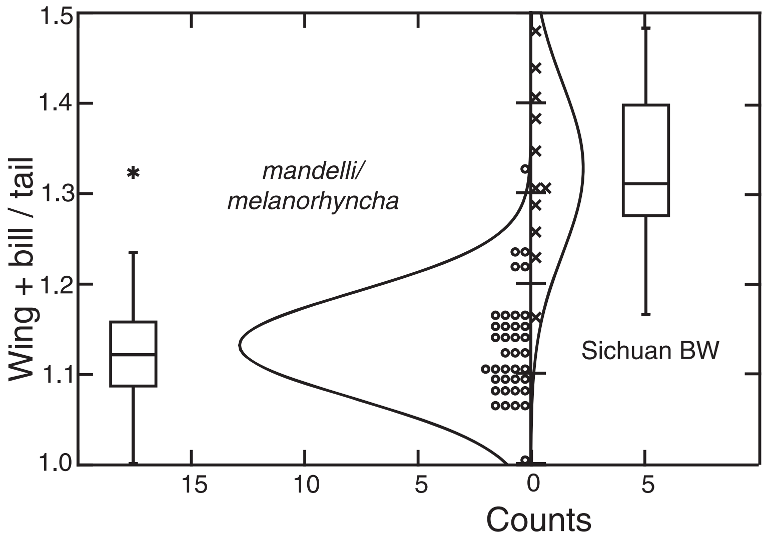

Figure 8 [Wing (flattened) length + culmen (from skull) length]/tail length ratios for *Locustella m. mandelli* and *L. m. melanorhyncha* (combined) and *L. chengi* sp. nov. Mann–Whitney U = 18.00, chi-square approximation = 14.70, df = 1, *p*-value = 0.000.

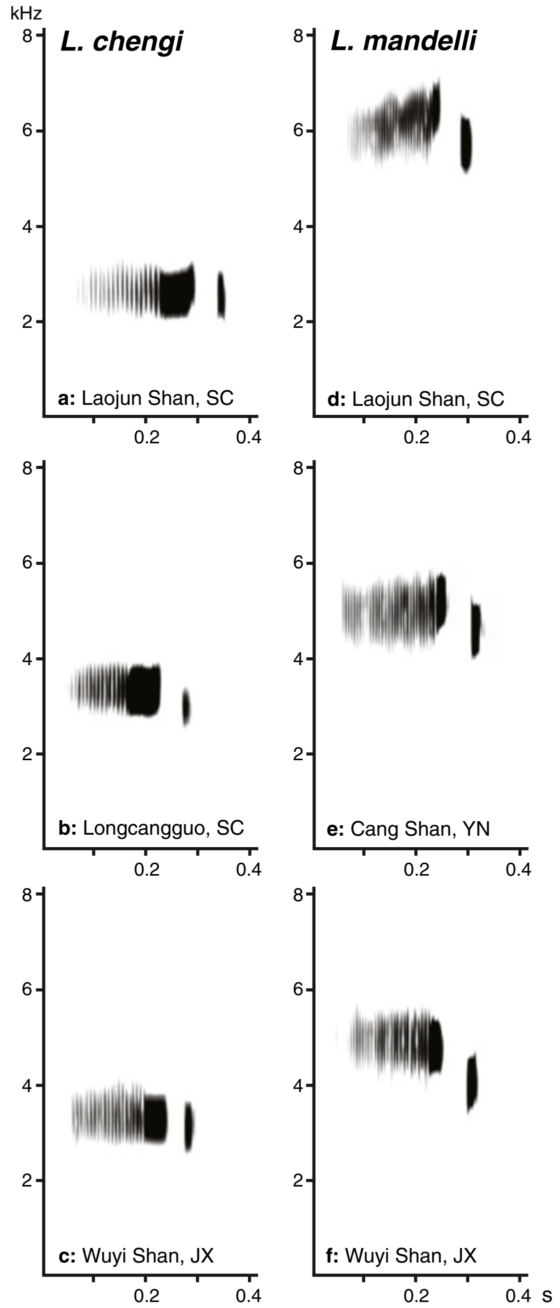

Figure 9 Sonograms and their corresponding oscillograms of single strophes of *Locustella chengi* sp. nov. (a–c), *L. mandelli mandelli/melanorhyncha* (d, e) and *L. mandelli melanorhyncha* (f). **a**: Laojun Shan, Sichuan, China, 1350 m, 27 May 2014 (AV18791; same individual as IOZ19663 in Figures 6a and 14); **b**: Longcangguo, Sichuan, China, 1785 m, 27 May 2013 (AV18792]; same individual as IOZ19662 in Figures 6b and 14); **c**: Wuyi Shan, Jiangxi, China, 1000 m, April 2011 (AV19009); **d**: same locality and date as **a** (neighbours, see main text) (AV18793; same individual as IOZ19664 in Figures 6g and 14); **e**: Cang Shan, Yunnan, China, mid-June 2008 (AVoCet No. 18794); **f**: Wuyi Shan, Jiangxi, China, 1755 m, mid-May 2009 (AV18795). All recordings by Per Alström except c, by Jiansheng Lin and f, by Paul I. Holt. See also Figures 2 and 11.

principal note (see further DFA, below), and birds from Bhutan (Figure 10×) have on average higher-pitched endings of the principal note than the others.

The song of Sichuan Bush Warbler from Shaanxi, Sichuan, Guizhou, Hubei and northwest Hunan (Figures 9a-c, 10a-i, Table 2, Additional file 3: Table S3) is less variable in pitch and detailed structure than that of *mandelli/melanorhyncha*. It is markedly lower-pitched than the song of *mandelli*/*melanorhyncha* (midfreq of principal note mean [calculated as mean of midfreq of first and second parts of principal note] 2.828 ± 0.269 kHz, range 2.438–3.525 kHz, as opposed to mean 5.203 ± 0.753 kHz,

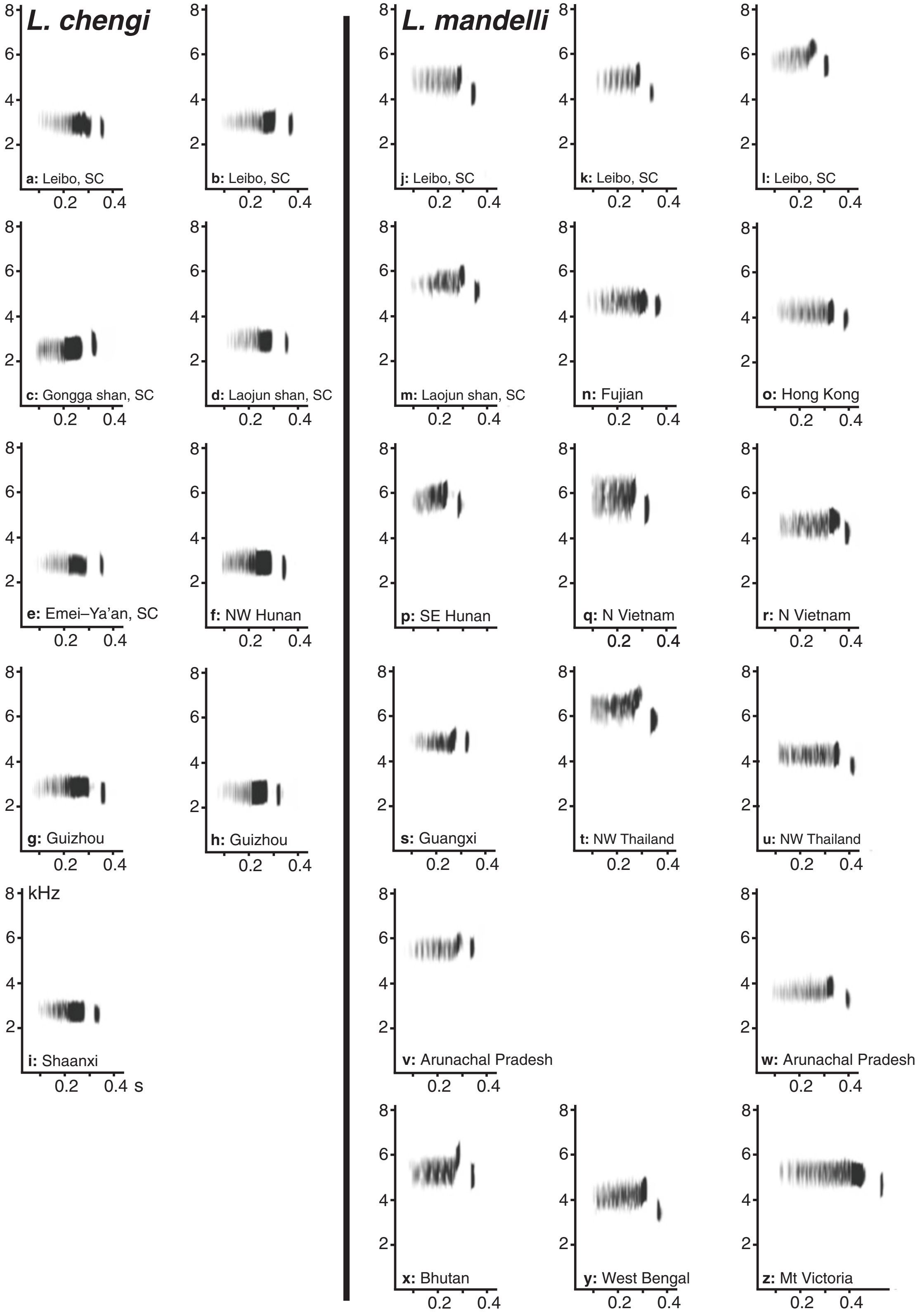

Figure 10 (See legend on next page.)

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Figure 10 Sonograms of single strophes of *Locustella chengi* sp. nov. (a–i) and *L. mandelli* (j–z) from different localities. **a**: Leibo, Sichuan, China, 1410 m, 29 May 2014 (AV18796) (Per Alström); **b**: Leibo, Sichuan, China, 1385 m, 29 May 2014 (AV18797) (Per Alström); **c**: Gongga Shan, Sichuan, China, 1820 m, late May 2012 (AV18798) (Per Alström); **d**: Laojun Shan, Sichuan, China, 1040 m, 27 May 2014 (AV18799; same individual as IOZ19665 in Figures 6c and 14) (Per Alström); **e**: Emei–Ya'an, Sichuan, China, 1260 m, late May 2012 (AV18800) (Paul I. Holt); **f**: Badagong Shan, Hunan, China, 1615 m, early June 2010 (AV18801) (Geoff J. Carey); **g**: Kuankuoshui, Guizhou, China, 1515 m, mid-July 2010 (AV18802) (Canwei Xia); **h**: Kuankuoshui, Guizhou, China, 1290 m, mid-April 2009 (AV18803) (Canwei Xia); **i**: Honghegu, Shaanxi, China, 1640 m, late May 2011 (AV18335; IOZ62959, holotype, also in Figure 14) (Per Alström); **j**: Leibo, Sichuan, China, 2100 m, 29 May 2014 (AV18805) (Per Alström); **k**: Leibo, Sichuan, China, 1900 m, 29 May 2014 (AV18806; same individual as IOZ19666 in Figure 14) (Per Alström); **l**: Leibo, Sichuan, China, 2100 m, 29 May 2014 (AV18807) (Per Alström); **m**: Laojun Shan, Sichuan, China, 1400 m, July 2012 (AV18808) (Chentao Wei); **n**: Mangdang Shan, Fujian, China, 1100 m, early July 2013 (AV18809) (Menxiu Tong/Yang Liu); **o**: Hong Kong, 200 m, early March 2004 (AV18810) (Geoff J. Carey); **p**: Taoyuandong, SE Hunan, China, 1500 m, late May 2013 (AV18811) (Jian Zhao); **q**: Fansipan, Tonkin, Vietnam, 1600/1700 m, mid-May 1999 (AV18812) (Per Alström); **r**: Fansipan, Tonkin, Vietnam, 1600/1700 m, mid-May 1999 (AV18813) (Per Alström); **s**: Anjiangping, Guangxi, China, 1240 m, mid-July 2013 (AV18814) (Jian Zhao); **t**: Doi Angkang, NW Thailand, March 1992 (AV18815) (Per Alström); **u**: Doi Angkang, NW Thailand, March 1992 (AV18816) (Per Alström); **v**: Eaglenest, Arunachal Pradesh, India, 2135 m, 15 April 2008 (AV18817) (Pratap Singh); **w**: Jengging–Yingkiong, Arunachal Pradesh, India, 900 m, 25 March 1998 (AV18818) (Pratap Singh); **x**: Bhutan, 2250 m, early April 2010 (AV18819) (Paul I. Holt); **y**: West Bengal, India, c. 2000 m, late May 1997 (AV18820; same individual as DZUG U1339 in Figure 14) (Per Alström); **z**: Mt Victoria, Myanmar, 1700/1800 m, mid-April 2000 (AV18821) (Per Alström). See also Figures 2 and 10.

range 3.675–6.750 kHz, in *mandelli*/*melanorhyncha*). In sonograms, the thin elements at the beginning of the principal note usually look "cleaner", and the entire principal note tends to be "straighter", especially towards the end, never showing the inflected ending frequently shown in *mandelli*/*melanorhyncha*. Moreover, the highamp part of the principal note is longer in relation to the lowamp part than in *mandelli*/*melanorhyncha* (mean 49% ± 0.12, range 31–76%, of length of principal note, as opposed to mean 13% ± 0.04, range 8–28%, in *mandelli*/*melanorhyncha*; and the duration of the highamp part of the principal note is on average more than three times as long as the secondary note, as opposed to virtually the same length as the secondary note in *mandelli*/*melanorhyncha*). The secondary note differs on average less from the principal note in midfreq than in *mandelli*/*melanorhyncha*, and therefore does not seem to be "hanging down" so much in relation to the principal note as in *mandelli*/*melanorhyncha*. There is less variation among male Sichuan Bush Warblers than in *mandelli*/*melanorhyncha*.

The song of *L. mandelli idonea* is insufficiently known, and we have only three recordings, two from South Annam and one from Central Annam, Vietnam (Figure 11b-c, Additional file 3: Table S3). These show a single rather "straight" principal note with an extensive highamp part, most reminiscent of Sichuan Bush Warbler, but unlike both Sichuan Bush Warbler and *mandelli*/*melanorhyncha*, there is no secondary note. However, unlike in the previously described taxa there are one or two very short "introductory elements", either with similar pitch as the principal note or decidedly lower. The pitch of the principal note (midfreq mean 4.350 kHz ± 0.185, range 4.144–4.500 kHz) is considerably lower than the mean of *mandelli*/*melanorhyncha*, but similar to the lowest-pitched individuals of that group, i.e. higher-pitched than any Sichuan Bush Warbler. Sonograms are most similar to songs of *L. montis* from Mt Bromo (Figure 11i1–i3), though higher-pitched.

Our small sample of songs of *L. seebohmi* ($n = 7$; Figure 11d1–d3, Additional file 3: Table S3) suggests that there is little variation within this taxon. It is most similar to *idonea*, *montis* from Mt Sundoro/Mt Sumbing and putative *timorensis* from Alor, having a single "straight" note that increases markedly in amplitude towards the end. However, it is on average lower-pitched (midfreq mean 4.112 kHz ± 0.262, range 3.750–4.350 kHz) and lacks the former's "introductory elements". The notes are on average shorter than in all other taxa except assumed *timorensis* from Alor.

In contrast to *L. seebohmi*, the song of *L. montis* ($n = 34$; Figure 11e1–l3, Additional file 3: Table S3, Additional file 4: Table S4) shows considerable interlocality variation, while generally being fairly consistent within a locality. It is on average lower-pitched than the other taxa, except Sichuan Bush Warbler (all populations combined midfreq mean 3.289 kHz ± 0.374, range 2.688–3.919 kHz). Sonograms from the neighbouring central Javan Mt Sumbing ($n = 1$ measured) and Mt Sundoro ($n = 7$ measured) (Figure 11e1–e3, Additional file 5: Table S5) are reminiscent of *L. seebohmi*, although on average lower-pitched (midfreq mean 3.474 ± 0.238 kHz, range 3.188–3.919 kHz) and more drawn-out. In contrast, the songs from Mt Merapi ($n = 2$ [only one measurable]; Figure 11f, Additional file 5: Table S5) and Mt Lawu ($n = 3$; Figure 11g1-g2, Additional file 5: Table S5) somewhat further east are more drawn-out, more so than in all previous taxa, and the single note droops markedly in pitch to form a prominent "step" at the end, with the lowest part having highest amplitude; at least one of the recordings from Mt Merapi also has a trace of an introductory element. Our single recording from Mt Merbabu (Figure 11h), just south of Mt Merapi, is most reminiscent of one of our

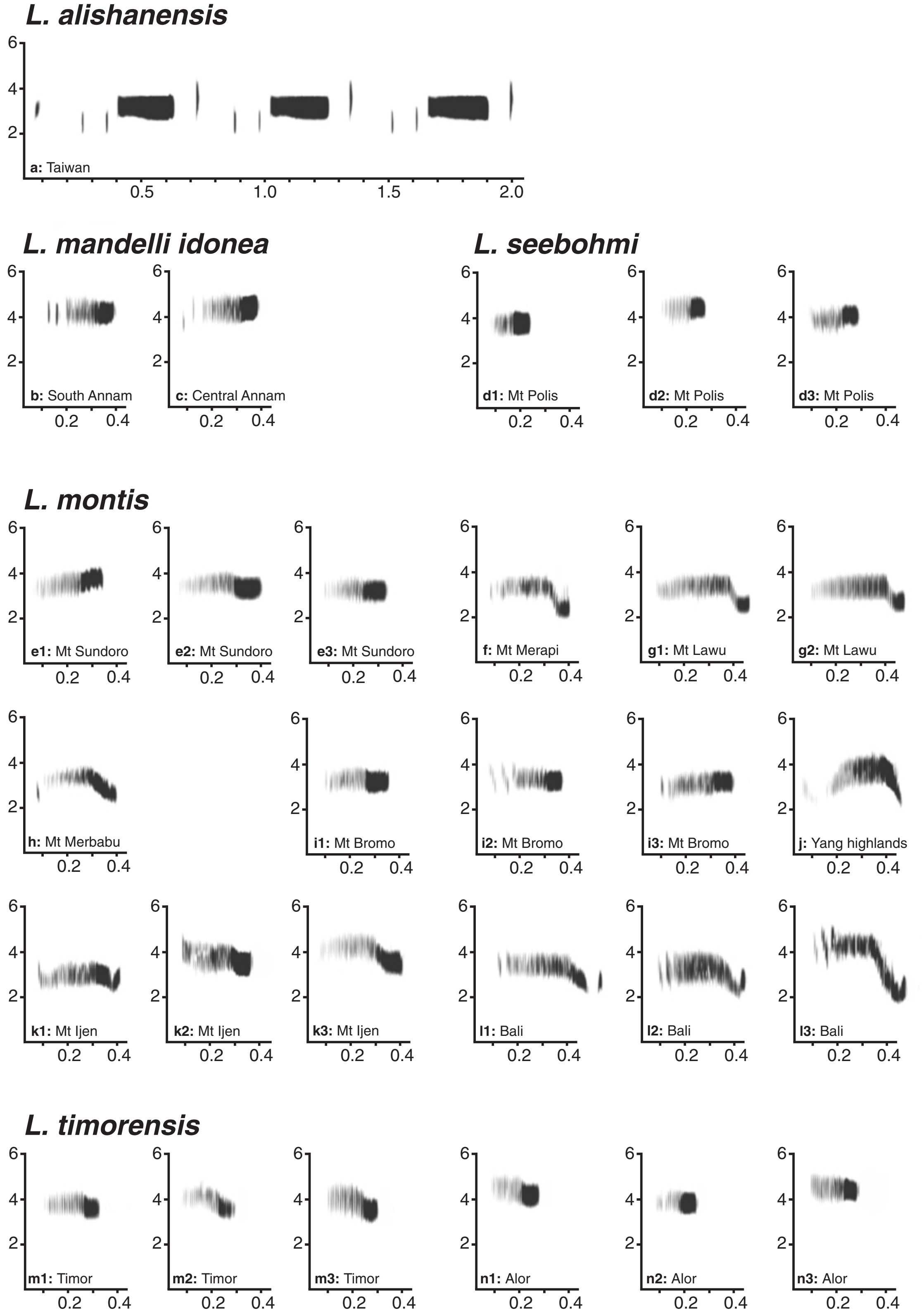

Figure 11 (See legend on next page.)

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Figure 11 Sonograms of single strophes of songs of *Locustella alishanensis* (a; three strophes), *L. mandelli idonea* (b, c), *L. seebohmi* (d), *L. montis* (e–l), topotypical *L. timorensis* (Timor, m) and putative *L. timorensis* (Alor, n). a: Hohuan Shan, Taiwan, late May 1999 (AV18822) (Per Alström); **b**: Tuyen Lam, Dalat, South Annam, Vietnam, 10 May 2005 (photos of same individual on www.orientalbirdimages.org) (AV18823) (Kim Chuah Lim); **c**: Kontum, Central Annam, Vietnam, 1750 m, 26 March 2013 (Macaulay Library No. 176999) (Mark B. Robbins); **d1**: Mt Polis, Luzon, Philippines, 1700 m, mid-March 2007 (XC23074) (George Wagner); **d2**: Bontoc, Mountain province, Luzon, Philippines, c. 1200 m, February 2000 (AV18825) (Des Allen); **d3**: Mt Polis, Luzon, Philippines, 16 April 2001 (AV18826) (Magnus Jäderblad); **e1**: Mt Sundoro, Java, Indonesia, 1785 m, 20 July 2014 (AV18736) (Pamela C. Rasmussen); **e2**: Mt Sundoro, Java, Indonesia, 1750 m, 20 July 2014 (AV18737) (Pamela C. Rasmussen); **e3**: Mt Sundoro, Java, Indonesia, 1730 m, 20 July 2014 (AV18740) (Pamela C. Rasmussen); **f**: Mt Merapi, Java, Indonesia, 1325 m, 15 November 1995 (XC36858) (Bas van Balen); **g1**: Mt Lawu, Java, Indonesia, 1825 m, 7 October 1988 (AV18827) (Bas van Balen); **g2**: Mt Lawu, Java, Indonesia, 30 June 1989 (Macaulay Library No. 70685) (Arnoud van den Berg); **h**: Mt Merbabu, Java, Indonesia, c. 2100 m, 14 September 2014 (AV18718) (Imam Taufiqurrahman); **i1**: Mt Bromo, Java, Indonesia, 5 May 2002 (XC35925) (Frank Lambert); **i2**: Mt Bromo, Java, Indonesia, 2450 m, 13 March 1991 (AV18828) (Bas van Balen); **i3**: Mt Bromo, Java, Indonesia, 4 April 2001 (AV18829) (Magnus Jäderblad); **j**: Yang highlands, Java, Indonesia, 4 April 1989 (AV19011) (Bas van Balen); **k1**: Mt Ijen, Java, Indonesia, 1850 m, 8 February 2013 (XC121769) (Yann Muzika); **k2**: Mt Ijen, Java, Indonesia, 1470 m, July 2005 (AV18830) (Rob Hutchinson); **k3**: Mt Ijen, Java, Indonesia, 2360 m, 17 August 2014 (AV18831) (Pamela C. Rasmussen); **l1**: Bali, Indonesia, 23 May 2013 (AV18832) (Bas van Balen); **l2**: Bali, Indonesia, 8 August 2014 (AV18833) (Philippe Verbelen); **l3**: Bali, Indonesia, 31 March 2001 (AV18834) (Magnus Jäderblad); **m1**: Timor Leste, Indonesia, c. 1850–1950 m, 1 May 2010 (AV 18835) (Colin Trainor); **m2**: Timor Leste, Indonesia, c. 1850–1950 m, 30 April 2010 (AV18836) (Colin Trainor); **m3**: Timor Leste, Indonesia, c. 1850–1950 m, 20 December 2009 (AV18837) (Colin Trainor); **n1**: Alor, Indonesia, 1070 m, 23 October 2011 (AV18838) (Rob Hutchinson); **n2**: Alor, Indonesia, 1000 m, 13 January 2013 (XC105859) (Colin Trainor); **n3**: Alor, Indonesia, 1400 m, 9 September 2009 (XC91907) (Philippe Verbelen).

recordings from Mt Ijen (see below; Figure 11k3), though it has a single distinct "introductory element". Sonograms of recordings from Mt Bromo in eastern Java ($n = 3$; Figure 11i1–i3, Additional file 5: Table S5) are reminiscent of songs of birds from Mt Sundoro and Mt Sumbing, although one of them has two short series of "introductory elements", whereas the two others have ill-defined "introductory elements". The sonogram of the single recording available from Taman Hidup, Yang highlands, even further east (Figure 9j, Additional file 5: Table S5) has a distinct inverted U-shape, and a short series of thin "introductory elements". The sampled recordings from Mt Ijen on easternmost Java ($n = 9$; Figure 11k1–k3, Additional file 5: Table S5) are somewhat variable; they are more or less distinctly down-turned at the end, but less clearly "stepped" than at Mt Merapi and Mt Lawu, and overall more similar to recordings from Mt Sundoro/Mt Sumbing. Finally, the songs of birds from Bali ($n = 10$; Figure 11l1–l3) are strongly descending and up-turned at the end, with marked variation in the degree of the descent, and the end may be disconnected, forming an isolated terminal element; they also have two short series of "introductory elements". The sonogram in Figure 11l3 resembles a recording from Bali published in Dickinson et al. (2000).

Sonograms of our recordings of *L. timorensis* from Timor Leste ($n = 5$; Figure 11m1–m3, Additional file 3: Table S3), from where this taxon was originally described, are most similar to a drawn-out, down-slurred *L. seebohmi*, and very similar to some *L. montis* from Mt Sundoro/Mt Sumbing, although on average higher-pitched and more drawn-out. Recordings from the recently discovered population on Alor (Figure 11n1–n3, Additional file 3: Table S3) that has been considered to be *L. timorensis* due to the geographical proximity with Timor, or perhaps an undescribed taxon (Verbelen and Trainor 2012) are very similar to recordings of *L. seebohmi* and *L. timorensis*. In contrast, *L. alishanensis* is strikingly different from the taxa in the *L. mandelli* complex, having a clear pure drawn-out low-pitched "straight" note preceded and succeeded by short clicking elements (Figure 11a).

In the DFA including all samples based on 11 song variables (Figure 12, Additional file 5: Table S5), discriminant functions (F) 1–4 had Eigenvalues >1 (1.38–22.22). These four functions explained in total 95.7% of the variance: F1 51.6%, F2 30.3%, F3 10.6% and F4 3.2%. Wilk's Lambda was highly significant for the first seven functions. In this analysis, *mandelli/melanorhyncha* and Sichuan Bush Warbler were clearly separated from the others according to F1, which mainly represented duration, midfreq of the lowamp part and lowfreq of the highamp part, whereas F2, which had a strong contribution from midfreq of the highamp part, highfreq of the lowamp part and lowfreq of the highamp part (Additional file 6: Table S6), fully separated *mandelli/melanorhyncha* and Sichuan Bush Warbler. *L. montis* from Bali ($n = 10$), Mt Merapi ($n = 1$), Mt Lawu ($n = 2$) and Yang highlands ($n = 1$) clustered together, along with two *montis* from Mt Ijen. The other *montis* from Mt Ijen ($n = 7$), Mt Bromo ($n = 3$) and Mt Sumbing/Mt Sundoro ($n = 8$) clustered tightly with *seebohmi* ($n = 7$), *timorensis* ($n = 5$) and presumed *timorensis* from Alor ($n = 6$). *L. m. idonea* ($n = 3$) was separated from the first *montis* cluster on F1 and from the *montis*/*seebohmi*/*timorensis*/presumed *timorensis* Alor cluster on F2.

In the DFA of *mandelli*, *melanorhyncha* and Sichuan Bush Warbler based on 18 song variables (Figure 13, Additional file 5: Table S5), two discriminant functions with

Table 2 Univariate measurements of song variables of *Locustella m. mandelli/melanorhyncha* and *L. chengi* sp. nov.

Taxon		Duration 1a (s)	Low freq 1a (kHz)	High freq 1a (kHz)	Bandw 90% 1a (kHz)	Midfreq 1a (kHz)	Duration 1b (s)	Low freq 1b (kHz)	High freq 1b (kHz)	Bandw 90% 1b (kHz)	Midfreq 1b (kHz)
***L. chengi*, sp. nov.**		0.136 ± 0.021 (0.083 – 0.193)	**2.119 ± 0.289 (1.434 – 2.858)**	*3.557 ± 0.302 (2.972 – 4.336)*	0.743 ± 0.060 (0.563 – 0.900)	**2.836 ± 0.280 (2.438 – 3.525)**	*0.064 ± 0.010 (0.045 – 0.104)*	**2.234 ± 0.266 (1.795 – 2.911)**	*3.441 ± 0.273 (2.955 – 4.174)*	0.604 ± 0.056 (0.563 – 0.750)	**2.820 ± 0.263 (2.438 – 3.563)**
L. m. mandelli, L. m. melanorhyncha		0.185 ± 0.029 (0.118 – 0.249)	**4.346 ± 0.712 (3.027 – 5.825)**	*5.794 ± 0.745 (4.227 – 7.321)*	0.869 ± 0.109 (0.563 – 1.163)	**5.090 ± 0.728 (3.600 – 6.563)**	*0.024 ± 0.009 (0.011 – 0.055)*	**4.653 ± 0.783 (3.163 – 6.239)**	*5.925 ± 0.815 (4.190 – 7.586)*	0.663 ± 0.080 (0.563 – 0.975)	**5.316 ± 0.786 (3.750 – 6.938)**
One-way ANOVA	**F**	99.001	442.343	408.445	54.042	440.676	459.625	451.678	441.116	19.291	478.318
	P	***	***	***	***	***	***	***	***	***	***

Taxon	Duration 1 (s)	Duration 2 (s)	Low freq 2 (kHz)	High freq 2 (kHz)	Bandw 90% 2 (kHz)	Midfreq 2 (kHz)	Total duration (s)	Mid freq 2/Midfreq 1b	N
***L. chengi*, sp. nov.**	0.204 ± 0.020 (0.150 – 0.259)	0.019 ± 0.008 (0.013 – 0.060)	*2.151 ± 0.209 (1.743 – 2.772)*	*3.354 ± 0.197 (2.981 – 3.987)*	0.634 ± 0.069 (0.563 – 0.750)	*2.750 ± 0.198 (2.438 – 3.375)*	0.261 ± 0.021 (0.207 – 0.320)	0.978 ± 0.045 (0.882 – 1.123)	53
L. m. mandelli, L. m. melanorhyncha	0.213 ± 0.034 (0.142 – 0.302)	0.019 ± 0.005 (0.011 – 0.039)	*4.056 ± 0.736 (2.699 – 5.278)*	*5.203 ± 0.777 (3.639 – 6.443)*	0.639 ± 0.073 (0.563 – 0.938)	*4.631 ± 0.749 (3.188 – 5.813)*	0.274 ± 0.040 (0.199 – 0.372)	0.870 ± 0.045 (0.778 – 0.985)	51
One-way ANOVA	2.843	0.027	328.043	281.673	0.098	311.766	4.573	149.116	
	0.095	0.87	***	***	0.754	***	*	***	

1a – lowamp part of principal note; 1b – highamp part of principal note; 2 – secondary note; see Figure 2 for further explanation of terms. MANOVA was used to assess the overall differences between all 18 variables (Pillai's Trace = 0.943, F = 78.664, $p < 0.001$), followed by one-way ANOVA for each variable (* = $p \leq 0.05$; *** = $p \leq 0.001$). Values in columns that are non-overlapping between the two species are in bold, and those that are very marginally overlapping are in italics.

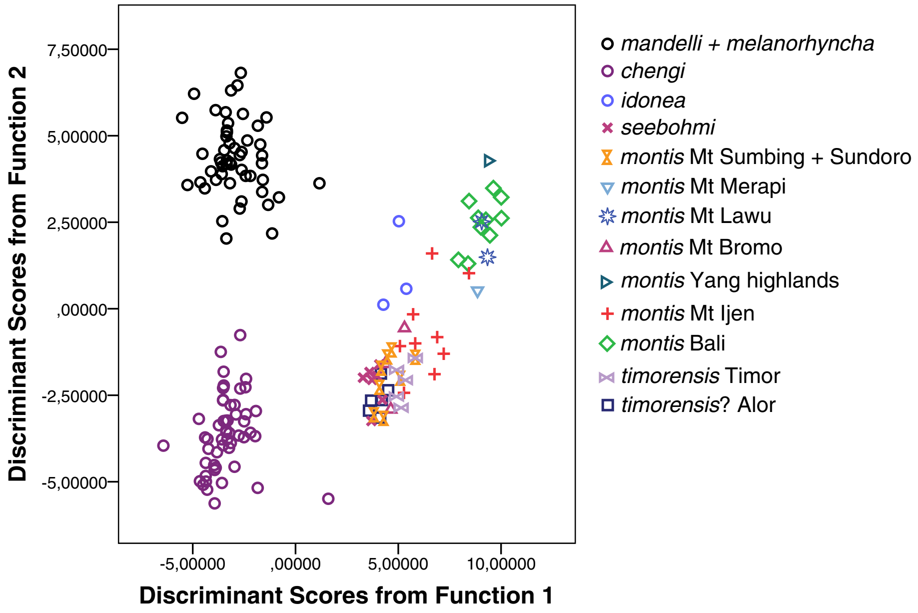

Figure 12 Discriminant Function Analysis of songs in the *Locustella mandelli* complex based on 11 variables. Note clear separation of *L. chengi* sp. nov. and *L. mandelli mandelli/melanorhyncha* from each other and from the other taxa; tight clustering of *L. seebohmi*, topotypical *L. timorensis* (Timor), assumed *L. timorensis* from Alor, and some *L. montis* populations; a second *L. montis* cluster; and *L. mandelli idonea* with a somewhat intermediate position between the two latter clusters.

Eigenvalues >1 were extracted, with F1 explaining 91.8% of the variance; Wilk's Lambda was significant for the first four functions. In this analysis *mandelli/melanorhyncha* and Sichuan Bush Warbler were well separated by F1, with 100% of the cases correctly identified; in a cross-validation, one Sichuan Bush Warbler was classified as *melanorhyncha*. Moreover, *L. m. mandelli* from Mt Victoria, SW Myanmar were almost completely separated from *mandelli* from India and Bhutan and *melanorhyncha* by F1, and completely separated from the others by F2. F1 was

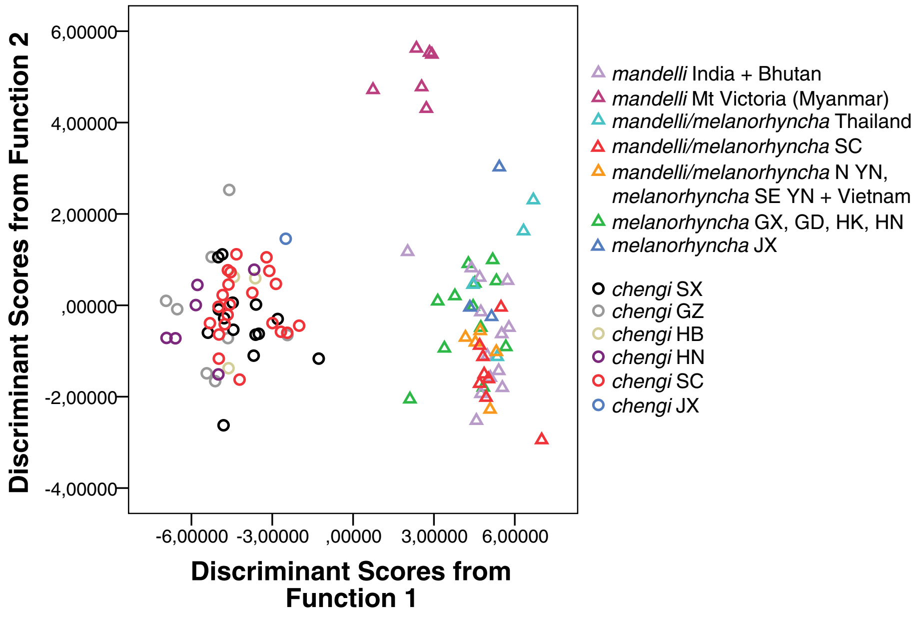

Figure 13 Discriminant Function Analysis of songs of *Locustella mandelli* and *L. chengi* sp. nov. based on 18 variables. Note clear separation of *L. chengi* sp. nov. and *L. mandelli mandelli/melanorhyncha* from each other, and lack of differentiation within these taxa, except for distinct Mt Victoria (Myanmar) *mandelli*.

determined mostly by the midfreq of the highamp part of the principal note, high- and lowfreq of the same part, duration and lowfreq of the lowamp part of the principal note, and highfreq of the secondary note, and F2 mainly by the high- and lowfreq of the lowamp part of the principal note, highfreq of the highamp part of the same note, lowfreq of secondary note, midfreq of both parts of the principal note, and total duration (Additional file 6: Table S6).

DNA

The cyt*b* alignment contained 1038 base pairs (bp), with a few missing bases for some of the samples sequenced from toepads. No stop codons, anomalous amino acids or other indications of amplification of pseudogenes were found. All sequences have been submitted to GenBank (Additional file 1: Table S1).

In the MrBayes tree based on cyt*b* sequences (Figure 14) the samples of *L. m. mandelli*/*melanorhyncha* from NE India, NW Thailand, N Vietnam, S Sichuan, Hong Kong and SE Hunan and the samples of Sichuan Bush Warbler from Shaanxi, Sichuan, Guizhou and NW Hunan formed separate clades. In neither of these clades was there any geographical structuring; in particular, the *mandelli* samples from India were undifferentiated from the *melanorhyncha* and *mandelli/melanorhyncha* from China, Thailand and NW Vietnam. The *mandelli*/*melanorhyncha* clade had posterior probability (PP) 1.00 and maximum likelihood bootstrap (MLBS) 77%, whereas the Sichuan Bush Warbler clade had PP 0.87 and MLBS 65%. However, the Sichuan Bush Warbler clade excluding the Hunan sample IOZ 19990, which was sister to the other Sichuan Bush Warblers, received PP 1.00/MLBS 79%. Sichuan Bush Warbler IOZ 19990 had plesiomorphic character states at three out of four positions that had synapomorphic character states in the other Sichuan Bush Warblers. *L. m. idonea* from S/C Vietnam was sister to *L. m. mandelli*/*melanorhyncha* (PP 0.98, MLBS 77%), and these together formed the sister clade to the Sichuan Bush Warbler clade, although the support was low (PP 0.87, MLBS 64%). The other relationships among the different taxa in the *L. mandelli* complex were very poorly supported, and even the monophyly of *L. montis* received low support (0.74/60%). All terminal and internal branches within the *L. mandelli* complex were very short compared to the three outgroup species.

The BEAST chronogram based on cyt*b* sequences and a lognormal relaxed molecular clock rate of 2.1%/million years, a GTR + G model and a constant size coalescent tree prior (Figure 14, inset) differed from the MrBayes tree in recovering a clade with Sichuan Bush Warbler as sister to *L. seebohmi*, *L. timorensis* and *L. montis* and another one with *L. m. mandelli*/*melanorhyncha* and *L. m. idonea*, although the support was low (PP 0.80) for the former clade, and the support for the latter clade was considerably lower (<0.50) than in the MrBayes analysis. The Sichuan Bush Warbler clade, including the somewhat aberrant IOZ 19990, received higher support (PP 0.94) than in the MrBayes analysis. The BEAST analysis suggested very recent divergences among the different taxa in the *L. mandelli* complex, with the deepest split at 0.85 million years ago (Mya) (95% highest posterior density [HPD] interval 0.46–1.33 Mya). Another BEAST analysis with a "speciation: birth-death incomplete sampling" tree prior, but otherwise same settings as above, inferred on average younger ages, especially towards the root, with the main difference being the deepest split (0.63 Mya; 95% HPD 0.39–0.91 Mya). Neither of these analyses was favoured over the other in a Bayes Factor (BF) analysis (Newton and Raftery 1994; Kass and Raftery 1995) (ln BF second analysis vs. first 0.812), but we chose to present the first analysis as our main result as a coalescent tree prior seemed more appropriate than a speciation tree prior due to the large proportion of samples representing intraspecific variation and the overall shallow divergence of the different taxa within the *L. mandelli* complex (as previously shown for a few taxa by Alström et al. 2011).

The mean pairwise genetic cyt*b* divergences were low, generally <1%, in the *L. mandelli* complex (Table 3).

Distribution

The distributions of the different taxa are shown in Figure 1. All of them are allopatric, except that we have found *mandelli/melanorhyncha* and Sichuan Bush Warbler sympatrically, although almost entirely altitudinally segregated (see below), at six locations in Leibo, Pingshan and Mabian counties in southern Sichuan (Figure 15). We have also received one sound recording of Sichuan Bush Warbler from Wuyi Shan, NE Jiangxi, where *melanorhyncha* occurs at a higher elevation (see below).

Habitat and elevation

All taxa in the *Locustella mandelli* complex inhabit dense, low, herbaceous, grassy, scrubby, bushy vegetation, often tea plantations, and sometimes in glades in open secondary forest, in mountainous areas (Madge 2006; Kennerley and Pearson 2010; pers. obs.). *L. m. mandelli* is said to breed mainly between 1000 and 2200 m in the Indian Subcontinent (Rasmussen and Anderton 2012), concentrated at 2100–2200 m (Spierenburg 2005). We have noted it regularly at 1910–2420 (once at 2690 m and 2800 m) at a number of sites in Bhutan. Our observations from Mt Victoria, W Myanmar are from 1700–1800 m. We have found *melanorhyncha* on Fansipan in N Vietnam at 1600–1700 m, and *mandelli/melanorhyncha* is believed to breed at 1800–2000 m in NW Thailand (Philip D. Round, in litt., who suggested that the range 1300–1900 m given in Dickinson et al. 2000, and other observations down to 1000 m, are probably incorrect, as these might

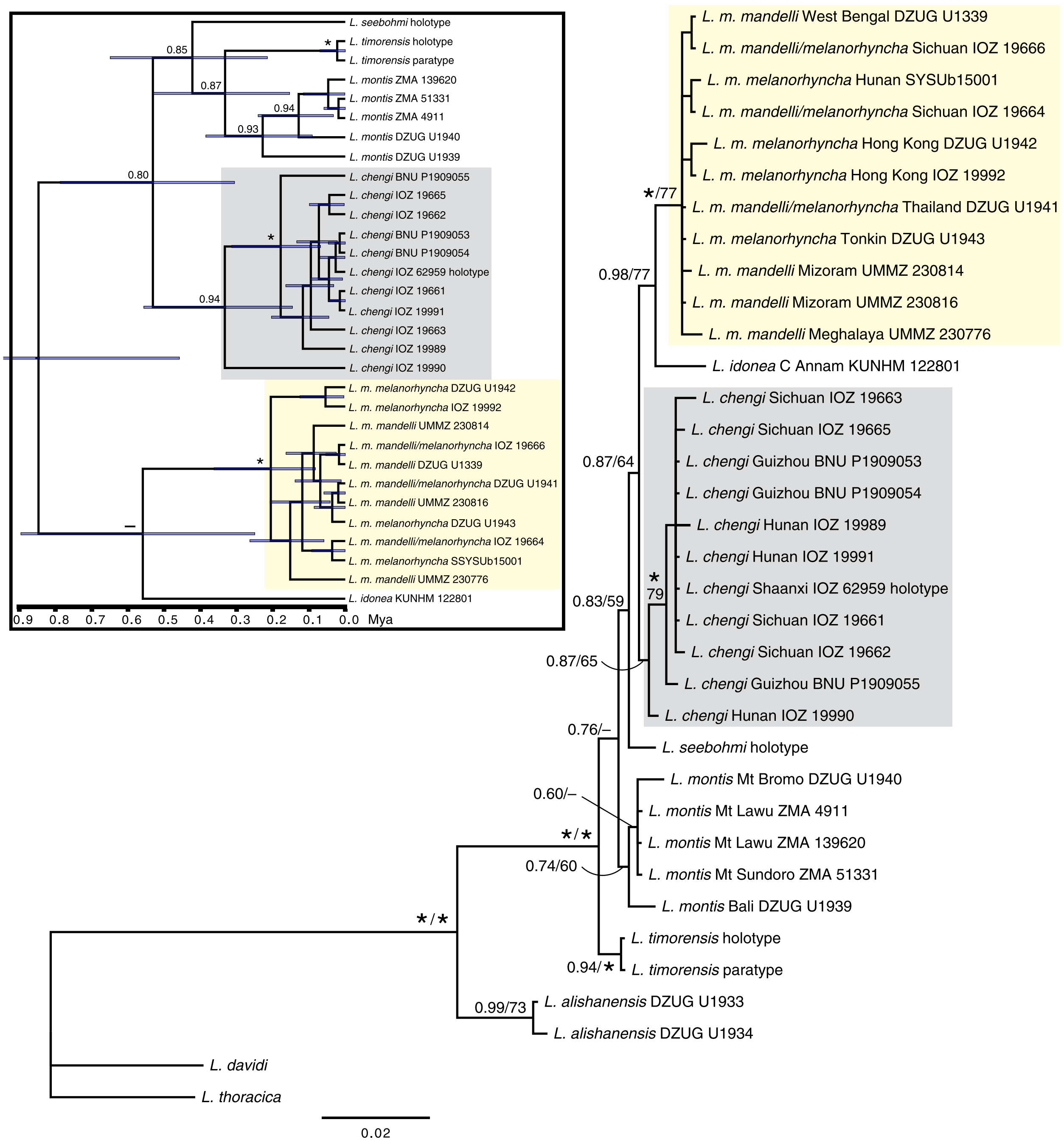

Figure 14 Cytochrome *b* tree for the *Locustella mandelli* complex and *L. alishanensis*, with *L. davidi* and *L. thoracica* as outgroups (details in Additional file 1: Table S1). Values at nodes are posterior probabilities (PP) and maximum likelihood bootstrap values (MLBP), in this order (only marked for primary clades). * indicates PP or MLBP 1.00/100%. Inset: Cytochrome *b* chronogram. Blue bars are 95% highest posterior density distributions for node height; note that the bar at the deepest node should be equally long on both sides of the node (cut off towards the past).

include non-breeding altitudinal migrants). In China, we have observed *melanorhyncha* and *mandelli/melanorhyncha* in Yunnan at 2190–2615 m; in southern Sichuan at 1350–2120 m; in Guangxi at 150–350 m (early April to early August, so evidently on breeding grounds despite low elevation; Jonathan Martínez, in litt.) and 1100–1290 m; in Guangdong at 25–310 m (singing in early to late March in suitable breeding habitat, but uncertain if on migration or

Table 3 Pairwise genetic distances within and between some of the taxa in the *Locustella mandelli* complex and the outgroups

Taxa	Divergence (%) uncorr. P (mean ± SD, range)	Divergence (%) Maximum Composite Likelihood + Γ (mean ± SD, range)
L. montis Java – *L. montis Java*	0.22 ± 0.24 (0.00 – 0.44)	0.23 ± 0.25 (0.00 – 0.45)
L. montis Java – *L. montis Bali*	0.55 ± 0.23 (0.44 – 0.89)	0.57 ± 0.23 (0.45 – 0.91)
L. chengi – *L. chengi*	0.24 ± 0.21 (0.00 – 0.74)	0.25 ± 0.21 (0.00 – 0.75)
L. mandelli – *L mandelli*	0.20 ± 0.10 (0.00 – 0.30)	0.21 ± 0.14 (0.00 – 0.90)
L. chengi – *L. mandelli*	1.01 ± 0.16 (0.59 – 1.33)	1.03 ± 0.17 (0.60 – 1.37)
L. mandelli – *L. m. idonea*	0.79 ± 0.12 (0.59 – 0.89)	0.80 ± 0.12 (0.60 – 0.90)
L. seebohmi – *L. mandelli/L. m. idonea/L. chengi*	0.82 ± 0.17 (0.59 – 1.19)	0.84 ± 0.17 (0.60 – 1.21)
L. seebohmi – *L.montis/L. timorensis*	0.87 ± 0.22 (0.74 – 1.19)	0.88 ± 0.23 (0.75 – 1.22)
L. timorensis – *L. montis*	0.48 ± 0.23 (0.30 – 0.74)	0.48 ± 0.23 (0.30 – 0.76)
L. montis – *L. mandelli/L. m. idonea/L. chengi*	1.00 ± 0.25 (0.44 – 1.48)	1.02 ± 0.26 (0.45 – 1.53)
L. seebohmi – *L. montis*	0.92 ± 0.25 (0.74 – 1.19)	0.94 ± 0.26 (0.75 – 1.22)
L. timorensis – other taxa in the *L. mandelli* complex	0.76 ± 0.19 (0.30 – 1.04)	0.77 ± 0.19 (0.30 – 1.05)
L. alishanensis – *L. mandelli* complex	3.35 ± 0.22 (2.96 – 3.85)	3.55 ± 0.24 (3.11 – 4.11)
L. davidi – *L. thoracica*	4.4	4.9

L. mandelli includes both *L. m. mandelli* and *L. m. melanorhyncha*. See Additional file 1: Table S1 for samples used.

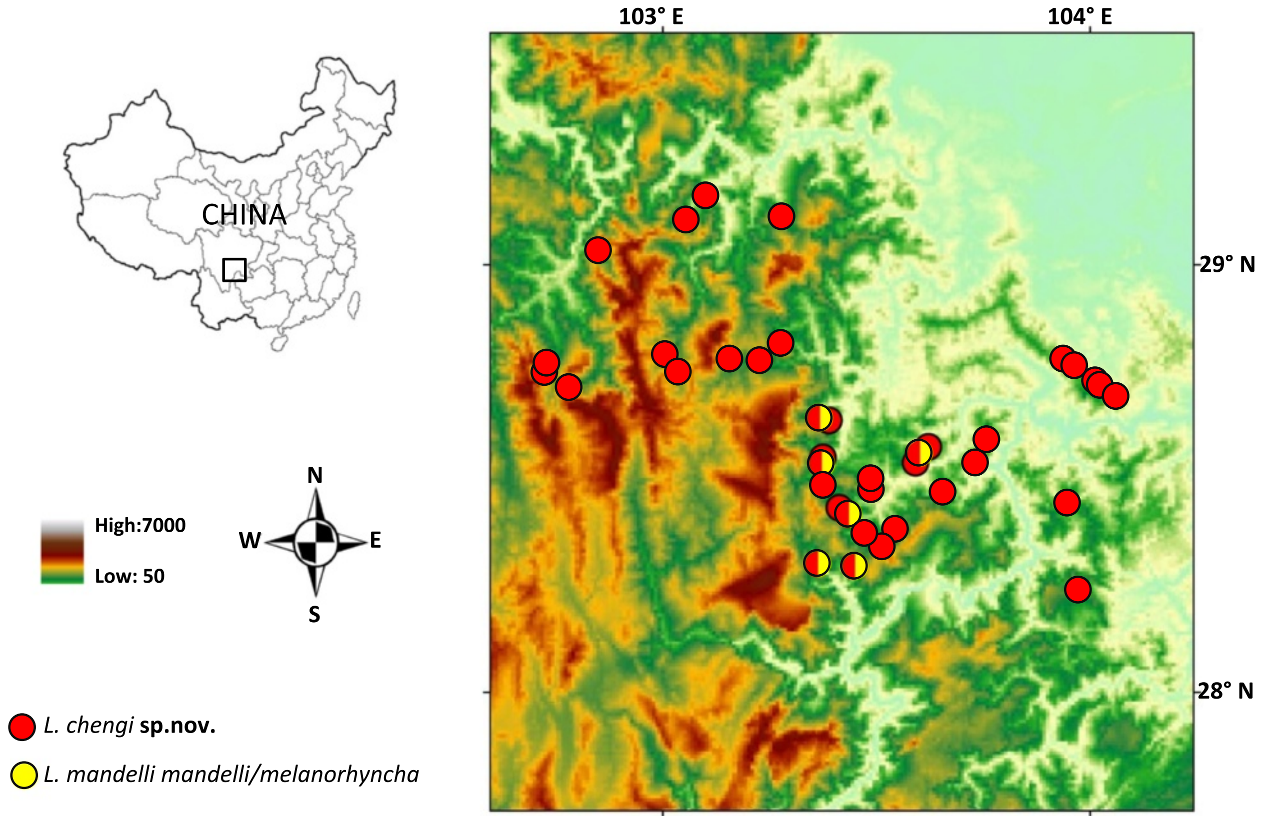

Figure 15 **Detailed map of southern Sichuan, with localities where *Locustella chengi* sp. nov. and *L. mandelli* have been observed by us.** The bicoloured (red + yellow) circles are places where both *L. chengi* sp. nov. and *L. mandelli* have been found in sympatry.

on breeding grounds), 500–850 m (late April–late May; Jonathan Martínez, in litt.) and 1000–1700 m; in Hong Kong at c. 900 m; in SE Hunan at 1150–1560 m; and in Jiangxi/Fujian at 1150–1900 m. We have observed Sichuan Bush Warbler in Sichuan at 1000–2275 m; in Shaanxi at 1290–1675 m; in Hubei at 1350–1670 m; in NW Hunan at 1400–1615 m; and in Guizhou at 1290–1515 m. We have also obtained one sound recording from 1000 m at Wuyi Shan, NE Jiangxi (i.e. at lower elevation than *melanorhyncha* from the same location, in agreement with the situation in south Sichuan).

In south Sichuan, we found *mandelli/melanorhyncha* and Sichuan Bush Warbler to be mostly altitudinally segregated, the former occurring mainly above 1850 m, whereas the latter was almost entirely below 2000 m (only six observations in total above 1900 m; Figure 16). At the sites where we observed *melanorhyncha* and Sichuan Bush Warbler in sympatry, they were exclusively segregated by elevation except at 1350 m on Laojun Shan, Pingshan county, where the single male *mandelli/melanorhyncha* observed at that site was holding a territory right next to the highest singing male Sichuan Bush Warbler. In Leibo county in late May 2014, Sichuan Bush Warbler was rather common at 1250–1475 m in lush subtropical herbaceous vegetation and ferns with scattered bushes and trees, whereas *mandelli/melanorhyncha* were found in basically similar habitat, although in a climate zone with decidedly more temperate character at 1895–2100 m, with the highest density around 2100 m.

Interaction between *L. m. melanorhyncha* and Sichuan Bush Warbler

The *Locustella m. mandelli/melanorhyncha* and Sichuan Bush Warbler males (sexed by song and later, in the hand, by prominent cloacal protuberance and lack of brood patch) that were observed at 1350 m on Laojun Shan (see above) held territories that were adjacent, and probably at least partly overlapping. Most of the time, the two birds were singing from different sides of a road, at close distance from each other, although the *mandelli/melanorhyncha* male was also heard on two occasions singing within what was undoubtedly the Sichuan Bush Warbler's territory. The Sichuan Bush Warbler was seen chasing the *mandelli/melanorhyncha* male across the road once. Neither of the two birds ever showed any strong response towards playback of the other song type (Sichuan Bush Warbler recorded in Shaanxi and *mandelli/melanorhyncha* in Yunnan), while responding strongly to its own song type by giving alarm calls instead of song, and vigorously searching for the source of the sound. We caught the Sichuan Bush Warbler in a mistnet placed on the road by playing Sichuan Bush Warbler song from a speaker underneath the net and shortly afterwards caught the *mandelli/melanorhyncha* male in the same net by playing *mandelli/melanorhyncha* song.

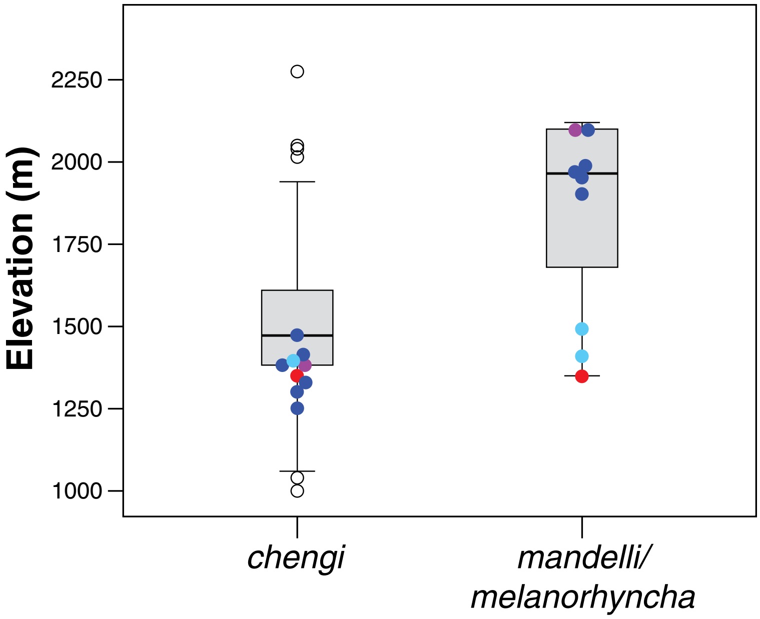

Figure 16 Elevational distributions of *Locustella m. mandelli/melanorhyncha* and *L. chengi* sp. nov. in southern Sichuan, China (localities in Figure 1 and Additional file 1: Table S1). Localities where both species have been found in sympatry are indicated with coloured dots: red – Laojun Shan, Pingshan county; purple – Ledugou, Lanbazi township, Leibo county; pale blue – Tongmuxi, Xining town, Leibo county; dark blue – Baiyanwan–Laolinkou, Lanbazi township, Leibo county.

Discussion

Distinctness of Sichuan Bush Warbler

With respect to Sichuan Bush Warbler vs. *mandelli*/*melanorhyncha*, there are congruent differences in plumage, structure, song and cyt*b* from within a large geographical area, and accordingly these represent separately evolved lineages. Based on morphometrics, Sichuan Bush Warbler is the most distinctive of all taxa analysed here, and differs from *mandelli/melanorhyncha* especially by its proportionately longer bill and shorter tail, with hardly any overlap in (wing + culmen)/tail ratios. It should be noted here, in relation both to univariate and multivariate analyses, that all sexed specimens of Sichuan Bush Warbler available are males. Given that both sexes are present in samples of the other taxa for which multiple specimens are available, it is almost certain that the morphological distinctiveness of Sichuan Bush Warbler is underestimated here due to the absence of females, which can be expected to have even shorter tails. In addition, in relation to univariate statistical testing, it should be borne in mind that the sexes are pooled, and additionally that the two-way *t*-tests systematically underestimate significance levels, especially when measurements are Bonferroni-adjusted as they are here for measurements.

The songs of Sichuan Bush Warbler and *mandelli*/*melanorhyncha* are easily separable by ear, with no intermediates ever heard, and with no overlap in measurements of lowfreq and midfreq of the principal note, and hardly any overlap in the highfreq part of the principal note and duration of the highamp part of the principal note, and lowfreq, highfreq and midfreq of the secondary note. Sichuan Bush Warbler and *mandelli*/*melanorhyncha* are also reciprocally monophyletic in cyt*b*. Moreover, there are general differences in habitat choice, as shown by elevational distributions, with almost complete segregation where both taxa are syntopic (as is the case also with *L. thoracica* and *L. davidi* in central China; Alström et al. 2008). In the Xining and Xisujiao catchment areas, Leibo county, Sichuan Bush Warbler is common at low to mid elevation, whereas *mandelli/melanorhyncha* is common higher up, with hardly any altitudinal overlap.

The two Sichuan Bush Warblers and two *mandelli*/*melanorhyncha* that we caught at places where they occurred in sympatry in southern Sichuan in late May 2014 were diagnosably different in morphometrics (the two *mandelli*/*melanorhyncha* both having wing/tail ratios of 0.92, and the two Sichuan Bush Warblers with wing/tail ratios of 1.03 and 1.04, i.e. wing shorter than tail in *mandelli*/*melanorhyncha* and the opposite in Sichuan Bush Warbler), song (Figures 10a, d, 11d, k) and cyt*b* (Figure 14, IOZ 19663, IOZ 19664, IOZ 19665, IOZ 19666). Moreover, the two individuals with adjacent, probably partly overlapping, territories that we caught at 1350 m on Laojun Shan in the same mistnet responded strongly to playback of their own song type, but not to the other one. Although, as suggested by the chronogram and cyt*b* distance, Sichuan Bush Warbler and *L. mandelli* are in the early stages of divergence, our data suggest that they are nevertheless reproductively isolated where they occur in sympatry in S Sichuan. The reproductive isolation between them is extraordinary in view of their cyt*b* divergence of only 0.6–1.3/1.4% (mean 1.0%). Although genetic distances from different studies are not directly comparable (Fregin et al. 2012), this genetic distance is considerably smaller than between other taxa generally treated as species (cf. Aliabadian et al. 2009), and is much lower than the distance between the two outgroup species, *L. thoracica* and *L. davidi* (4.4% uncorrected/4.9% corrected; Table 3), which were previously treated as conspecific, but which have recently been found to breed sympatrically, mostly altitudinally segregated, in C China (Alström et al. 2008). Further studies are required to evaluate whether the low cyt*b* distance between Sichuan Bush Warbler and *L. mandelli* represents true recent divergence, or whether it may have been affected by past introgression (cf. Wang et al. 2014). Nevertheless, our evidence shows that Sichuan Bush Warbler should be treated as specifically different from *L. mandelli* under any species concept.

Description of a new species

As concluded above, the Sichuan Bush Warbler is a distinct species, and as it has not previously been described, we here name it.

Locustella chengi, sp. nov.

Sichuan Bush Warbler.

Holotype

Institute of Zoology, Chinese Academy of Sciences, Beijing, No. IOZ 62959, adult male, Honghegu, Shaanxi Province, China (E107.47′45″, N34.01′07″), 1640 m a.s.l., 30 May 2011, collected by Per Alström, Gang Song, Xuebin Gao, Zuohua Yin and Fumin Lei, specimen prepared by Zuohua Yin. The cyt*b* sequence has GenBank accession No. KP773459 (see position in tree in Figure 14), and the song AVoCet (www.avocet.zoology.msu.edu) catalogue No. AV18335 (sonogram Figure 11i).

Paratypes

All other specimens of *L. chengi* known to us are also listed in Table 4, and have been examined by us. The specimens BNU-P1909051, BNU-P1909052, BNU-P1909053, BNU-P1909054 and BNU-P1909055 are hereby designated as paratypes.

Table 4 Specimens and measured live birds of *Locustella chengi* sp. nov., with their data

Museum acronym	Specimen number	Number on Figures 3 and 4	Documentation	Locality	Coordinates	Number on Figure 1	Altitude (m)	Date	Sex	Age
MNHN	2013.234[a]	6	Specimen	Sichuan; Tatsienlou (Kangding)	30°05′N, 101°97′E	\	\	No date	Unsexed	Adult
BMNH	1914.6.12.102[b]	7	Specimen	Hubei; Ichang, Upper Yangtse (Yichang)	30°7′N, 111°.3′E	\	\	No date	Male	Adult
BMNH	1914.6.12.101[b]	8	Specimen	Hubei; Ichang, Upper Yangtse (Yichang)	30°7′N, 111°.3′E	\	\	No date	Male	Juv
IOZ	62959 (holotype)	9	Specimen, song	Shaanxi; Honghegu	34°01′07″N,107°.47′45″E	1	1640	30 May 2011	Male	Adult
BNU	P1909051 (paratype)	1	Specimen	Kuankuoshui, Guizhou, China	28°13′N,107°9′E	8	1516	13 Jul 2011	Male	Adult
BNU	P1909052 (paratype)	2–4	Specimen	Kuankuoshui, Guizhou, China	28°13′N,107°9′E	8	1516	14 Jul 2011	Male	Adult
BNU	P1909053 (paratype)	2–4	Specimen	Kuankuoshui, Guizhou, China	28°13′N,107°9′E	8	1516	14 Jul 2011	Male	Adult
BNU	P1909054 (paratype)	2–4	Specimen	Kuankuoshui, Guizhou, China	28°13′N,107°9′E	8	1516	14 Jul 2011	Male	Adult
BNU	P1909055 (paratype)	5	Specimen	Kuankuoshui, Guizhou, China	28°13′N,107°9′E	8	1516	18 Jul 2011	Male	Adult
IOZ	19988	\	Photo, song	Hunan; Badagong Shan	29°40.820′N,109°45.214′E	6	1615	5 June 2010	Male	Adult
IOZ	19989	\	Photo, song	Hunan; Badagong Shan	29°40.820′N,109°45.214′E	6	1500	5 June 2010	Male	Adult
IOZ	19990	\	Photo, song	Hunan; Badagong Shan	29°40.820′N,109°45.214′E	6	1550	6 June 2010	Male	Adult
IOZ	19991	\	Photo, song	Hunan; Badagong Shan	29°40.820′N,109°45.214′E	6	1500	6 June 2010	Male	Adult
IOZ	19661	\	Photo, song	Sichuan: Longcangguo	c.29°6′N,102°.9′E	12	1810	26 May 2013	Male	Adult
IOZ	19662	\	Photo, song	Sichuan: Longcangguo	c.29°6 N′,102°.9′E		12	27 May 2013	Male	Adult
IOZ	19663	10	Photo, song	Sichuan: Laojunshan	28°70′N,104°.033′E	14	1350	27 May 2014	Male	Adult
IOZ	19665	11	Photo, song	Sichuan: Laojunshan	28°70′N,104°.033′E	14	1040	27 May 2014	Male	Adult

[a] Listed as MNHN 1896 in Dickinson et al. 2000; registered in 2013. [b] Considered *B. mandelli melanorhyncha* in Dickinson et al. 2000.

Diagnosis of species

If singing, *Locustella chengi* is easily distinguishable from *L. m. mandelli*/*melanorhyncha* by song, which is lower-pitched (midfreq of principal note <3.6 kHz and lowfreq of principal note <3.0 kHz; vs. ≥3.6 kHz and ≥3.0 kHz, respectively, in *mandelli/melanorhyncha*; Table 2), with relatively more drawn-out highamp part of the principal note (Figures 9 to 10). Morphologically, *L. chengi* typically differs in breeding plumage from *L. m. mandelli/melanorhyncha* by its greyer overall colour, lacking strong russet tones, especially pronounced above and on flanks (although there is overlap). Its non-breeding plumage is unknown. The tail of *L. chengi* is shorter and the wing longer, and therefore its (wing + culmen)/tail ratio (1.22–1.48) is larger than nearly all *L. m. mandelli* (1.00–1.23, one 1.33) and *L. m. melanorhyncha* (1.08–1.23) (Table 1).

Description of holotype

Upperparts from forehead to uppertail-coverts uniformly warm grey-brown. Folded wings and tail same colour as upperparts; centres to alula, secondary coverts, tertials, remiges and rectrices marginally darker and greyer. Ear-coverts slightly greyer than upperparts, with a few very thin pale streaks. Lores rather dark brown-grey. Rather thin supraloral stripe and crescent above eye pale greyish-white with a faint buffy tinge, forming short supercilium. Diffuse pale crescent below eye same colour. Throat whitish centrally, pale brownish-grey on the side with a faint yellowish tinge. Centre of breast pale brownish-grey with a faint yellowish tinge, side of breast slightly darker and browner. Barely visible darker spots at junction of throat and breast. Flanks uniformly warm grey-brown, similar to upperparts. Belly whitish with a pale dingy yellowish tinge, appears whitish from a distance. Undertail-coverts cold grey-brown with greyish-white tips on average 3.6 mm wide, basal ones narrower, more diffuse and more buffy-tinged (hence less distinct than terminal ones). Feathering on tibia similar to flanks. Underwing-coverts whitish, with a faint buffy tinge, stronger buffy on the under primary coverts. Bill black, slightly paler grey distally on lower mandible, especially on underside, and very tip of upper mandible. Gape pale yellowish-grey. Tarsus pale greyish-pink, paler on rear side, soles similar to rear side of tarsus, claws medium grey. Iris dark grey-brown. See photos of holotype accompanying recordings of the same individual on AVoCet (http://avocet.zoology.msu.edu.recordings/18335).

Measurements of holotype

Culmen length from skull 14.9 mm, from feathers 10.6 mm; wing length (flattened) 55 mm; tarsus length 17.8 mm; tail length 56.9 mm.

Phenotypic variation

All *L. chengi* specimens (Table 4) except BMNH 1914.6.12.101 (a juvenile; see below) are very similar to the holotype in plumage pattern and colour. The main variation relates to the colour of the central breast and dark spotting on the lower throat/upper breast (Figure 6). The base colour of the central breast varies from rather pale grey to medium dark grey-brown. Most individuals are either unspotted on the throat/breast or have very faint darker spots at the junction of the throat/breast, although one of the birds that we caught had quite profuse dark spotting. Also, a few individuals have a pale yellowish tinge to the belly.

Because *L. chengi* was not then recognized, a juvenile *L. chengi* (BMNH 1914.6.12.101; henceforth BMNH 101) was among those used as the basis for the description of the juvenile plumage of *L. mandelli* in Dickinson et al. (2000); however, two other juveniles, one of *L. m. mandelli* (BMNH 1886.7.8.1882) and the other of *L. m. melanorhyncha* (BMNH 1914.6.12.104), are very similar in plumage to *L. chengi* BMNH 101 (Dickinson et al. 2000), the only apparent differences being that the juvenile of *L. chengi* is slightly less reddish above, and that the dark flanks grade more into the belly in juvenile *L. chengi*, than in the juveniles of *L. m. mandelli* and *L. m. melanorhyncha*. In brief, the juvenile *L. chengi* BMNH 101 has very dark russet upperparts, a nearly unpatterned dark brown face, and unspotted dark greyish-brown breast, buffy-yellowish mid-underparts, dull fulvous-brown flanks and undertail-coverts, the latter with weak pale tips.

The iris colour has been found to vary noticeably among different individuals of *L. chengi* (and *L. mandelli*, previously also *L. thoracica* and *L. davidi*; pers. obs.), some having dark grey-brown irides, while others having markedly more rufous-coloured irides. We believe that the former are second-calendar year (first-summer) birds, whereas the latter are older.

Etymology

We are pleased to name *Locustella chengi* after the late Professor Cheng Tso-hsin (modern pinyin transcription Zheng Zuoxin) (1906–1998) in recognition of his unparalleled contributions to Chinese ornithology, of which his monumental work *A Synopsis of the Avifauna of China* (Cheng 1987) is the most widely known outside of China. We recommend the use of the English name Sichuan Bush Warbler.

Distribution, status, habitat, life history and conservation

Locustella chengi is endemic to China, breeding in Shaanxi, Sichuan, Guizhou, Hubei and northwest Hunan, with a single record from NW Jiangxi (Figures 1, 15). The winter range is unknown. It is locally common and does not seem to be under any imminent threat, as its habitat is widespread and not threatened. It occurs in mountainous areas, and we have observed it at 1000–2275 m a.s.l. (see Habitat and elevation, above). It is found on slopes as well as on flat ground, in open habitats with dense low vegetation of herbs and/or ferns, often in association with trees, such as in forest clearings and in sparse secondary forest. We have also observed *L. chengi* inside tea plantations. We have heard song activity from late April to mid-June, indicating that the breeding season begins mainly in May. We have no other data on breeding. Like other *Locustella* species, *L. chengi* is extremely secretive and usually difficult to observe, and normally keeps in dense cover; it creeps effortlessly through thick vegetation, and is capable of running quickly on the ground. During the breeding season, however, it may be brought into view by playback.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2012), and hence the new name contained herein is available under that Code from the electronic edition of this article. This published work and the nomenclatural act it contains have been registered in ZooBank, the online registration system for the International Commission of Zoological Nomenclature. The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: zoobank.org:act:CE89AF59-A3D5-4496-A8EC-84AC0CF4DAAA. The electronic edition of this work was published in a journal with ISSN 2053–7166, and has been archived and is available from the digital repository http://www.ncbi.nlm.nih.gov/pmc/.

Taxonomy of the other taxa in the *Locustella mandelli* complex

The *Locustella mandelli* complex, which was treated as a single species (e.g. Watson et al. 1986) until it was suggested that it be split into *L. mandelli*, *L. seebohmi*, *L. montis* and *L. timorensis*, mostly based on morphology (Dickinson et al. 2000), and the newly described *L. alishanensis* (Rasmussen et al. 2000), is clearly a clade of recently diverged taxa. Alström et al. (2011) suggested, based on a small sample of sequences, that the cyt*b* divergence between *L. mandelli* and *L. montis* was so slight that their status as separate species required further study. All except *L. m. mandelli*/*melanorhyncha* and *L. chengi* have disjunct distributions, either isolated continental (*L. mandelli idonea*) or island populations. *Locustella alishanensis*, despite being so similar to other taxa in morphology that it was overlooked as a new taxon for many years (Rasmussen et al. 2000), is most divergent, both with respect to cyt*b* and song, and would qualify as a species under any species concept. The taxonomic rank of the others is more open to discussion, and the interpretations of some suffer from a lack of data.

The Mt Victoria population of what is presently classified as *L. m. mandelli* is vocally distinct, although in most respects it agrees well with other populations of *L. m. mandelli/melanorhyncha*. No DNA samples or specimens are available from Mt Victoria. Our sequences from two specimens from the nearby Lushai hills in Mizoram are not divergent from other *mandelli/melanorhyncha*, indicating that the same might be true also for the Mt Victoria population. However, as both the Mizoram specimens were collected in February, they may represent more northerly-breeding populations wintering in that area. DNA samples and specimens from Mt Victoria would be needed to evaluate the distinctness of that population.

With respect to the geographically isolated and poorly known south and central Vietnamese *L. mandelli idonea*, further data beyond that available to Dickinson et al. (2000) allow a better supported taxonomic conclusion. The three specimens we have examined differ consistently from *L.m. mandelli/melanorhyncha* in plumage, and photos of another (www.orientalbirdimages.org) show a fourth bird sharing these characters. Our three recordings of this taxon suggest that its song is consistently different, even more from *L. m. mandelli*/*melanorhyncha* and *L. chengi* than the two latter are from each other. The cyt*b* divergence is marginally smaller than between *mandelli/melanorhyncha* and *L. chengi* (though the sample of only one *idonea* precludes evaluation of the variation). Given that we conclude that *mandelli/melanorhyncha* and *L. chengi* are separate species, we consider that the even more striking vocal and plumage differences between *mandelli*/*melanorhyncha* and *idonea* indicate that species status is warranted for the latter.

With regard to *L. seebohmi* vs. *L. montis*, the morphological differences between adults are as strong as between any two members of this complex (though only one specimen of *L. seebohmi* exists). The vocal differences between *L. seebohmi* and *L. montis* from Mt Sundoro/Sumbing and, especially, compared to the putative *L. timorensis* from Alor are relatively trivial. There is conflict between our two phylogenetic analyses regarding the position of *seebohmi*, although both are uncertain. The cyt*b* divergence is slight, although it approaches the divergence between *mandelli/melanorhyncha* and *L. chengi*. Based on the distinct plumage and the slight song and cyt*b* differentiation, coupled with the large range discontinuity between this taxon (Luzon, northern Philippines) and *L. montis* (Java and Bali, Greater Sundas), *L. timorensis* (Timor-Leste) and the taxon on Alor, which would be a biogeographically anomalous distribution if treated as a single species to the exclusion of the other taxa, we provisionally continue to recognise *L. seebohmi* as a distinct species, acknowledging that more data are needed.

L. montis is morphologically distinct from the other taxa, and differs markedly in song from *L. m. mandelli/melanorhyncha* and *L. chengi*. However, especially the Mt Sundoro/Mt Sumbing birds have songs that are close to those of *L. seebohmi*, *L. timorensis* and the Alor taxon. The cyt*b* divergence is on a similar level to that between *L. m. mandelli/melanorhyncha* and *L. chengi*, and *L. montis* is monophyletic in the cyt*b* tree, albeit with low support (higher in BEAST than in MrBayes). In conclusion, based on morphology, song and cyt*b*, we support continued treatment of *L. montis* as a distinct species (but see circumscription, below). However, as noted above, we believe that there may be one or more undescribed taxa within what is presently treated as *L. montis*, especially given that plumage and mensural differences exist between birds from central vs. east-central and eastern mountains, and that there are pronounced vocal differences among localities within the range of *L. montis*. The variation in song among some of the mountains within Java and between Java and Bali is marked, and would seem to be on a level suggesting different species. However, cyt*b* does not support this: the cyt*b* divergence between our single sample from the vocally distinct, geographically isolated Bali population and our samples from Java is only 0.6 ± 0.2% (range 0.4–0.9%), and the divergences among our samples from Mt Sundoro, Mt Bromo and Mt Lawu, of which at least the latter is vocally distinct, are even lower (0.4 ± 0.0%), and the topology of the tree suggests variation similar to that within *L. m. mandelli/melanorhyncha* and *L. chengi*. Given the strong patterns of geographic variation in montane birds of Java (e.g., there are four well-marked subspecies of Island Thrush *Turdus poliocephalus* in the mountains of Java; Collar 2005), the lack of recognized taxa within the *L. montis* complex might be due to lack of specimens and thorough study; more research is needed.

The taxon *L. timorensis* is still poorly known, as there are only two specimens and few sound recordings of what is undoubtedly this taxon. Morphologically, the specimens differ from the other taxa (except *L. alishanensis*) mainly in being distinctly paler above and drabber below with very weak pale undertail-covert edgings. The song of birds from Timor-Leste is reminiscent of songs of *L. montis* from especially Mt Sundoro and Mt Sumbing. The cyt*b* divergence from *L. montis* is only 0.5 ± 0.2% (range 0.3–0.7), which is higher than the intraspecific variation within *L. m. mandelli/melanorhyncha* and *L. chengi*, but with the same maximum value as within the latter. The cyt*b* trees indicate that *timorensis* might represent a separately evolving lineage, although more data are desirable. The song of the recently discovered population on Alor appears to be sufficiently similar to *L. timorensis* from Timor-Leste to most probably represent the same species. We provisionally favour treatment of *L. timorensis* as a subspecies of *L. montis*, and urge further study, especially of the Alor population, which might require designation as a new taxon.

Identity of one of the paralectotypes of *Cettia russula*

The name *Cettia russula* Slater, 1897, was based on a series of three syntypes from Fujian. Dickinson et al. (2000) showed that this series is a taxonomic composite, with two of the specimens being *Locustella luteoventris*, while the third (Museum of Comparative Zoology [MCZ] 129138) is *L. mandelli* (*sensu lato*). Dickinson et al. (2000) designated a lectotype of *Cettia russula* (BMNH 1898.1.28.65), thereby fixing the meaning of *russula* as a synonym of *luteoventris*. However, given our findings that *L. mandelli melanorhyncha* as understood by Dickinson et al. (2000) includes *L. chengi*, we sought to verify the identity of MCZ 129138 for the record, even though the meaning of the name *russula* was unambiguously fixed long prior to our realization that a new species is involved. On our request (and with detailed instructions on our measurement techniques), J. Trimble measured the wing and tail of MCZ 129138. The measurements he provided (wing length = 51 mm; tail length = 62 mm, which gives a wing/tail ratio of 82.3) are unambiguously those of *L. mandelli melanorhyncha* (*sensu stricto*; Table 1).

Revised distribution of *melanorhyncha*

The subspecies *Locustella mandelli melanorhyncha* (Rickett, 1898), described from Fujian province, China, has usually been restricted to birds of southeastern China, from Hubei to Fujian and wintering to Hong Kong (e.g., Dickinson et al. 2000, followed by Bairlein et al. 2006), although earlier treatments were highly variable in this respect (see e.g. Dickinson et al. 2000). Although Dickinson et al. (2000) argued for this restriction based on the shorter tail and often paler upperparts of *L. m. melanorhyncha* compared to *L. m. mandelli*, we now know that these data and observations were influenced by the presence of a few *L. chengi* in the sample (notably the two BMNH specimens 1914.6.12.101 and 102, especially because many of the comparisons were made at the NHM UK).

In reevaluating the data partly in light of the removal of *L. chengi* specimens from the sample of *L. m. melanorhyncha*, it became clear that the circumscription of *melanorhyncha* to southeast China was artificial. Based on broad patterns of avian distribution, biogeographically it seems more likely that birds from Tonkin (N Vietnam) and northern Laos would be of the same taxon as those from southeast China than identical to Himalayan birds.

Indeed, when birds from these areas are pooled with southeast Chinese birds, variances of univariate measurements are typically lower both for *L. m. mandelli* and *L. m. melanorhyncha*, and PCAs show that the two cluster largely separately, even though only bill and wing lengths are significantly different. However, with a larger sample it seems almost certain that greater levels of statistical significance would be found between measurements of *L. m. mandelli* and *L. m. melanorhyncha* (*sensu stricto*), the latter being on average smaller in many measurements than the former. Despite this, no genetic or vocal differences between the two subspecies were found in the present study.

In summary, on the basis of this evidence we recommend continued recognition of *L. m. melanorhyncha* as a subspecies of *L. mandelli*, but with an expanded range including northern Laos and Tonkin. The subspecific allocation of the population in northern Thailand is unclear because all Thai specimens studied were too incomplete to include in multivariate analyses. Sichuan birds best fit with *L. m. mandelli* on size but cannot be definitely determined to subspecies on the basis of available material. Whether differences are clinal and exactly where the range limits lie requires further investigation that is outside the scope of this study.

Conclusions

The Sichuan Bush Warbler *Locustella chengi*, which we describe herein, is endemic to China, where it breeds locally commonly at mid-elevations in the mountains of Sichuan, Shaanxi, Hubei, Hunan and Guizhou provinces, with a single record from NW Jiangxi province. It is unknown from the non-breeding season. It differs consistently from *L. m. mandelli/melanorhyncha* in song and morphology, and these two species are reciprocally monophyletic in our analyses of cyt*b*, although their exact positions in the tree are unresolved. *Locustella chengi* and *L. m. mandelli/melanorhyncha* are locally sympatric in S Sichuan, where they are almost exclusively altitudinally segregated, and we believe that they are reproductively isolated. That is remarkable in view of their slight cyt*b* divergence (0.6–1.3/1.4%, mean 1.0%), which is considerably lower than between most other bird species. The other taxa, *seebohmi*, *montis* and *timorensis*, which are currently classified as separate species, and *idonea*, which is treated as a subspecies of *L. mandelli*, are all allopatric. Their taxonomic ranking is open to question, mainly because of recent divergence and slight differentiation, but also due to lack of data. However, with respect to *seebohmi*, *montis* and *idonea*, their overall differences from each other and from *L. m. mandelli/melanorhyncha* and *L. chengi* are almost on the same scale as those between *L. m. mandelli/melanorhyncha* and *L. chengi*, although the variation in song is greater within what is presently treated as *L. montis* than between some of these taxa. Accordingly, we tentatively consider *L. seebohmi*, *L. montis* and *L. idonea* to be separately evolving lineages, which deserve treatment as species, although we prefer to treat the taxon *timorensis* as a subspecies of *L. montis*. We note that further research will probably show further differentiation within *L. montis*, and should also cast light on the recently discovered population on Alor, for which only vocal data are presently available. We show that the Mt Victoria population is vocally distinctive but lacks a name and is unrepresented by specimens. We redefine the ranges of *L. m. mandelli* and *L. m. melanorhyncha*. Future research should focus on the Mt Victoria population of *L. m. mandelli* and different populations of *L. montis*, including Timor and Alor birds.

Availability of supporting data

All new sequences have been submitted to GenBank (Additional file 1: Table S1), and all sound recordings used to produce sonograms are available either in AVoCet (http://avocet.zoology.msu.edu), xeno-canto (http://www.xeno-canto.org) or Macaulay Library (http://macaulaylibrary.org).

Additional files

Additional file 1: Table S1. Localities of DNA and song samples for the *Locustella mandelli* complex.

Additional file 2: Table S2. Summary statistics for PCAs for the *Locustella mandelli* complex. First external measurement character set was maximized for inclusion of specimens of all taxa, so no bill measurements were included. Second external measurement character set includes only birds in adult or first-winter plumage sexed as males or unsexed. Loadings deemed especially important in bold italic, those of intermediate importance in bold only.

Additional file 3: Table S3. Univariate measurements of song variables of the *Locustella mandelli* complex. 1a – lowamp part of principal note; 1b – highamp part of principal note; see Figure 2 for further explanation of terms. MANOVA was used to assess the overall differences between all 18 variables (Pillai's Trace = 0.943, F = 78.664, $p < 0.001$), followed by one-way ANOVA for each variable.

Additional file 4: Table S4. Univariate measurements of song variables of different *L. montis* populations. 1a – lowamp part of principal note; 1b – highamp part of principal note; see Figure 2 for further explanation of terms.

Additional file 5: Table S5. Summary of function results of DFAs on song of (A) the *L. mandelli* complex (see Figure 12) and (B) *L. mandelli* and *L. chengi* (see Figure 13). Only results for functions with significance levels $p < 0.05$ are presented.

Additional file 6: Table S6. Function Coefficients. Standardized Canonical Discriminant Function Coefficients for DFAs on song of (A) the *L. mandelli* complex (see Figure 12) and (B) *L. mandelli* and *L. chengi* (see Figure 13). Only results for functions with significance levels $p < 0.05$ are presented. See Additional file 1: Table S1 for relevant statistics.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

The original planning was done by PA, CX and UO, with later input from PCR In addition, PA collected specimens, DNA samples, sound recordings, morphometrics and other data in the field, carried out the vocal and phylogenetic analyses, and wrote the first draft; CX collected specimens, DNA samples and sound recordings, and measured and statistically analysed the vocal variables; UO collected DNA samples and sequenced 60% of the samples (including all of the toepad samples); PCR collected and analysed the morphological data, and wrote the first draft of those sections; LD sequenced several *L. chengi*; BD collected much data in the field; JZ and YL collected DNA samples, sound recordings and other data in the field; PJL and GJC. collected DNA samples, morphometrics, sound recordings and other data in the field; HLM. collected a specimen and DNA sample of *idonea*; PIH collected sound recordings and other data in the field; S.G. participated in the collection of the holotype of *L. chengi*; TC sequenced three *L. chengi*; YL, YZ and FL conceived the study, and YL prepared the map figures. All of the authors read and approved of the manuscript.

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