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# Description of the song of the Nilgiri Thrush (*Zoothera [aurea] neilgherriensis*) and song differentiation across the *Zoothera dauma* species complex

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## Abstract

**Background:** Taxonomic treatment of the *Zoothera dauma* species complex is highly variable and has been hampered by the absence of song recordings for the Nilgiri Thrush (*Zoothera [aurea] neilgherriensis*).

**Methods:** I obtained two recordings of the song of *neilgherriensis* from southern Indian. Here I publish sonograms and analyze song recordings for all but one currently described taxon from the Eurasian portion of the geographic range of this species complex. Principal component analyses were used to investigate song differences between taxa.

**Results:** The song of *neilgherriensis* is a highly complex series of strophes remarkably similar to the song of the insular *Zoothera major*. Vocal analyses across the complex indicate four key groups of taxa differentiated in their songs: (1) simple flat whistled songs which include the northern *aurea*, *toratugumi* and the undescribed Taiwan population; (2) eastern populations of *dauma* (reported here for the first time) which sing like northern birds but with much broader bandwidth, (3) strongly down-slurred, thin whistles of tropical resident *imbricata* of Sri Lanka and *horsfieldi* of Indonesia, and (4) highly complex songs of Himalayan *dauma*, *neilgherriensis* and *major*.

**Conclusions:** *Zoothera dauma* is unlikely to represent a single species given the simple singing populations from its eastern range and highly complex song from the Himalayan portion of its range. *neilgherriensis* should either be transferred from *Zoothera aurea*, where it is currently classified as a subspecies, and be placed as a subspecies within *Z. dauma* from the Himalayas or it should be recognized as a distinct species. Given the small number of songs available for analyses, I suggest the former course until it can be clearly demonstrated that *neilgherriensis* and Himalayan *dauma* are vocally distinct.

**Keywords:** Nilgiri Thrush, *neilgherriensis*, *Zoothera dauma*, Song, Taxonomy

## Background

The *Zoothera dauma* species complex contains eight taxa (*dauma*, *aurea*, *toratugumi*, *iriomotensis*, *major*, *horsfieldi*, *neilgherriensis*, *imbricata*) on the Eurasian side of Wallace's Line (Fig. 1), with additional taxa distributed in Australasia which will not be considered here. The Eurasian taxa are often considered to comprise a single, highly

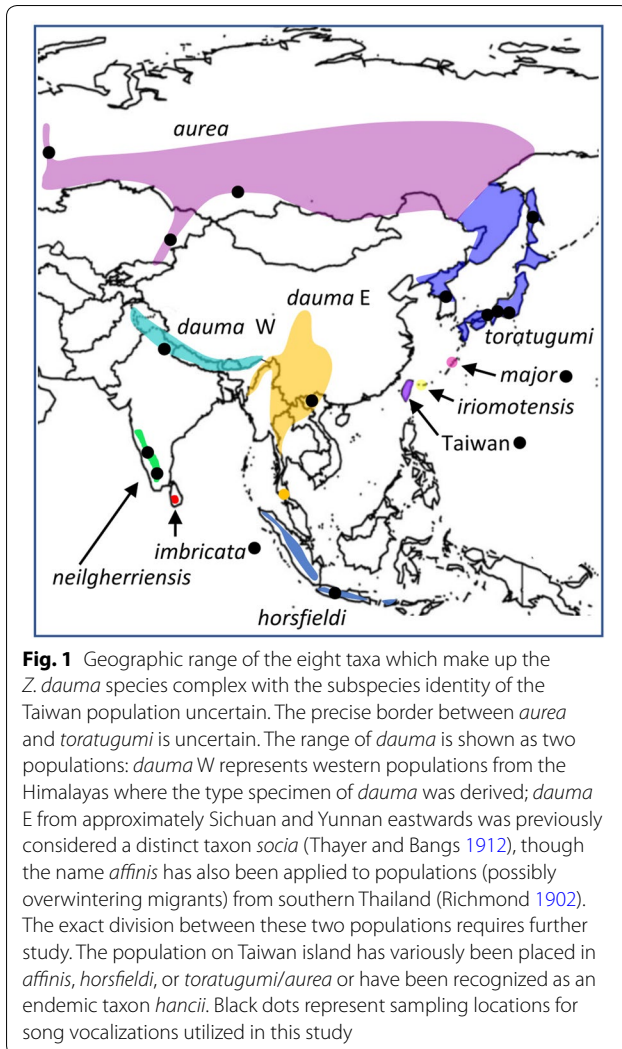
polytypic species, with taxa differing in body dimensions and/or plumage and some of them also in song (del Hoyo et al. 2005). Alternatively, these differences have led to recognition of as many as six species (*Z. dauma*, *Z. aurea* which also includes *toratugumi* and *iriomotensis*, *Z. major*, *Z. horsfieldi*, *Z. neilgherriensis*, and *Z. imbricata*) (Sangster et al. 1998; Rasmussen and Anderton 2005), though del Hoyo and Collar (2016) recently recognized only three species: (1) *Z. dauma* with a highly variable song, (2) *Z. major* with a song like *Z. dauma* but with larger body size, and (3) *Z. aurea* which combines all the

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other Eurasian taxa on the pretense that they shared a similar simple song consisting of a flat whistle.

The song of the Nilgiri Thrush (*neilgherriensis*)—geographically isolated in the Western Ghats of India—has never been described, leading Clement and Hathway (2000) to conclude that if “*neilgherriensis* does in fact sing, it may be of such quality and/or given for so short a period that it has remained undetected.” del Hoyo and Collar (2016) assigned *neilgherriensis* to *Z. aurea*, given its geographic proximity to *Z. a. imbricata* of Sri Lanka, which, like other taxa assigned to *Z. aurea*, has a simple song comprised of long whistled notes. Alternatively, *neilgherriensis* could be allied with *Z. dauma* distributed to the north.

Like *neilgherriensis*, recordings of many forms of the *Z. dauma* complex are scarce. For example, despite its broad geographic range, only a single recording of *dauma* was available in the Macaulay Library and none were found

on Xeno-Canto. Likewise, while the song of *horsfieldi* was verbally described (Clement and Hathway 2000), only a single song was available from a private recording and no sonograms have previously been published or analyzed. The song of *imbricata* was first recorded in 1997 (Clement and Hathway 2000). In contrast, many recordings are available for the migratory forms *aurea* and *toratugumi* and for the insular form *major*. This dearth of recordings for many taxa has made assessment of species limits in this complex difficult.

Here I describe the song of *neilgherriensis* from recordings I made from two separate individuals at different localities in 2008. I obtained at least one recording for all Eurasian members of the *Z. dauma* complex, with the sole exception of the recently described insular subspecies *Z. a. iriomotensis* of Japan. I performed a principal component analysis of songs from across the species complex to determine if *neilgherriensis* is vocally distinctive, and whether it groups more closely with *Z. aurea* or *Z. dauma*. Using this dataset I discuss the biogeographic patterns of song differentiation in the *Z. dauma* complex and its taxonomic implications.

## Methods

Digital recordings were obtained using a Sennheiser K6/ME-62 omnidirectional microphone mounted in a Mineroff Electronics SME-PR-1000 parabolic reflector and recorded in 16-bit wav format into an Edirol digital recorder. On March 16, 2008, I obtained a recording of the song of *neilgherriensis* at 1930 m from Pampadumchola National Park, Kerala, near Top Station (in the vicinity of 10.125°N, 77.252°W) at around 7 AM under clear conditions. The bird was not seen prior to or during the recording, but the individual briefly responded to playback of the recording immediately afterward. That evening, I edited the song in RAVEN Pro 1.5 (Cornell Laboratory of ornithology, Ithaca, USA) to shorten a long interval between two episodes of singing on the recording, and to minimize background noises. The next day I encountered a second individual of *Z. neilgherriensis* in a different section of the park (ca. 10.132°N; 77.252°W; 1860 m) at 10 AM. The bird was not vocalizing. I placed a Pignose field speaker 12 m from the bird and played the edited recording. The bird approached to 9 m from the speaker and flew back and forth several times in the vicinity of the speaker without approaching any closer. The song of a second bird was recorded and the bird observed well and positively identified at close range at ca. 2200 m in Cairn Hill Reserve Forest near Ooty, Tamil Nadu on March 19, 2008 at 11:30 AM under light rain.

Songs of all other taxa except *iriomotensis* (song undescribed) were obtained from Xeno-canto (2017), the Macaulay Library (2017), AvoCET (2017), and the

private holdings of Craig Robson and Bas van Balen and were analyzed together with my *neilgherriensis* vocalizations in Raven Pro using the default settings. Eight transformed measurements were obtained for each song strophe (a single phrase usually consisting of one note, more rarely of two or more notes strung in quick succession, with strophes separated by a pause) in these recordings (see RAVEN Pro manual for precise definitions): (1) centre frequency, (2) 90 percentile bandwidth, (3) strophe length, (4) aggregate entropy, and (5) change in frequency. The latter was the difference in centre frequency of the first and last 0.1 s of the song strophe averaged across five or more song strophes and divided by the standard deviation across song strophes. This value is positive if strophes decline in frequency and negative if they increase. When possible, I analyzed 10 or more strophes per song. Mean values across strophes within a recording were obtained for the first four measurements and these were log transformed. A principal component analysis was performed in R 3.4.0 (R Core Team 2017) using the *prcomp* function with data centered and scaled.

## Results

Table 1 compares strophe length and frequency between taxa and Fig. 2 shows examples of the range of song variation across and within taxa. The song of *neilgherriensis* (Table 1, Fig. 2) is comprised of a slow series of highly variable strophes that varied greatly in pitch. Harmonics were not observed on either sound recording. Notes were blurry rather than pure whistles and strophe shape varied greatly and included various fast warbles, as well as both strongly down-slurred and up-slurred strophes, and a variety of strophes with more complex shape. Strophe length was similar for the two recordings and ranged from 0.1 to 0.8 s (Table 1). Spacing between notes differed between the two recordings

with the Top Station recording at a much slower pace. (Top Station, range = 2.8–8.5 kHz; mean = 5.4 kHz,  $n = 13$ ; Ooty, range = 0.2–4.39 s; mean = 2.2 s,  $n = 36$ ).

The first PC was positively loaded mostly by bandwidth and aggregate entropy and negatively loaded by song length. I interpret large values to represent short strophes possessing high variability in frequency within each strophe. *neilgherriensis*, *dauma* (Himalayas) and *major* had large values for PC 1, while *aurea*, *toratugumi*, the Taiwan population, *imbricata* and *horsfieldi* had small values. The Vietnam recording of *dauma* had intermediate values. The second PC was negatively loaded by centre frequency and positively loaded by change in frequency. Large values indicate songs with low frequency in which frequency declined through the song. This PC clearly differentiated *imbricata* and *horsfieldi* from other species. Both these species show a strong downturn (i.e. negative slope) through their songs (Fig. 2). I also plotted change in frequency versus log bandwidth (Fig. 3c) as these two variables clearly separate out the various groups.

## Discussion

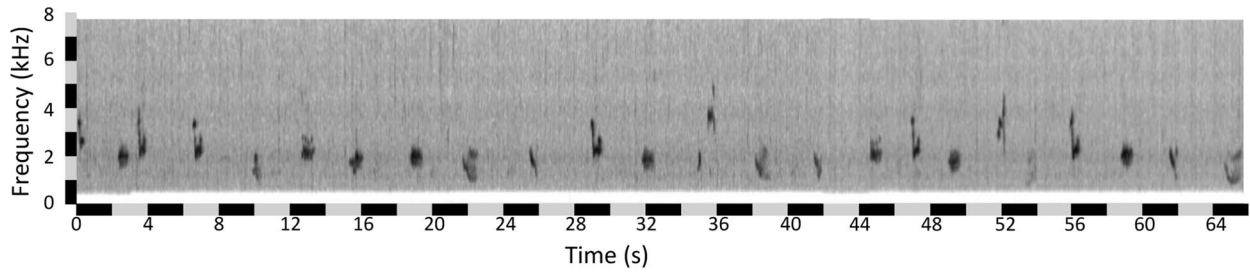
Songs of the various taxa fall into four, mostly distinct groupings: (1) simple flat whistled songs sung by the migratory *aurea*, *toratugumi*, and the sedentary population from Taiwan island; (2) simple songs similar to group 1, but with much broader bandwidth sung by *dauma* from Vietnam; (3) simple down-slurred whistled songs sung by *imbricata* and *horsfieldi*; and (4) complex songs with varied strophes sung by *major*, western Himalayan *dauma*, and *neilgherriensis* (Figs. 2, 3). These four vocal groupings are at odds with the taxonomic treatment in del Hoyo and Collar (2016) in two respects. First, del Hoyo and Collar (2016) treated *neilgherriensis* as a subspecies of *Z. aurea*. However, the complex strophes that

**Table 1** Mean (range) for 5 measurements from songs of the *Z. dauma* species complex

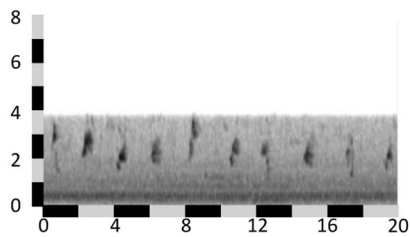
Taxon	<i>n</i>	Length (s)	Bandwidth (s)	Centre frequency (kHz)	Lower frequency (kHz)	Upper frequency (kHz)
<i>neilgherriensis</i>	2	0.31 (0.1–0.8)	0.81 (0.34–1.98)	2.26 (1.38–3.70)	1.86 (0.95–3.53)	2.67 (1.98–4.05)
<i>major</i>	10	0.34 (0.04–0.9)	1.38 (0.38–6.80)	2.85 (1.50–8.72)	2.26 (1.13–8.53)	3.65 (1.81–10.59)
<i>dauma</i> (Himalayas)	1	0.15 (0.1–0.3)	1.72 (0.52–5.34)	4.06 (1.46–7.06)	3.27 (1.29–6.20)	4.99 (2.15–8.53)
<i>dauma</i> (Vietnam)	1	0.46 (0.4–0.5)	0.52 (0.26–0.60)	2.67 (2.15–3.62)	2.42 (2.07–3.53)	2.93 (2.50–3.79)
<i>aurea</i>	11	0.57 (0.3–1.1)	0.14 (0.09–0.26)	2.70 (1.29–4.91)	2.63 (1.29–4.82)	2.77 (1.38–5.00)
<i>toratugumi</i>	9	0.45 (0.3–0.7)	0.17 (0.09–0.34)	2.64 (1.81–5.86)	2.56 (1.72–5.68)	2.73 (1.89–6.03)
Taiwan Is.	2	0.57 (0.3–0.8)	0.16 (0.09–0.26)	2.75 (1.55–5.25)	2.67 (1.46–5.17)	2.84 (1.64–5.34)
<i>imbricata</i>	2	0.40 (0.3–0.6)	0.29 (0.17–0.43)	2.03 (1.98–2.15)	1.91 (1.81–1.98)	2.20 (2.15–2.41)
<i>horsfieldi</i>	1	0.49 (0.4–0.6)	0.49 (0.34–0.52)	2.70 (2.58–2.76)	2.57 (2.50–2.67)	3.02 (2.93–3.10)

Frequency measurements and bandwidth are in units of kilohertz and length in seconds. Lower Frequency is measured at the 5th percentile of energy and Upper Frequency at the 95th percentile. Bandwidth occurs between these. Song length is measured between the 5th and 95th percentile energies. Mean values for each measurement were obtained across strophes within a recording and then were averaged across recordings for each taxon to obtain mean values. The range represents low and high values obtained across replicate strophes both within and between individuals

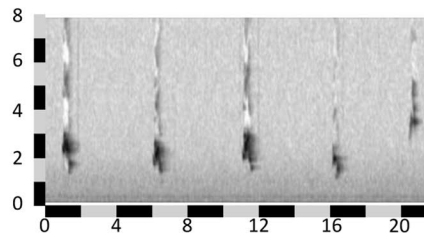
**a** *neilgherriensis* (Ooty, Tamil Nadu; India)



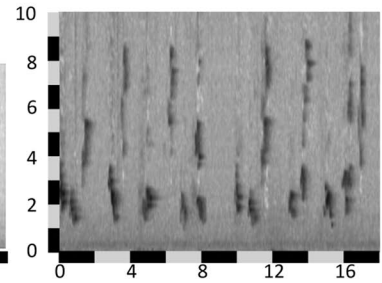
**b** *neilgherriensis* (Top Station, Kerala)



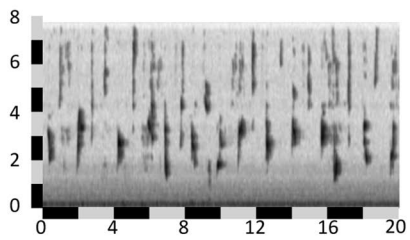
**c** *major* (Amami Ōshima Is., Japan)



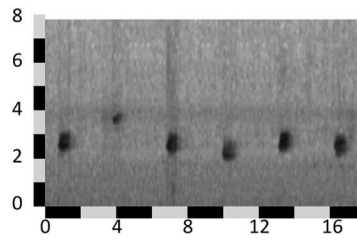
**d** *major* (Amami Ōshima Is)



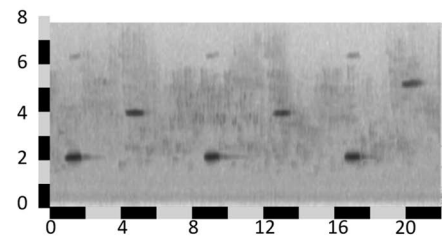
**e** *dauma* (Uttaranchal, India)



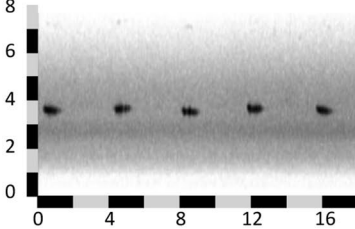
**f** "*dauma*" (N. Vietnam)



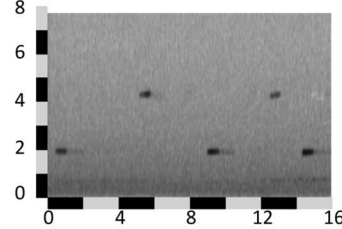
**g** *aurea* (Ural Mtns, Russia)



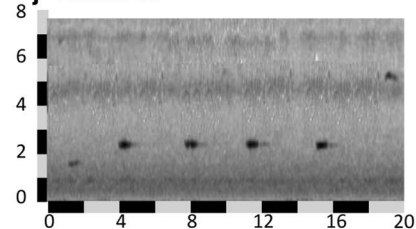
**h** *toratugumi* (Japan)



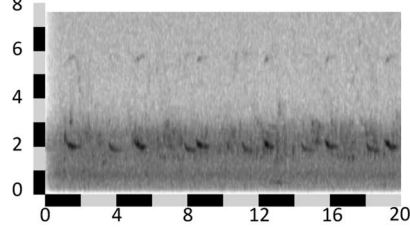
**i** *toratugumi* (Japan)



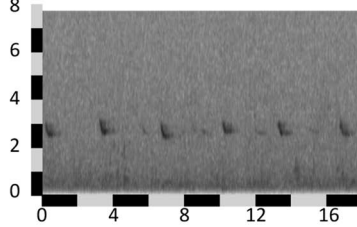
**j** Taiwan Is.



**k** *imbricata* (Sri Lanka)



**l** *horsfieldi* (Java)



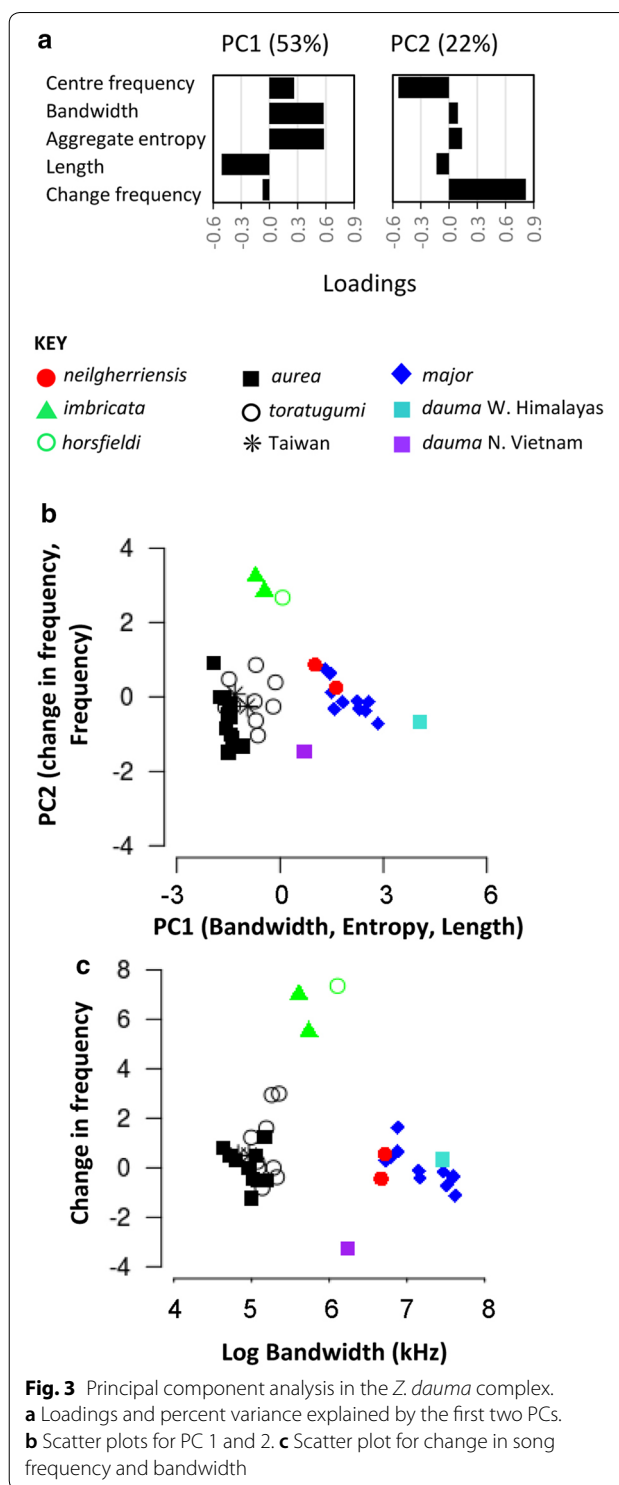
**Fig. 2** Sonograms of *neilgherriensis* and other Eurasian taxa belonging to the *Z. dauma* species complex. Accession numbers from left to right: **a** *neilgherriensis* (ML111731231), **b** *neilgherriensis* (ML111727651), **c** *major* (AV18778), **d** *major* (AV18779), **e** *dauma* India (ML16952), **f** *dauma* N. Vietnam (Craig Robson recording); **g** *aurea* (XC118523); **h** *toratugumi* (XC286220); **i** *toratugumi* (XC79382); **j** Taiwan Is. (XC268893); **k** *imbricata* (AV6763); **l** *horsfieldi* (Van Balen recording). Sonograms are drawn to scale. Background bird songs were edited out of some sonograms. Sonogram in **b** has intervals between strophes shortened. Intervals were not manipulated in other sonograms

**Table 2 Recordings analyzed**

Taxon	Country	Region	Accession number
<i>toratugumi</i>	Japan	Kyoto	XC305906, XC362118, XC193561
<i>toratugumi</i>	Japan	Tokyo	XC372124, XC372117
<i>toratugumi</i>	Japan	Mt. Fuji	ML14145
<i>toratugumi</i>	South Korea	Daejeon	XC128641, XC128642, XC79669
<i>toratugumi</i>	Russia	Sahalinskaja	ML99837
<i>aurea</i>	Russia	Primorskiy	XC268117, ML91840; ML91844
<i>aurea</i>	Russia	Krasnoyarsk	XC377207
<i>aurea</i>	Russia	Perm	XC364885
<i>aurea</i>	Khazakistan		XC150106, XC373092
?	China	Taiwan	XC48162, XC278274
<i>major</i>	Japan	Amami-Oshima Is.	AV18778, AV18779, XC191079, XC155984, XC191083, XC191080, XC286175, XC191087, XC363833, XC363831
<i>dauma</i>	India	Uttarakhand	ML169652
<i>dauma</i>	Vietnam	Tam Dao	Craig Robson recording
<i>neilgherriensis</i>	India	Tamil Nadu (Ooty)	ML111731231
<i>neilgherriensis</i>	India	Kerala (Top Station)	ML111727651
<i>imbricata</i>	Sri Lanka	Horton Plains	AV6763 (2 individuals on recording)
<i>horsfieldi</i>	Indonesia	Java	Bas van Balen recording

Libraries: XC = Xeno-cantos, ML = Macaulay Library, AV = AvoCET

comprise the song of *neilgherriensis* are starkly different from the simple down-slurred whistles of *Z. a. imbricata* or the mostly flat whistles of *aurea* and *toratugumi*, and instead are similar to the recording of *Z. dauma* from the western Himalayas and remarkably similar to certain individuals of *Z. major* (Table 2, Figs. 2, 3). Second, the songs from northern Vietnam comprised simple, flat whistles similar to those from *aurea*, *toratugumi* and the unassigned Taiwan population, and starkly different from the recording of *Z. dauma* from the western Himalayas. However, the Vietnam recording differed from all sampled individuals of *aurea*, *toratugumi* and the Taiwan population in possessing a much larger strophe bandwidth (intermediate in this respect between these taxa and *major*) and thus is unlikely to represent the song of an overwintering or migrant individual of these other taxa. While this larger strophe bandwidth results in the Vietnam recording appearing intermediate between the



simple (generally narrow bandwidth) and complex (large bandwidth) groupings in PCA (Fig. 3), these recordings are otherwise consistent with the simple flat whistles produced by other members of the simple grouping

(Fig. 2). These results suggest the presence of a distinct taxon allied with *Z. aurea* rather than *Z. dauma* in the eastern part of its range (e.g. birds of Yunnan, Sichuan and surrounding areas were previously described as *Z. d. socia*; Thayer and Bangs 1912). Alternatively, possible plumage intergradation between *Z. aurea* and *Z. dauma* in south-east Asia has been reported (del Hoyo and Collar 2016) suggesting that these populations could be of hybrid origin.

The presence of birds with simple songs in Vietnam means that the simple singing *horsfieldi* of Indonesia no longer forms a geographic leapfrog pattern with the migratory simple singers of the far north, as was thought to be the case if the geographic range of complex singing *Z. dauma* extended from the Himalayas all the way to Vietnam (Fig. 1). However, other leapfrog patterns still do exist. Foremost, the insular range of *Z. major* is now even more strongly dissociated from the ranges of other complex singers if complex singing *Z. dauma* is restricted to the Himalayas. To the north of *Z. major* lies the range of the simple singing *toratugumi* in Japan, and simple singers also occur on Taiwan island to the south. The simple songs from the two birds from Taiwan island have narrow bandwidths and are similar to, and probably indistinguishable from the migratory *toratugumi*, but are distinct from geographically adjacent continental birds (e.g. Vietnam) which sing with increased bandwidth. A final leapfrog pattern involves the Sri Lankan endemic *imbricata* which is isolated from other simple singers in the far north and Southeast Asia, by the combined geographic ranges of the proximate *neilgherriensis* from the Western Ghats and the Himalayan *dauma*. Interestingly, *imbricata* groups closely with Indonesian *horsfieldi* in possessing strongly down-slurred whistled notes, a result that was not previously reported (e.g. by Clement and Hathway 2000). The presence of flat singing birds in Vietnam indicates another leapfrog pattern between these down-slurred singing taxa, or the possibility of an over-water dispersal event leading to the formation of these taxa. Assuming flat, down-slurred and complex singing taxa represent reciprocally monophyletic groupings (an assumption which cannot be verified without phylogenetic analysis of the complex), these geographic patterns suggest that long distance colonisations, or the generation of relict populations following a complex series of range expansions and contractions resulted in the current leapfrog patterns.

Should *neilgherriensis* be considered a distinct species? The complex song of this taxon clearly indicates it is vocally distinct from the simple singing taxa of *Z. aurea* with which it is currently considered conspecific by del Hoyo and Collar (2016). Whether *neilgherriensis* is specifically distinct from other complex singing taxa is

more difficult to assess. Both *neilgherriensis* recordings grouped closely in PCA space, but these were somewhat differentiated along PC 1 from the sole recording available of *Z. dauma* from the western Himalayas. The latter had considerably greater strophe bandwidth. However, *Z. major*, for which I analyzed 10 recordings, occupied a large region of PCA space and possessed considerable variation in bandwidth across recordings. Some recordings of *major* possessed bandwidths as narrow as those of *neilgherriensis* (these lacked high pitched strophes above 5 kHz) while others had bandwidths greater than those of Himalayan *dauma* (these had strophes that extended up to 8 kHz or more). *Z. major* also possessed considerable variation in strophe length across recordings which overlapped that of Himalayan *dauma*. The large variation observed within *Z. major* suggests that other complex singing taxa could have considerable variation in song across individuals, but more recordings are needed to verify this. If Himalayan *dauma* also possesses the same range of variation as *Z. major*, then *neilgherriensis* might not differ substantially from it and would probably best be considered a subspecies of *Z. dauma* when considering song characters alone. Given the low sample size of song recordings for *neilgherriensis* and *dauma* and the likely high variance in songs of *dauma*, I refrain from recommending that *neilgherriensis* be treated as specifically distinct from the Himalayan *dauma* at this time, though specific distinction may ultimately be the best option. Complex singers of the *Zoothera mollissima* complex have recently been shown to comprise at least two morphologically cryptic, sympatric species that separate elevationally and whose songs, though complex across all taxa involved, are nevertheless distinctive (Alström et al. 2016). These results for the *Z. mollissima* complex suggest that population differences in song composition amongst complex singers may contribute importantly to reproductive isolation, and the same may apply to the complex singers of the *Z. dauma* complex.

My data also suggest considerable variation in strophe shape and bandwidth amongst taxa which sing a simple, whistled song. On the basis of song differences alone, I suspect that the three groupings of simple singing taxa reported above could each represent distinct species level taxa. Additional species level taxa could be warranted if taking plumage divergence into account (i.e. *imbricata* and *horsfieldi* differ strongly in plumage, but less so in song). However, it would be premature to split these taxa now on the basis of so few vocal recordings.

## Conclusions

These results suggest that the widespread taxon currently described as *dauma* sings simple songs in the east portion of its range and complex songs in the western

Himalayas. Future work should aim to increase the sample size of recordings for *dauma* from both the east and west to determine if two taxa are involved, and if so, what their respective range limits are. My analyses also suggest that *neilgherriensis* sings complex songs highly distinct from *Z. aurea* with which it has been considered conspecific by del Hoyo and Collar (2016) and that it should either be regarded as a subspecies of *Z. dauma* or as its own distinct species. Additional species level taxa likely occur amongst the simple singing taxa, but a full taxonomic revision of the *Z. dauma* species complex will require a much larger sample size of vocal recordings, playback experiments between various taxa pairs, and detailed analyses of morphometrics, plumage, and genetics.

#### Authors' contributions

JTW obtained field recordings of the Nilgiri Thrush, performed analyses and wrote the manuscript. The author read and approved the final manuscript.

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#### Competing interests

None.

#### Availability of data and materials

See Table 2.

#### Consent for publication

Several private recordings were provided to me as indicated in Table 2.

#### Ethics approval

Not applicable.

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