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Cryptic species-level diversity in Dark-throated Oriole *Oriolus xanthonotus*

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SUMMARY.—Borneo is part of the Sundaland biodiversity hotspot, yet this large tropical island still harbours much unrecognised biodiversity. In this integrative study, we combine the results from phylogenomic, bioacoustic, biometric and morphological analyses, and show that the Sundaic species Dark-throated Oriole *Oriolus xanthonotus* comprises two species-level taxa, both of which occur on Borneo. The eastern species, here re-named Ventriloquial Oriole *O. consobrinus*, is characterised by plumage distinctions, most notably a more male-like coloration in females, and a characteristic ventriloquial song unique among the region's orioles. The precise contact zone of the two species on Borneo is incompletely mapped. Their populations on Borneo show pronounced character displacement whereby individuals of *O. xanthonotus* on other landmasses are significantly larger than Bornean individuals, presumably to prevent non-adaptive hybridisation with the larger Ventriloquial Oriole along their Bornean contact zone.

Borneo, the third largest island on Earth, forms part of the South-East Asian equatorial rainforest belt known as Sundaland (Fig. 1). The island boasts unusually high avian diversity and is well known ornithologically for its distinct montane endemic avifauna, featuring roughly 1–2 dozen endemic bird species depending on taxonomic treatment (MacKinnon & Phillipp 1993, Eaton *et al.* 2021). However, despite being c.500 km from the nearest part

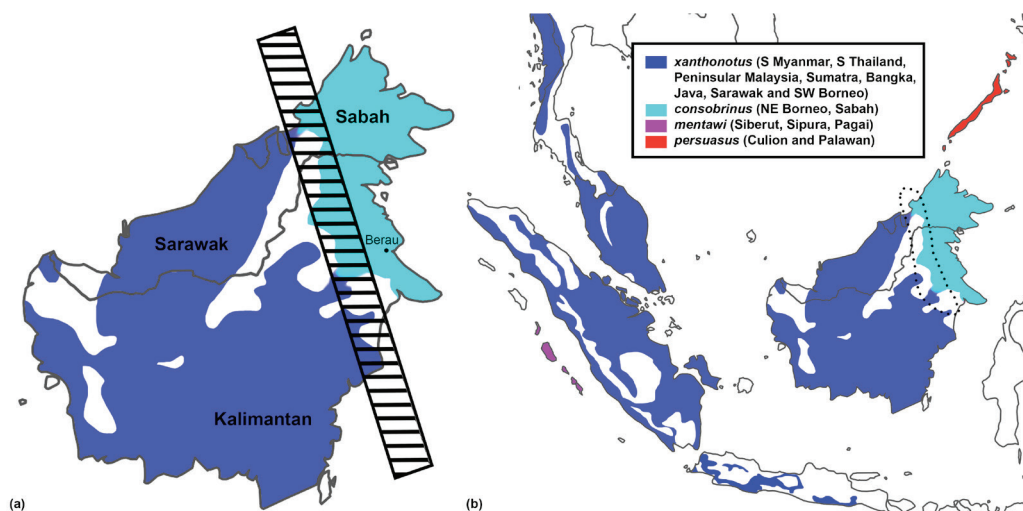


Figure 1. Distribution map of Dark-throated Oriole *Oriolus xanthonotus*, following Walther & Jones (2020). (a) Distribution of Bornean *O. x. xanthonotus* and *O. x. consobrinus*. Barred rectangle refers to possible contact zone between the two taxa. (b) Distribution map of all four taxa within the *O. xanthonotus* complex.

of the Asian mainland in the Malay Peninsula, Borneo's endemic lowland avifauna has traditionally been considered rather limited. In the taxonomic traditions of the 20th century, the vast majority of Borneo's lowland rainforest birds were considered part of more widely distributed Sundaic species whose ranges often also include Sumatra, Java and Peninsular Malaysia (MacKinnon & Phillipps 1993, Sheldon *et al.* 2015). It has taken a steady stream of molecular and bioacoustic work to reveal that the populations of some Bornean lowland or hill forest birds are more distinct than previously anticipated, a few even at species level, thereby further boosting the island's number of endemic species (Moyle *et al.* 2005, Lim *et al.* 2010, 2017, Moyle *et al.* 2011, Ng *et al.* 2016, 2017a, Gwee *et al.* 2019, Cros *et al.* 2020).

Borneo's distribution of lowland endemism constitutes one of the world's most unusual biogeographic patterns, whose origin continues to require a satisfactory explanation. The greatest part of Borneo's lowland endemic birds—both among species traditionally recognised and those elevated to species via recent research—is restricted to the north-east of the island. Here labelled 'Sabah endemics' or 'Sabah specialists', these species are almost entirely confined to the state of Sabah, although some are known to spill over slightly into adjacent parts of North and East Kalimantan, Sarawak, and even Brunei. Most Sabah endemics are replaced over the rest of Borneo by a more widespread sister species that usually also occurs on Sumatra, Peninsular Malaysia, and sometimes even Java. This biogeographic division into Sabah and the remainder of Borneo along a suture zone, comprising multiple roughly parallel contact zones among avian taxa, exists against the backdrop of a conspicuous lack of geographic boundaries (Sheldon *et al.* 2009, Rheindt 2021), as the position of Borneo's largest rivers and mountains is incongruent with the divide.

The cataloguing of Borneo's avian endemism remains far from complete. Recent taxonomic treatments have suggested that splits between Sabah and the rest of Borneo may become necessary in approximately another dozen bird species (Eaton *et al.* 2021). In this study, we present evidence for one such taxonomic split in the Dark-throated Oriole *Oriolus xanthonotus* complex. This species is a typical Sundaic rainforest denizen, distributed from the southernmost tip of Myanmar in the Thai-Malay Peninsula through Sumatra, Java and Borneo to Palawan, in the south-west Philippines. Four subspecies have long been recognised, two of which occupy smaller marginal islands (*mentawi* on the three main Mentawai Islands of Siberut, Sipora and Pagi, off western Sumatra, and *persuasus* on Palawan and some smaller satellites; Fig. 1). Among the two more widespread subspecies, *consobrinus* is said to be restricted to northern, central and eastern Borneo (including Sabah), whilst nominate *xanthonotus* occurs in the remainder of Borneo, Sumatra, Java and the Thai-Malay Peninsula. The precise boundary between the two subspecies on Borneo remains to be elucidated.

Recent genomic work on Old World orioles (Jönsson *et al.* 2019) has uncovered unexpected relationships and divergences among Asian oriole species that possibly warrant taxonomic adjustments. Most of these refer to island taxa or populations otherwise isolated geographically. However, one complex that stands out is the Dark-throated Oriole, with two distinctive forms co-occurring on one landmass (Borneo) and presumably overlapping or abutting in range. Here we present parts of Jönsson *et al.*'s (2019) genomic data and add bioacoustic, biometric and morphological analyses to propose dividing Dark-throated Oriole into two species.

Materials and Methods

For genomic analyses and methods we refer to Jönsson *et al.* (2019). For phenotypic analyses, we measured 59 specimens of Dark-throated Orioles deposited in the Raffles

TABLE 1
List of specimens measured. All specimens are from the Raffles Collection in the Lee Kong Chian Museum of Natural History, Singapore.

| Taxon | Landmass or state of collection | Locality | Collection date | Sex | Specimen registration number |
|--------------------|---------------------------------|---|-------------------|--------|------------------------------|
| <i>xanthonotus</i> | Sarawak | ‘Belingeang’ (probably Bukit Belingan south of Miri) | 17/05/1917 | Male | 3.18788 |
| <i>xanthonotus</i> | Sarawak | ‘Bukar’, Samarahan (near Kuching) | 25/10/1919 | Male | 3.18789 |
| <i>xanthonotus</i> | Sarawak | ‘Bukar’, Samarahan (near Kuching) | 15/11/1919 | Male | 3.1879 |
| <i>xanthonotus</i> | Sarawak | ‘Saribas’ | 01/03/1932 | Male | 3.18795 |
| <i>xanthonotus</i> | Sarawak | ‘Lio Matu, Baram District’ (now Lio Matoh, near Miri) | 13/10/1920 | Male | 3.1878 |
| <i>xanthonotus</i> | Sarawak | ‘Lio Matu, Baram District’ (now Lio Matoh, near Miri) | 23/10/1920 | Male | 3.18781 |
| <i>xanthonotus</i> | Sarawak | ‘Long Musan’, Baram, Sarawak | 05/10/1920 | Male | 3.18782 |
| <i>xanthonotus</i> | Sarawak | ‘Borneo, Baram’ | 05/03/1905 | Male | 3.18783 |
| <i>xanthonotus</i> | Sarawak | ‘Sungei Lenian, Tenjar, Baram’ | 24/08/1919 | Male | 3.18786 |
| <i>xanthonotus</i> | Sarawak | ‘Saribas’ | 01/01/1917 | Male | 3.18791 |
| <i>xanthonotus</i> | Sarawak | ‘Saribas’ | 15/05/(illegible) | Male | 3.18794 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 11/08/1927 | Male | 3.18702 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 14/08/1927 | Male | 3.18704 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 22/08/1927 | Male | 3.18707 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 22/08/1927 | Male | 3.18708 |
| <i>consobrinus</i> | Sabah | Kudat | 19/09/1927 | Male | 3.18713 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 08/08/1927 | Male | 3.18698 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 27/07/1927 | Male | 3.18697 |
| <i>consobrinus</i> | Sabah | Rayoh | 28/06/1928 | Male | 3.18718 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 09/08/1927 | Male | 3.18700 |
| <i>consobrinus</i> | Sabah | ‘Banguay Island’ (now Banggi) | 6/09/1927 | Male | 3.18694 |
| <i>consobrinus</i> | Sabah | Kudat | 17/09/1927 | Male | 3.18714 |
| <i>consobrinus</i> | Sabah | ‘Malawalle Island’ (now Malawali) | 08/1927 | Male | 3.18716 |
| <i>consobrinus</i> | Sabah | ‘Banguay Island’ (now Banggi) | 02/09/1927 | Male | 3.18693 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 11/08/1927 | Male | 3.18701 |
| <i>consobrinus</i> | Sabah | Rayoh | 19/06/1928 | Male | 3.18717 |
| <i>xanthonotus</i> | Sarawak | Baram | 05/03/1905 | Female | 3.18784 |
| <i>xanthonotus</i> | Sarawak | ‘South Paku, Paku Saribas’ | 28/10/1916 | Female | 3.18793 |
| <i>xanthonotus</i> | Sarawak | Baram, Borneo | 05/03/1905 | Female | 3.18785 |
| <i>xanthonotus</i> | Sarawak | Wai Sa... Baram, Borneo | 27/10/1920 | Female | 3.18787 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 08/1927 | Female | 3.18712 |
| <i>consobrinus</i> | Sabah | Kudat | 09/1927 | Female | 3.18715 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 13/08/1927 | Female | 3.18703 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 24/08/1927 | Female | 3.18711 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 27/07/1927 | Female | 3.18696 |

| | | | | | |
|--------------------|-----------------------|------------------------------------|------------|--------|---------|
| <i>consobrinus</i> | Sabah | ‘Banguey Island’ (now Banggi) | 07/09/1927 | Female | 3.18695 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 09/08/1927 | Female | 3.18699 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 19/8/1927 | Female | 3.18705 |
| <i>consobrinus</i> | Sabah | ‘Bettotan’ (now Betotan), Sandakan | 21/08/1927 | Female | 3.18706 |
| <i>xanthonotus</i> | Malay Peninsula | Chong Trang, North Malay Peninsula | 01/12/1909 | Male | 3.18755 |
| <i>xanthonotus</i> | Malay Peninsula | Temengoh now Temengor, Perak | 02/08/1909 | Female | 3.18751 |
| <i>xanthonotus</i> | Malay Peninsula | Cheras, Selangor | 18/3/1908 | Male | 3.18769 |
| <i>xanthonotus</i> | Malay Peninsula | Pelipak, Johor | 29/3/1905 | Male | 3.18776 |
| <i>xanthonotus</i> | Malay Peninsula | Pelipak, Johor | 27/3/1905 | Female | 3.18775 |
| <i>xanthonotus</i> | Malay Peninsula | Gunung Angsi, Negri Sembilan | 4/1906 | Female | 3.18771 |
| <i>xanthonotus</i> | Malay Peninsula | Klang, Selangor | 14/1/1909 | Male | 3.18770 |
| <i>xanthonotus</i> | Sumatra | Kota Pinang | 4/6/1937 | Male | 3.18797 |
| <i>xanthonotus</i> | Sumatra | Kota Pinang | 5/7/1937 | Male | 3.18798 |
| <i>xanthonotus</i> | Sumatra | Kota Pinang | 7/8/1937 | Male | 3.18799 |
| <i>xanthonotus</i> | Sumatra | Kerinci, Sumatra | 28/11/1914 | Female | 3.18796 |
| <i>xanthonotus</i> | Sumatra | Padang, Sumatra | 14/11/1934 | Male | 3.18800 |
| <i>xanthonotus</i> | Java | Wynkoops Bay now Pelabuhan Ratu | 13/3/1920 | Male | 3.18804 |
| <i>xanthonotus</i> | Java | Wynkoops Bay | 8/3/1920 | Male | 3.18803 |
| <i>xanthonotus</i> | Java | Wynkoops Bay | 8/3/1920 | Male | 3.18802 |
| <i>xanthonotus</i> | Java | Wynkoops Bay | 7/3/1920 | Male | 3.18801 |
| <i>xanthonotus</i> | Java | Wynkoops Bay | 19/3/1920 | Male | 3.18805 |
| <i>persuasus</i> | Palawan (Philippines) | Puerto Princesa | 17/09/1925 | Female | 3.18808 |
| <i>persuasus</i> | Palawan (Philippines) | Puerto Princesa | 08/08/1925 | Female | 3.18806 |
| <i>persuasus</i> | Palawan (Philippines) | Puerto Princesa | 13/08/1925 | Male | 3.18807 |
| <i>mentawi</i> | Sumatra | Siberut Island | 24/9/1924 | Male | 3.3968 |
| <i>mentawi</i> | Sumatra | Sipora Island | 20/10/1924 | Female | 3.3969 |
| <i>mentawi</i> | Sumatra | Siberut Island | 16/9/1924 | Male | 3.3967 |

Collection of the Lee Kong Chian Museum, Singapore, including three *persuasus*, three *mentawi*, 21 *consobrinus* and 32 nominate *xanthonotus* (Table 1). The latter taxon was represented by specimens from across multiple major landmasses (Table 1). Specimens were arranged according to taxon, landmass, collection date and sex, and were measured as follows: flattened wing length (from the carpal joint to the tip), maxilla length (from the tip to where the bill meets the skull), tail length (from the longest rectrix tip to the uropygial gland) and tarsus length (from tibiotarsus). Measurements of each parameter were performed by a single person (MYW: tail and wings; NM: maxilla and tarsus). All specimens were inspected for plumage coloration. Biometric comparisons of individuals from different landmasses and taxa were undertaken using principal component analysis (PCA) via the ‘prcomp’ function in R version 4.0.2 (R Core Team 2020), with PCA plots drawn using the ‘ggplot2’ package. We also carried out t-tests in R to identify any traits that might be significantly different between taxa.

Old World orioles are known for their fluty and variable songs. Song structure, including number of elements as well as their frequency and duration, varies greatly within and

among populations. Therefore, bioacoustic analyses that include sonogram measurements of individual call notes are not meaningful because of difficulties in assigning homology. Bioacoustic variability notwithstanding, Dark-throated Oriole calls can be assigned to particular call types within each population based on composite properties such as call structure, number of elements and frequency modulation. Some of these call types are specific to a particular taxon, whereas others are shared. Our bioacoustic analysis therefore centred on mapping the overlap of call types among different taxa. We gathered a total of 147 sound recordings from xeno-canto (www.xeno-canto.org), the Macaulay Library (<https://macaulaylibrary.org>) and private recordings (B. van Balen; available on request) for qualitative inspection. These vocalisations were categorised into 11 and ten call types for the eastern and western populations, respectively.

Results

Genomic analysis.—Jönsson *et al.* (2019) analysed two mitochondrial and two genome-wide DNA data partitions across the genus *Oriolus*. We summarise and provide additional detail on the results of each of these four datasets with emphasis on the Dark-throated Oriole complex (Fig. 2).

Analysis of the single mitochondrial gene ND2 (1,041 base pairs [bp]) uniquely encompassed individuals of all four subspecies, including island representatives for Java, Sumatra, the Thai-Malay Peninsula, Borneo, Palawan and Mentawai. This analysis revealed

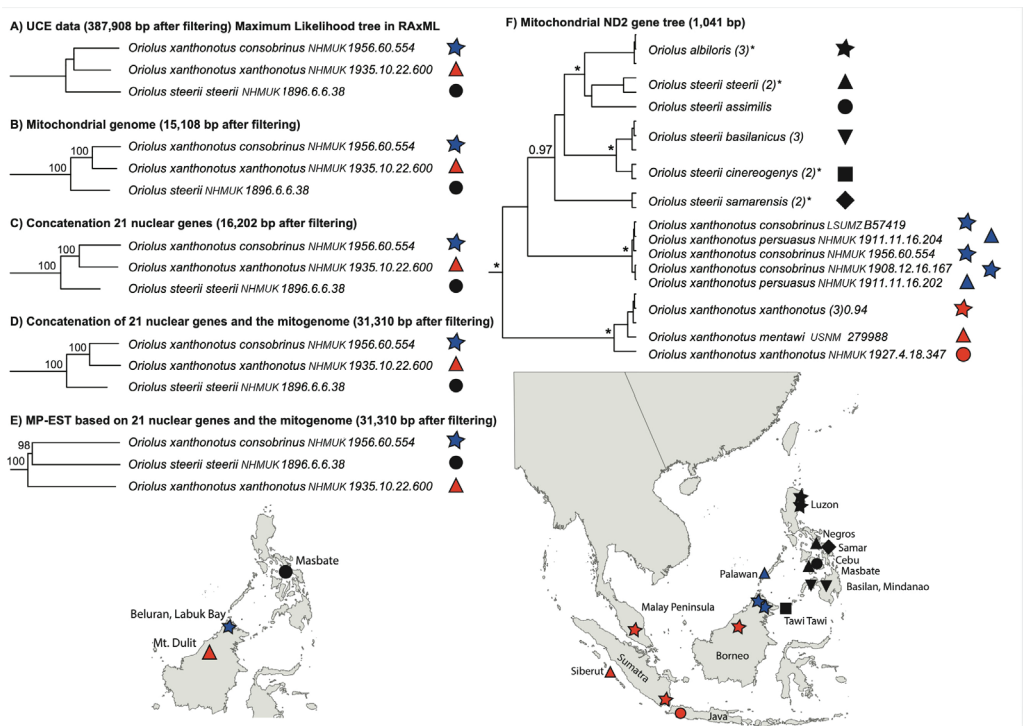


Figure 2. Phylogenetic trees based on four different data partitions adapted from Jönsson *et al.* (2019). A: nuclear ultraconserved element (UCE) loci; B: mitochondrial genomes; C: 21 independent nuclear sequence loci; F: mitochondrial NADH dehydrogenase 2 (ND2) gene sequences. D–E show trees based on a combination of the 21 nuclear sequence loci (C) and the mitochondrial genomes (B), constructed using the concatenation approach (D) and the species-tree approach as implemented in MP-EST (E). Maps show sampling localities for the phylogenetic trees placed above.

O. xanthonotus to be paraphyletic, with strong support for a closer relationship between the two eastern subspecies, *O. x. consobrinus* and *O. x. persuasus*, and the Philippine species White-lored Oriole *O. albiloris* and Philippine Oriole *O. steerii*, to the exclusion of the two western subspecies *O. x. xanthonotus* and *O. x. mentawi* (Fig. 2). Basal divergence between the 'western' dark-throated taxa (*O. x. xanthonotus* and *O. x. mentawi*) and the remaining orioles was estimated to have occurred c.7 million years ago, whereas divergence between 'eastern' dark-throated taxa (*O. x. consobrinus* and *O. x. persuasus*) and the two Philippine species was estimated to have occurred c.5 million years ago (fig. 1 in Jönsson *et al.* 2019).

For a smaller set of taxa representing all major *Oriolus* clades including an *O. x. xanthonotus* sample from Borneo, *O. x. consobrinus* and Philippine *O. steerii*, Jönsson *et al.* (2019) used shotgun sequencing to generate genome-wide sequences, resulting in the following four datasets:

In contrast to the single ND2 gene, analysis of more than 15,000 bp of the mitochondrial genome, containing ND2 and 15 other genes, supported monophyly of eastern and western representatives of Dark-throated Orioles (Fig. 2), with strong support for their being more closely related to each other than to Philippine Oriole (fig. 2B in Jönsson *et al.* 2019).

Analysis of a concatenation of 16 nuclear genes, amounting to >16,000 bp, agreed with the mitogenomic analysis in placing eastern and western Dark-throated Orioles closer to each other than to Philippine Oriole (Fig. 2; fig. 2C in Jönsson *et al.* 2019).

A concatenation of genome-wide ultra-conserved elements, amounting to almost 388,000 bp, and therefore surpassing the previous dataset almost 25-fold, had a more equivocal outcome: *O. x. xanthonotus* and *O. x. consobrinus* were placed as sister to each other, with Philippine Oriole as sister to these two, but with no strong branch support (Fig. 2). Moreover, the branch separating Philippine Oriole from the two dark-throated taxa was very short (fig. 2A in Jönsson *et al.* 2019).

In a species-tree analysis, as opposed to a concatenation analysis, using 21 nuclear genes and the entire mitogenome, *O. x. consobrinus* emerged as sister to Philippine Oriole, whilst nominate *O. x. xanthonotus* was more distant to these two, with fairly strong branch support (Fig. 2; bootstrap 98; see supplementary fig. S6 in Jönsson *et al.* 2019). This pattern was similar to the result of the ND2 analysis (Fig. 2). Species-tree analyses do not combine all loci into one super-alignment, but consider the phylogenetic information of each locus independently, and are widely regarded as the state of the art in phylogenetic analysis (e.g., Edwards *et al.* 2007).

Morphometric analysis.—The PCA plot for morphometric measurements clearly divided Sabah and Sarawak specimens along PC1, accounting for 38.8% of variation (Fig. 3). Generally, *O. x. xanthonotus* specimens from Sarawak grouped closer with *O. x. xanthonotus* individuals from the Thai-Malay Peninsula, Sumatra and *O. x. mentawi* from the West Sumatran Islands, whereas *O. x. consobrinus* from Sabah clustered more closely with *O. x. persuasus* from Palawan. Specimens of *O. x. xanthonotus* from Java were embedded with *O. x. xanthonotus* specimens from other landmasses (Fig. 3).

Morphometric measurements of Sabah vs. Sarawak specimens exhibited nearly non-overlapping ranges and significant differences in all parameters except tail length (Fig. 4). Javan *O. x. xanthonotus* emerged as significantly different in wing and tarsus length compared to other *O. x. xanthonotus* populations. In *O. x. mentawi* from the West Sumatran Islands, only wing length was significantly different from the nearby mainland Sumatran *O. x. xanthonotus* population.

Plumage inspection.—The plumages of *O. x. xanthonotus* from the Thai-Malay Peninsula were similar to those of *O. x. xanthonotus* from eastern Borneo but differed considerably

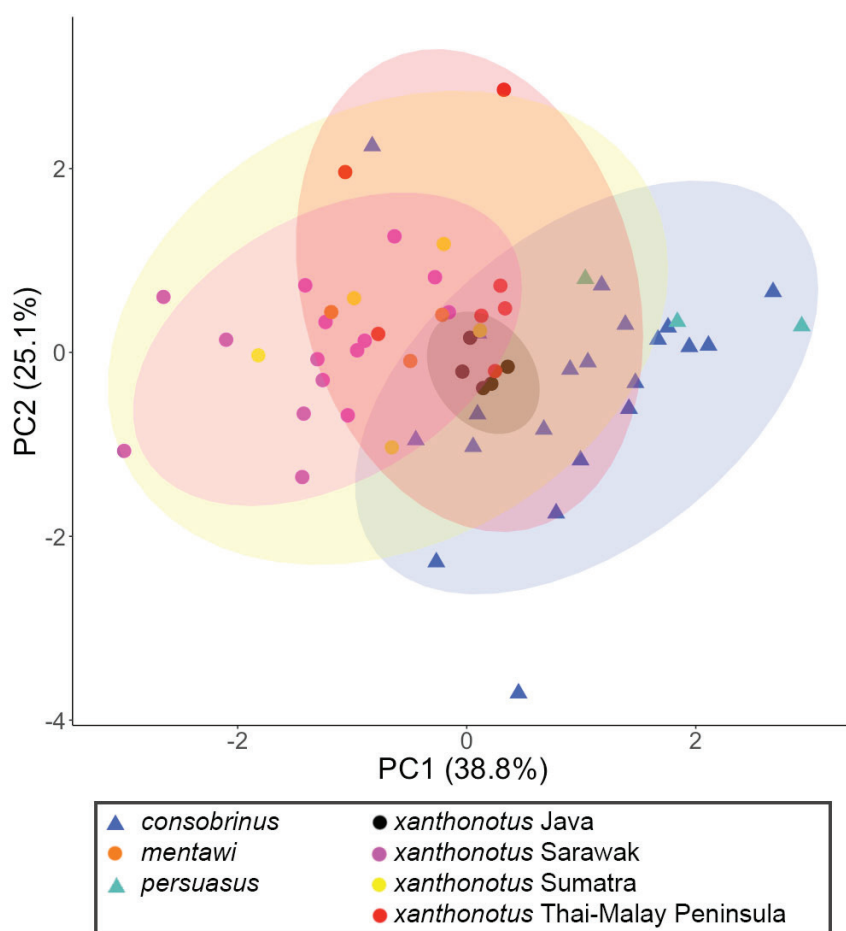


Figure 3. Principal component analysis plot for measurements across all four morphometric parameters. The 95% confidence interval ellipses are shown with the following colours: *O. x. consobrinus* (blue), *O. x. xanthonotus* Sarawak (pink), *O. x. xanthonotus* Java (grey) and the rest of the *O. x. xanthonotus* range (yellow). The percentage of total variation explained by each principal component (PC) is shown in parentheses.

from *O. x. consobrinus* in Sabah and *O. x. persuasus* on Palawan, which two showed similar plumage patterns.

Female *O. x. xanthonotus* has shorter, thinner and sparser streaking on the underparts, with a paler background coloration on the upper breast and a greyish-olive head that grades evenly into the upper mantle. This contrasts with female *O. x. consobrinus* and *O. x. persuasus*, which have longer, thicker and denser underparts streaking, a greyish background to the upper breast and a dark grey head that clearly contrasts with the upper mantle, giving their plumage a male-like character (Fig. 5).

Male *O. x. xanthonotus* also has shorter, thinner and sparser streaking on the underparts than both *O. x. consobrinus* and *O. x. persuasus*. Males of the latter show a diffuse border between the black throat and white upper breast, whereas *O. x. consobrinus* has a sharp divide between the black throat and white upper breast (Fig. 5).

Bioacoustic analysis.—We found two distinct vocal groups within the Dark-throated Oriole complex based on visual inspection of sonograms. Populations in the Thai-Malay Peninsula, Sumatra and Sarawak constitute one group separate from populations of Sabah and Palawan. Each of the two groups is characterised by sets of song and call types that

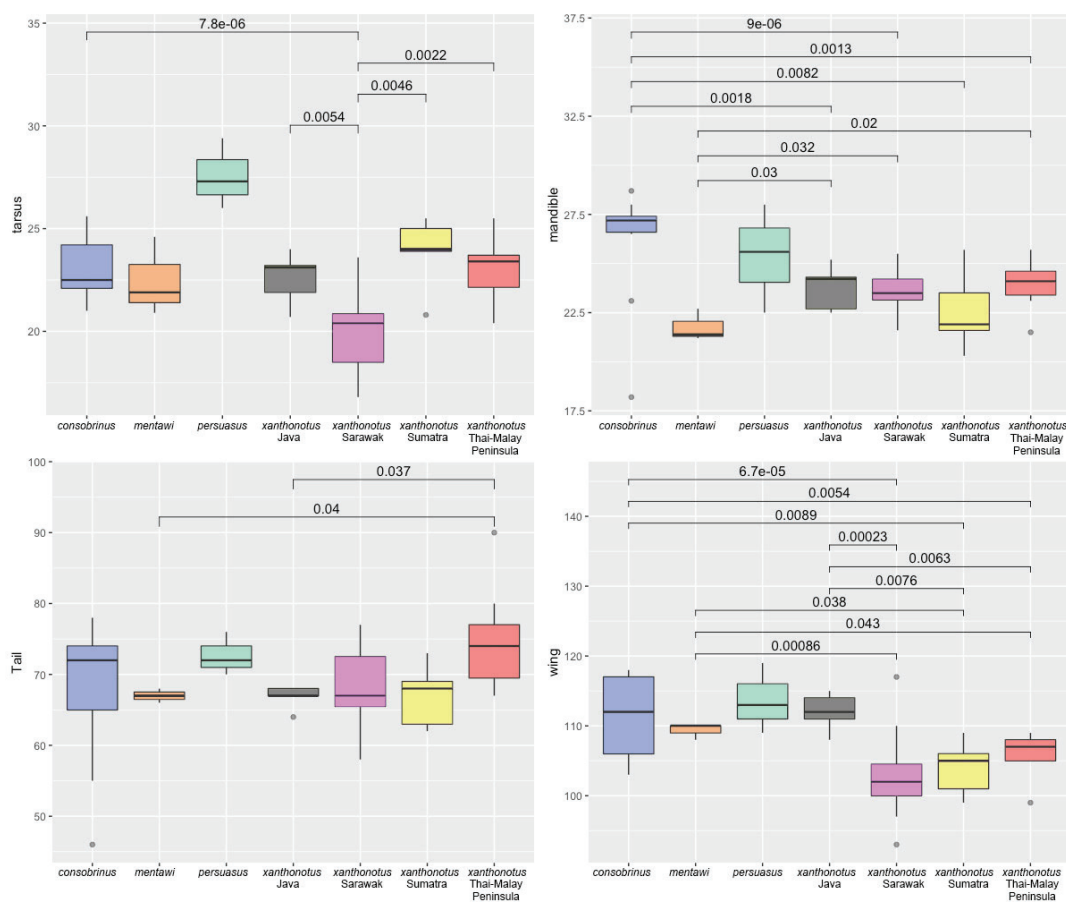


Figure 4. Box plots of morphometric measurements for tarsus (upper left), tail (lower left), maxilla (upper right) and wing length (lower right). Significant *p* values are shown above the plots for each corresponding pairwise comparison. Wing and tarsus comparisons involving *O. x. persuasus* overwhelmingly emerged as significant, and are not shown because of space constraints.

do not overlap (Figs. 6–7). At the same time, each group was found to emit call types of either inflected or deflected single notes which, however, differ greatly in duration between groups (Figs. 6–7: top row).

In contrast to the more conventional fluty multisyllabic oriole calls uttered by nominate *O. x. xanthonotus* (Fig. 6), the commonest calls in the Sabah and Palawan populations (*O. x. persuasus* and *O. x. consobrinus*) have a distinct ventriloquial quality (Fig. 7), more reminiscent of the sympatric Bornean Black Magpie *Platysmurus aterrimus*. Many of these ventriloquial calls exhibit a three-note structure, but with variations, sounding roughly like a monotonous *du-du-duuuu* with a variable ending, either inflected (e.g. XC 360969, XC 269344) or deflected (e.g. ML 202577).

Whilst *O. x. xanthonotus* from Java shares multiple call types with remaining nominate populations, we detected two unique call types (Fig. 6, blue frame) with a ‘bulbul-like’ (XC 618465) or ‘plaintive cuckoo-like’ (XC 393776) quality, quite unlike the typical fluty timbre that characterises the vocalisations of other populations. However, because of a low vocal sample size for Java, it is unclear whether these calls are of taxonomic importance or are merely rare vocal variants.



Figure 5. Photographs of female (left column) and male (right column) Dark-throated Oriole *Oriolus xanthonotus* specimens at the Lee Kong Chian Natural History Museum (Singapore). Dorsal (top row), ventral (middle row) and lateral views (bottom row). Specimens grouped by taxa, from left to right: Peninsular Malaysian *O. x. xanthonotus*, *O. x. mentawi*, *O. x. xanthonotus* and *O. x. persuasus* (females); Peninsular Malaysian *O. x. xanthonotus*, Javan *O. x. xanthonotus*, *O. x. mentawi*, *O. x. consobrinus* and *O. x. persuasus* (males) (Movin Nyanasengeran)

Discussion

Character displacement on Borneo.—Steep mensural differences between the two species on Borneo suggest that ecological and evolutionary character displacement may be moulding their body size and shape. Character displacement—also termed reinforcement—is an evolutionary phenomenon whereby populations of closely related species possess similar traits across most of their non-overlapping ranges, but adopt greater trait differences in areas where they co-occur thereby preventing competition (Brown & Wilson 1956, Hoskin *et al.* 2005). In South-East Asian birds, character displacement has been mapped for vocal traits in *Ptilinopus* fruit doves (Rheindt *et al.* 2011) and *Rhipidura* fantails (Ng *et al.* 2017b), but also for mensural characters in *Pachycephala* whistlers (Ashari *et al.* 2018) in a pattern reminiscent of Dark-throated Orioles on Borneo.

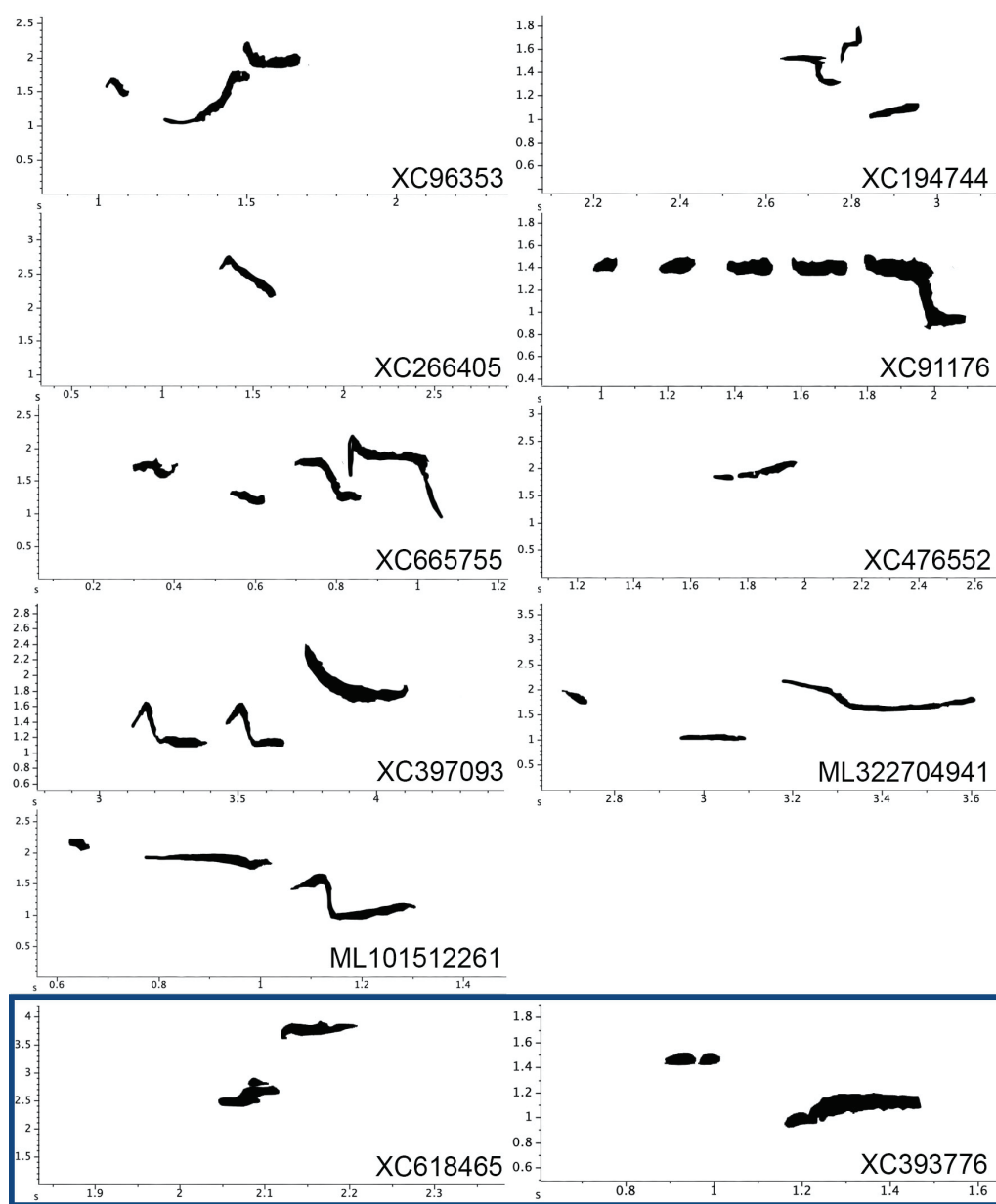


Figure 6. Sonograms of typical examples of the 11 song and call types identified across the Malay Peninsula, Sumatra, Java and Sarawak, reflecting the distribution of *O. x. xanthonotus*. Javan individuals were found to utter two unique call types that differ from all other recordings (blue frame). Frequency axis in kHz.

Measurements of tarsus length, wing length and bill length suggest that easterly *O. x. consobrinus* from Sabah is considerably larger than Bornean populations of nominate *O. x. xanthonotus*, with almost non-overlapping size ranges (Fig. 4). In a PCA combining all four morphometric characters, the 'clouds' of these two groups are nearly non-overlapping (Fig. 3). However, when Sabah *O. x. consobrinus* is compared with nominate *O. x. xanthonotus* outside Borneo, we find a large overlap in measurements, and differences are not significant (Figs. 3–4). Measurements of both Bornean populations (*O. x. xanthonotus* and *O. x.*

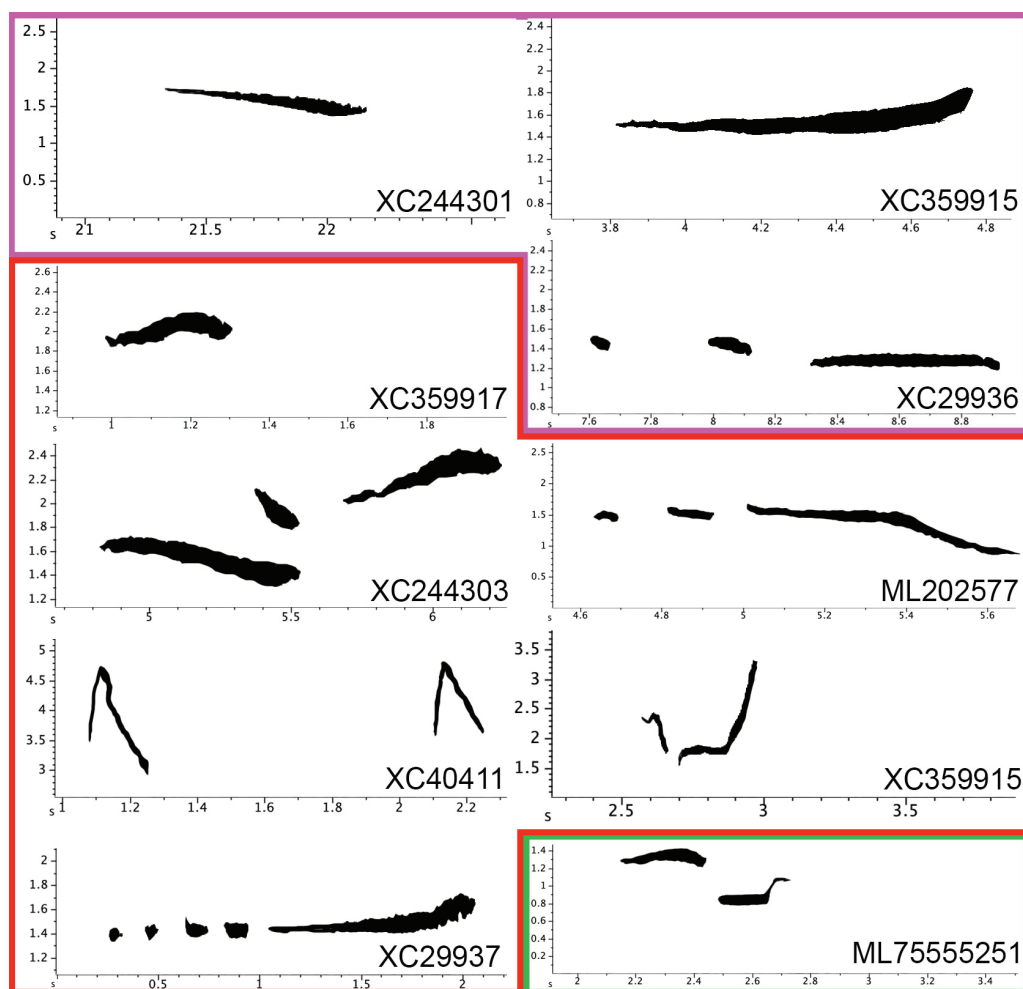


Figure 7. Sonograms of typical examples of the ten song and call types identified across Sabah and Palawan, reflecting the distribution of *O. x. consobrinus* and *O. x. persuasus*. The two populations shared three common call types (purple), whilst other call types may be distinct to each population, Sabah (red) and Palawan (green). Frequency axis in kHz.

consobrinus) may be driven apart to minimise the chances of reproductively suboptimal hybrid offspring in their contact zone. In biological terms, this has led to a Dark-throated Oriole (*O. x. xanthotus*) on Borneo that is much smaller than populations throughout the rest of the range, and outsized by the *O. x. consobrinus* which it encounters on Borneo.

Mapping the contact zone in Borneo.—The precise extent of the ranges of various Sabah endemics or Sabah specialties on Borneo remains incompletely known, especially for taxa that have only recently been recognised at species level (e.g. Glissando Babbler *Pellorneum saturatum* vs. Leaflietter Babbler *P. poliogene* and others; Eaton *et al.* 2021, Garg *et al.* 2022). The same uncertainty applies to Dark-throated Orioles. Whilst the internet permits access to much photographic and sound material from Sabah, there is hardly any such material from the rest of Borneo. As of November 2021, sound recordings deposited on www.xeno-canto.org indicated that *O. x. consobrinus* extends south from Sabah at least to the Berau District of East Kalimantan (Fig. 1), where a recording by I. Woxvold has the vocal hallmarks of eastern *O. x. consobrinus* (XC 65382). Further north, the transition

between the two appears to be close to the borders of Sabah, as recordings and personal observations from Brunei indicate the presence of the western (*O. x. xanthonotus*) fluty song and plumage types there (NM pers. obs.). Field ornithologists and hobby birdwatchers can contribute much to our understanding of Bornean ornithology by filling such knowledge gaps and thereby helping to achieve a more complete mapping of the distribution of the island's bird species.

Genomic evidence for a split.—Jönsson *et al.*'s (2019) extensive genomic analyses produced a surprisingly heterogeneous picture of the phylogenetic relationships of Dark-throated Oriole taxa and closely allied species in the Philippines. Analysis of a widely used mitochondrial gene unexpectedly pointed to a close relationship between the two eastern subspecies of Dark-throated Oriole (*O. x. consobrinus* and *O. x. persuasus*), Philippine Oriole and White-lored Oriole, whereas western dark-throated taxa (*O. x. xanthonotus* and *O. x. mentawi*) were phylogenetically more distant (Fig. 2). Importantly, this paraphyletic arrangement of the Dark-throated Oriole was backed by strong branch support and would have been widely interpreted as reflecting the true relationships in the complex c.10–20 years ago before the advent of modern next generation sequencing technology. After expanding the mitochondrial dataset to include 15 additional genes, however, Jönsson *et al.* (2019) found that the odd paraphyletic arrangement of Dark-throated Orioles was not corroborated (Fig. 2), and that they may—after all—form a monophyletic species.

Use of mitochondrial DNA in phylogenetics is known to generate artefactual relationships in cases when DNA introgression and instances of hybridisation may have confounded its gene tree (e.g. Rheindt & Edwards 2011, Andersen *et al.* 2021). A new era of phylogenomics based on genome-wide DNA has revolutionised the field and made routine the use of nuclear DNA loci. The most extensive nuclear dataset analysed by Jönsson *et al.* (2019) encompassed almost 388,000 bp from across the nuclear genome of these orioles, surpassing the volume of the mitogenomic dataset 25-fold. This expansive dataset provided only weak support for a monophyletic placement of eastern and western Dark-throated Orioles (Fig. 2). In addition, a species-tree analysis of 21 nuclear genes combined with the mitogenomes shifted support back to placing eastern *O. x. consobrinus* closer to Philippine Oriole rather than to western *O. x. xanthonotus* (Fig. 2).

In summary, the most likely explanation for the heterogeneous outcome of phylogenomic analyses—despite the massive DNA sequence volumes investigated—is a similar timing for the split among three lineages, one of which is the ancestor of White-lored and Philippine Orioles, whilst the other two represent the eastern and western subspecies groups of Dark-throated Oriole, respectively. The earlier timing of the split between eastern and western Dark-throated Orioles, preceding the diversification between this lineage of orioles in the Philippines, strongly supports elevation of the eastern genetic clade of Dark-throated Oriole to species level as *O. consobrinus*.

Biological evidence for a split.—Our morphometric and plumage analyses largely corroborate the work of early museum taxonomists who documented considerable differences in coloration especially in females. Eastern females are considerably more contrasting, saturated and male-like in appearance, and no cline in such coloration differences was evident in our sample of 59 specimens. Male differences, while less pronounced, are nevertheless readily discernible in the field and in specimens (Fig. 5). There is variation in the female plumage, with *consobrinus* exhibiting a more blackish crown similar to male plumage compared to *xanthonotus* on Borneo. This tendency for females to develop male-like plumage occurs elsewhere in the genus *Oriolus* but rarely in sympatry (e.g., Black-and-crimson Oriole *O. cruentus*; Kirwan *et al.* 2021). In the parapatric

populations of *consobrinus* and *xanthonotus* on Borneo, these differences in female plumage may present a prezygotic impediment to gene flow.

Furthermore, there are substantial bioacoustic differences between eastern and western Dark-throated Orioles, which may even outweigh the color differences in reproductive importance. The western subspecies group utters many versions of a typical multisyllabic fluty oriole song (Fig. 6) roughly reminiscent of other species in the region (e.g., Black-naped Oriole *O. chinensis*). This typical fluty song is unknown in the eastern subspecies group, whose primary vocalisations chiefly comprise a series of ventriloquial calls reminiscent of Bornean Black Magpie *Platysmurus aterrimus* (Fig. 7).

On the combined basis of phylogenomic, biometric, bioacoustic and plumage data, we propose that the two eastern subspecies of Dark-throated Oriole (*O. x. consobrinus* [northern and eastern Borneo] and *O. x. persuasus* [Palawan]) be recognised as a separate species, *O. consobrinus*. We propose ‘Ventriloquial Oriole’ as the vernacular name of this newly recognised species, reflecting its characteristic song, which is unique among the region’s orioles. The western subspecies group—nominate *O. x. xanthonotus* and *O. x. mentawi*—still occupies the largest part of the distribution of this complex; therefore retention of the name ‘Dark-throated Oriole’ for the western group appears to be the best solution leading to the least nomenclatural disruption.

Taxonomic uncertainty of the Javan population.—‘*Oriolus Xanthonotus*’ [sic] was first described by Horsfield in 1821 with ‘Java’ as its type locality, rendering the taxonomic identity of the Javan population of special importance. In plumage and morphometrics, Javan specimens squarely fit within the range of variation displayed by nominate *O. x. xanthonotus* on other landmasses, especially Sumatra and the Thai-Malay Peninsula (Figs. 3–5). Therefore, use of the subspecies name *xanthonotus* as a moniker for the more westerly species of Dark-throated Oriole is not in doubt. In mtDNA, Javan populations are characterised by the deepest divergence within the *O. x. xanthonotus* cluster (Fig. 2), but still compatible with subspecies status. Vocal material from Java is currently limited, consistent with the defaunation that has occurred here during the last three decades (Eaton *et al.* 2015, Symes *et al.* 2018, Verma *et al.* 2020) leading to this population’s decline and endangerment. Whilst the existing vocal material is suggestive of some potential differentiation of Java’s nominotypical population (Fig. 6, blue frame), the possibility of unusual call variants cannot be eliminated, and more extensive sampling of Javan call notes is required.

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