

# A taxonomic revision of Banda Myzomela Myzomela boiei (S. Müller 1843), including the description of a new species from Babar Island, Indonesia

Authors: Berryman, Alex J., Spencer, Andrew J., Sharma, Puja, and Eaton, James A.

Source: Bulletin of the British Ornithologists' Club, 145(1): 35-48

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v145i1.2025.a4

The BioOne Digital Library (<u>https://bioone.org/</u>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<u>https://bioone.org/subscribe</u>), the BioOne Complete Archive (<u>https://bioone.org/archive</u>), and the BioOne eBooks program offerings ESA eBook Collection (<u>https://bioone.org/esa-ebooks</u>) and CSIRO Publishing BioSelect Collection (<u>https://bioone.org/csiro-ebooks</u>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## A taxonomic revision of Banda Myzomela *Myzomela boiei* (S. Müller 1843), including the description of a new species from Babar Island, Indonesia

by Alex J. Berryman <sup>(D)</sup>, Andrew J. Spencer <sup>(D)</sup>, Puja Sharma <sup>(D)</sup> & James A. Eaton <sup>(D)</sup>

Received 19 August 2024; revised 24 December 2024; published 5 March 2025

http://zoobank.org/urn:lsid:zoobank.org:pub:931BA0CB-195E-4222-9A1F-35CB17FB2355

SUMMARY.—Banda Myzomela Myzomela boiei (S. Müller 1843) is a small honeyeater distributed in two subspecies across three island groups in Maluku Province, Indonesia: M. b. boiei on the Banda Islands, and c.350 km to the south, M. b. annabellae on the Tanimbar Islands and Babar. We compare data from 28 museum specimens and 21 sound recordings, and report the results of 152 playback experiments, to investigate the taxonomy of these three populations. Compared to M. b. annabellae, M. b. boiei has a c.10% longer wing, bill and tarsus, more extensive black breast-band, duskier posterior underparts, and a highly divergent song; in playback experiments, M. b. boiei proved unresponsive to recordings of M. b. annabellae. However, the songs of M. b. annabellae on the Tanimbars and Babar are also highly divergent, with populations on both islands unresponsive to the song of the other. Birds on Babar are also slightly larger than annabellae on the Tanimbars (with a *c*.10% longer tail) and may have more scarlet on the back. We consider the vocal differences between the three populations to be highly indicative of reproductive isolation and recommend they be treated as three independent species under a modern interpretation of the Biological Species Concept. Because no nomen is available for the Babar population, we name it as a new species.

Indonesia is the world's largest archipelagic state, comprising more than 18,000 islands which host—somewhat unsurprisingly—the largest number of birds endemic to a single country (528: BirdLife International 2024a). As foretold (Collar 2003), over the past 20 years this number has risen rapidly, with new species still described most years (e.g. Rheindt *et al.* 2020, Irham *et al.* 2022, 2023) and polytypic species being split into dozens more, particularly with the application of bioacoustic and molecular methods (e.g. Gwee *et al.* 2019, Berryman & Eaton 2020, Yue *et al.* 2020). There nonetheless remains a large volume of taxonomic work to be done.

Here we investigate the taxonomy of Banda Myzomela *Myzomela boiei* (S. Müller, 1843), a colourful, sexually dimorphic honeyeater distributed in two subspecies across three island groups in the Banda Sea, southern Maluku province: *M. b. boiei* (S. Müller, 1843) occurs on the Banda Islands, while *M. b. annabellae* P. L. Sclater, 1883, occurs on Babar (and possibly its satellites) and the Tanimbar Islands (recorded from at least Yamdena and Selaru, and probably throughout) (Fig. 1). With the addition of Damar, the Leti Islands, Kisar and other small islets between them, these islands comprise the 'Banda Sea Islands', a region of comparatively low avian diversity but predictably high endemism (Stattersfield *et al.* 1998, Trainor & Verbelen 2013, Eaton *et al.* 2021). A history of the ornithological exploration and collection on the Banda Sea Islands was presented by Trainor & Verbelen (2013), who were the first ornithologists to visit (in August 2009 and August 2011) and publish information

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



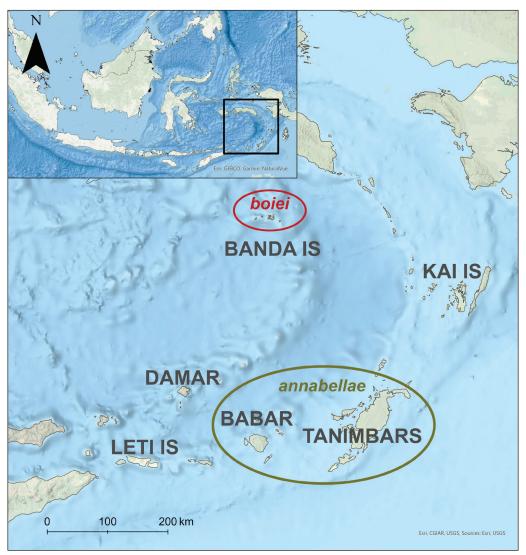


Figure 1. Distribution of Banda Myzomela Myzomela boiei taxa in relation to the Banda Sea Islands mentioned in the text.

on several of the Banda Sea Islands (including Babar), since summaries based exclusively on specimens in the early 20th century (e.g. Hartert 1900, Finsch 1901, Hartert 1904, 1906). More recently, there have been regular visits to many of the Banda Sea Islands by tour groups and independent birders, commencing in 2011 with the first 'Banda Sea Cruise' (Eaton & Hutchinson 2011).

*M. boiei* was described by Müller (in Müller & Schlegel 1843) from the Banda Islands (type locality: 'Banda Island'). Forty years later, based on a single specimen collected by H. O. Forbes, Sclater (1883) described *M. annabellae* as a new species from the Tanimbar Islands (type locality: 'Loetoe') and Finsch (1901) soon added Babar to its distribution, but considered specimens available to him from Babar to be undifferentiated from those procured on the Tanimbars. While Hartert (1901: 171) retained *M. annabellae* as a species separate from *M. boiei*, five years later he had evidently changed his mind (Hartert 1906:

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



301), noting that whilst *boiei* differed from *annabellae* in being 'larger, and the black area limiting the red throat much wider'...the two 'agree in all essential characters'. By this time, Hartert (1906) had a larger series of Kühn's material from Babar available to him and was presumably unable to find differences between them and the limited sample of *M. b. annabellae* from the Tanimbars.

37

M. boiei then underwent a period of taxonomic flux, with its two subspecies being variously lumped with other Wallacean taxa (e.g. Wolters 1982) or even more broadly with Scarlet Myzomela M. sanguinolenta of Australia (e.g. White & Bruce 1986, Inskipp et al. 1996). However, despite following the latter arrangement, White & Bruce (1986) did suggest that several Wallacean Myzomela-among them M. boiei-may merit separation. Subsequently, a more speciose treatment of the M. sanguinolenta complex achieved considerable support (Schodde & Mason 1999, Rheindt & Hutchinson 2007, Higgins et al. 2008) and has largely prevailed since, with M. boiei now almost unanimously treated as a polytypic species comprising two subspecies (e.g. Dickinson & Christidis 2014, Eaton et al. 2016, del Hoyo & Collar 2016, BirdLife International 2024b, Clements et al. 2024, Gill et al. 2024). However, the situation remains unsettled. More than a decade ago, Trainor & Verbelen (2013) implied that the geographic distance between M. b. boiei and M. b. annabellae was so great that the two may not be conspecific, and more recently Eaton et al. (2021) split these two, a decision said to be justified on the basis of 'strong vocal and some plumage differences'. To date, the details of these differences have remained unpublished, whilst more recently acquired vocal data from the three populations of M. boiei suggested that further study was warranted.

## Methods

*Museum specimens.*—All relevant skins were examined in the American Museum of Natural History, New York (AMNH) and the Natural History Museum, Tring (NHMUK), totalling: *M. b. boiei* Banda Islands (11 males, three females); *M. b. annabellae* Tanimbar Islands (three males); and *M. b. annabellae* Babar (nine males, two females) (specimen registration numbers are presented in Appendix 1). All measurements were taken by AJB with digital callipers as: (1) wing length from carpal joint to tip, while applying gentle pressure to the primary-coverts; (2) tail length from point of insertion to the tip; (3) tarsus from the notch on the back of the intertarsal joint to distal base of the longest toe; (4) bill length from the tip of the maxilla to the skull; (5) depth of the bill at the point at the front of the nostril; and (6) max. width of the bill at the same point. Immatures were not measured. Mensural differences were analysed using principal component analysis (PCA) and a PCA biplot was drawn. To compare differences in individual biometric traits between populations we used Welch's unpaired *t*-tests, applying a Bonferroni correction where the threshold for statistical significance is set at p<0.05/n<sub>v</sub>. Only males were analysed statistically due to a lack of female specimens from the Tanimbars.

In addition to specimens inspected personally, AJB solicited photographs of specimens of *M. b. annabellae* (n = 2 Tanimbars, n = 1 Babar [all males]) housed at the Museum für Tierkunde, Staatliche Naturhistorische Sammlungen Dresden (SMTD).

*Vocal analysis.*—Sound recordings were collated from Xeno-canto (xeno-canto.org) and the Macaulay Library (macaulaylibrary.org), and by contacting sound-recordists we knew had visited relevant islands (see Acknowledgements). We did not analyse contact or alarm calls, and concentrated on the more complex vocalisations we believe to represent each population's song, which is more likely to function as a barrier to mate recognition and reproduction. Across all recordings, as well as the authors' collective experience, we found no evidence for more than one song type on each island and believe them to be homologous

© 2025 The Authors; This is an open-access article distributed under the terms of the Creatine Commons Attribution. Non Commercial Licence subick summits and thick the Common state of th

ISSN-2513-9894 (Online)

Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,

vocalisations-this was directly tested further in our playback experiments (see below). In total, we collated 29 recordings of *M. boiei* song, but eight were of insufficient quality to measure parameters (although see Results), resulting in a final measurable sample of 21: Banda Islands (n = 6), Tanimbar Islands (n = 8) and Babar (n = 7) (see Appendix 2).

38

For each recording, we measured four basic parameters: (1) number of notes in a strophe; (2) length of the strophe; (3) minimum frequency (kHz) of the entire strophe; (4) max. frequency (kHz) of the entire strophe. Sonograms were visualised and measured in Raven Pro Version 1.6 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY) with an optimised window size of 1,048 for all recordings. In each recording, all strophes sung by the same bird were measured to account for individual variation and the mean of each parameter for each individual was taken (thus giving each individual equal weight in the final sample). Differences were analysed statistically using PCA and Welch's unpaired *t*-tests.

*Playback experiments.*—To test the ability of populations to discriminate sympatric from allopatric song, and thereby the likely reproductive significance of any vocal differences between populations, JAE, PS & AJS undertook playback experiments opportunistically during visits to Babar (JAE: 2014, 2016-18, 2022-24), the Tanimbar Islands (JAE: 2014, 2016–18, 2022–24, PS & AJS: 2023) and Banda Islands (PS & AJS: 2023). Although no formal or standardised protocol was followed, each experiment comprised a bird being played a loud recording of either sympatric song (i.e. a recording of a bird from the same island) or allopatric song (from another island) for up to two minutes and its behaviour observed for a response (if birds responded, they usually did so immediately). Behaviours were recorded as either 'no response' (bird behaved indifferently to recording), 'moderate response' (e.g., bird called back but did not approach) and 'strong response' (e.g. bird approached the speaker and vocalised). In total, 152 such experiments were carried out, including all possible combinations of population and song type (see Table 3). We calculated response scores as the proportion of birds in each population that responded to the song played.

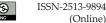
## Results

*Morphological comparison*. – All three populations of *M. boiei* are diagnosable in male plumage, with the greatest differences unsurprisingly evident between the two named taxa. Nominate *M. b. boiei* differs from both populations of *M. b. annabellae* in its larger size (see Table 1, Fig. 2), particularly wing and tarsus length, which did not overlap, and bill length, which overlapped only marginally; notably, there appears to be no difference in tail length between the two named populations, nor in bill depth or width. The breast-band of male M. b. boiei is also much broader, reaching the lower breast (vs. confined to neck/upper breast on *M. b. annabellae*); its posterior underparts are also duskier (Figs. 3–4).

Although they are very similar, there are some minor points of distinction that separate Tanimbar and Babar populations of *M. b. annabellae*: those from the Tanimbars are slightly smaller (Table 1, Fig. 2) and, while sample sizes are small, all measured specimens of males from the Tanimbars (n = 3) fall outside the range of Babar males (n = 9) for wing, tail and bill length. Most noticeably, tail length of Babar males is c.10% longer than that of Tanimbar birds (thus on Babar tail length is similar to the generally larger *boiei*). In the five Tanimbar males available for visual inspection (including photographs of the two males at SMTD), the back and mantle were considerably blacker, less admixed with scarlet vs. birds from Babar. As is typical for Myzomela, we could find no differences in adult females (except for the larger size of *M. b. boiei*: Table 1).

Vocal analysis.- The songs of the three populations of M. boiei differ so radically that numerical and statistical summaries alone do not adequately convey their distinctiveness,

 $\odot$   $\odot$ © 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



(Online)

#### TABLE 1

39

Morphometric comparison of *Myzomela boiei* from the Banda Islands (nominate *boiei*), Babar and the Tanimbar Islands (both *M. b. annabellae*). For specimens measured, see Appendix 1. Values in **bold** represent the mean  $\pm$  standard deviation, values in parentheses the range. Superscript letters A–C represent statistical significance of pairwise comparisons between taxa (males alone) at the threshold of <0.05 using Welch's unpaired *t*-tests applying a Bonferroni correction, where A = Banda Islands vs. Tanimbar Islands, B = Banda Islands vs. Babar, C = Tanimbar Islands vs. Babar.

Population		Wing	Tail	Bill length	Bill depth	Bill width	Tarsus
M. b. boiei	Males ( <i>n</i> = 11)	<b>55.9 ± 1.2</b> <sup>A,B</sup> (53.5–57.1)	<b>39.4 ± 3.0</b> (36.2–45.4)	<b>15.1 ± 0.7</b> <sup>A,B</sup> (14.0–16.2)	<b>2.6 ± 0.2</b> (2.3–2.9)	<b>2.6 ± 0.1</b> (2.4–2.8)	<b>16.5 ± 0.5</b> <sup>A,B</sup> (15.7–17.1)
(Banda Islands)	Females $(n = 3)$	<b>53.1 ± 1.0</b> (52.3–54.2)	<b>35.3 ± 1.3</b> (34.4–36.8)	<b>14.7 ± 0.6</b> (14.2–15.3)	<b>2.4 ± 0.1</b> (2.3–2.5)	<b>2.3 ± 0.1</b> (2.3–2.5)	<b>15.5 ± 0.2</b> (15.3–15.7)
M. b. annabellae	Males ( <i>n</i> = 3)	<b>49.8 ± 0.6</b> <sup>A,C</sup> (49.1–50.2)	<b>36.4 ± 0.9</b> <sup>C</sup> (35.8–37.4)	<b>13.2 ± 0.1</b> <sup>A,C</sup> (13.1–13.3)	<b>2.4 ± 0.1</b> (2.2–2.5)	<b>2.5 ± 0.1</b> (2.4–2.6)	<b>14.0 ± 0.1</b> <sup>A</sup> (13.9–14.1)
(Tanimbar Islands)	Females $(n = 0)$	NA	NA	NA	NA	NA	NA
M. b. annabellae (Babar)	Males $(n = 9)$	<b>51.9 ± 0.9</b> <sup>B,C</sup> (50.6–53.3)	<b>40.4 ± 1.4</b> <sup>C</sup> (39.2–43.6)	<b>13.8 ± 0.3</b> <sup>B,C</sup> (13.3–14.3)	<b>2.4 ± 0.2</b> (2.2–2.8)	<b>2.3 ± 0.1</b> (2.2–2.5)	$14.2 \pm 0.7^{\text{B}}$ (12.9–15.3)
	Females $(n = 2)$	<b>47.1 ± 2.1</b> (45.6–48.6)	<b>36.4 ± 3.5</b> (33.9–38.8)	<b>12.8 ± 0.3</b> (12.6–13.0)	<b>2.1</b> (NA; <i>n</i> = 1)	<b>2.1 ± 0.2</b> (2.0–2.2)	<b>13.5 ± 0.5</b> (13.1–13.8)

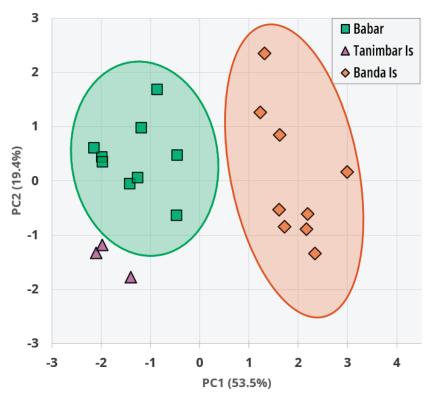


Figure 2. Principal component analysis (PCA) biplot for all morphometric parameters showing differences in populations of *Myzomela boiei* from the Banda Islands, Tanimbar Islands and Babar. Ellipses represent 95% confidence intervals of the principal component scores for each population. Explained variance for each axis is given in parentheses.

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



ISSN-2513-9894 (Online)



Figure 3. Ventral (above) and dorsal (below) views of male *Myzomela boiei* specimens. From left to right: *M. b. annabellae* (Tanimbars) AMNH 692710, 692709; *M. b. annabellae* (Babar) AMNH 692701, 692700, 692704; *M. b. boiei* (Banda Neira) AMNH 692712, 692714, 692713. Note the much broader black breast-band and duskier lower underparts of *M. b. boiei* (right). Compared to Tanimbars *M. b. annabellae* (left), birds from Babar (middle) have slightly more extensive scarlet on the upperparts.

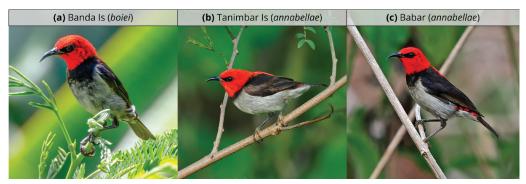


Figure 4. Photographs of the three populations of *Myzomela boiei s. s.* (a) *M. b. boiei*, Banda Neira, 8 December 2023 (Andrew J. Spencer); (b) *M. b. annabellae*, Tanimbar (Yamdena), 11 November 2024 (James A. Eaton); and (c) *M. b. annabellae*, Babar, 6 November 2024 (James A. Eaton)

but the sonograms (Fig. 5) show three populations whose songs bear almost no resemblance to one another at all. Unsurprisingly, the PCA plot very clearly separates the three

© 2025 The Authors; *This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,* 



ISSN-2513-9894 (Online)

populations along PC1 (which accounted for 63.4% of variance; Fig. 6). PC2, which accounted for 30.3% of variance, also separated Tanimbar birds from those on Babar and the Banda Islands.

The song of M. b. boiei (n = 6) comprises a series of 5–6 comparatively widely spaced high-pitched notes with a large bandwidth. These are sometimes followed by a 'flourish' of variable, lower-pitched more rapidly delivered notes (top row, Fig. 5). Strophes are the longest in the complex (1.7-2.5 seconds; mean 2.1) with the highest max. frequency (8.1-9.1 kHz, mean 8.4). The song of Tanimbar *M. b. annabellae* (n = 8) is a variable series of 3-5 simple notes, delivered over 0.5-0.8 second (mean 0.7) that fluctuate in frequency (mean range: 3.5–6.0 kHz) (middle row, Fig. 5). Tanimbar birds exhibit eventual variety (i.e. individuals sing a single song pattern multiple times [five examples shown in Fig. 5], then switch to a different song pattern that is repeated multiple times, then another, etc.) and while each of these song patterns differs slightly, all have a similar construction. In addition to the eight recordings we measured, seven additional songs of Tanimbar M. b. annabellae that could not be so analysed all audibly possessed the same structure. On Babar, M. b. annabellae has a totally different song, comprising 3-5 short introductory notes followed by a rapid, even-pitched trill, overall sounding rather like a bouncy ball (bottom row, Fig. 5). Strophes last 0.9–1.4 seconds (mean 1.1) and contain 13–23 notes (mean 17) delivered at a

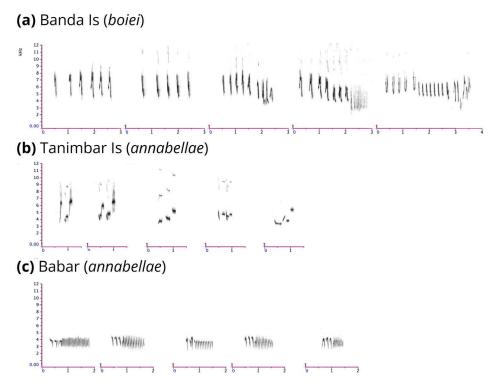


Figure 5. Example sonograms of  $Myzomela \ boiei \ sensu \ lato \ song (n = 5 \ for \ each \ population).$  (a)  $M. \ b. \ boiei \ Banda$ Islands; (b) M. b. annabellae Tanimbar Islands; and (c) M. b. annabellae Babar. Recordings and recordists (left to right, top to bottom): (a) ML 616087638, ML 616087419, ML 616087427, ML 616087421, ML 616087425 (all A. J. Spencer); (b) ML 613342338, ML 613342338, ML 613342355, ML 613342321, ML 613342331 (all A. J. Spencer); (c) XC 205056 (M. Nelson), XC 138359 (C. Trainor), ML 609070464 (P. Verbelen), ML 609070464 (P. Verbelen), ML 609070462 (P. Verbelen). Sonograms were visualised in Raven Pro Version 1.6 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY) with an optimised window size of 1,048 for all recordings.

© 2025 The Authors; This is an open-access article distributed under the terms of the

 $\odot$   $\odot$ Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,

ISSN-2513-9894 (Online)

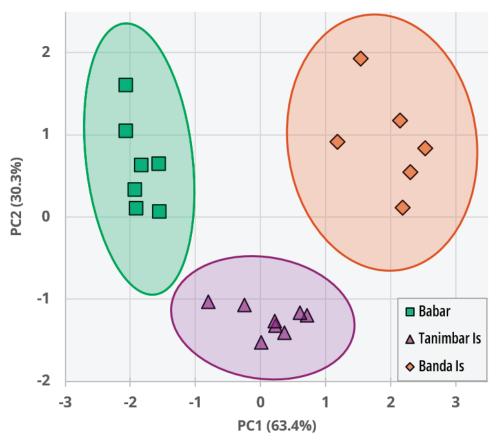


Figure 6. Principal component analysis (PCA) biplot for all vocal parameters (length of strophe, number of notes in each strophe, max. frequency, minimum frequency) showing differences in populations of *Myzomela boiei* from the Banda Islands, Tanimbar Islands and Babar. Ellipses represent 95% confidence intervals of the principal component scores for each population. Explained variance for each axis is given in parentheses.

rate of 16–18 notes/second. All notes are comparatively low-pitched, with the entire strophe having a mean frequency range of 2.8–4.4 kHz. Birds from Babar exhibit less variation in their songs than either *M. b. boiei* or birds from Tanimbar, but there are some differences (including between strophes delivered by a single individual) in the number and shape of the introductory notes, as well as the length of the trill.

**Playback experiments.**—The three populations of *M. boiei* can perfectly discriminate allopatric from sympatric song. In all playback experiments, birds ignored playback of allopatric song, and mostly responded (often aggressively) to sympatric song (Table 3). Although Banda song was played to only one individual each on Babar and Tanimbar, 38 playback experiments were performed on Banda birds (n = 20 played Tanimbar song, n = 18 Babar song) and all elicited no response. Playback experiments on Banda additionally tested whether birds were more likely to respond to allopatric populations after they had already been provoked with playback of sympatric songs, but this did not result in any differing response. While the songs of Tanimbar birds, and to a lesser extent those on Banda, are quite variable individually, birds were still observed to respond to songs from their own island, but not others (PS & AJS pers. obs.).

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



#### TABLE 2

Comparison of songs of *Myzomela boiei* from the Banda Islands (nominate *boiei*), Babar and the Tanimbar Islands (both *M. b. annabellae*). Values in **bold** represent the mean ± standard deviation, values in parentheses the range. Superscript letters A–C represent statistical significance of pairwise comparisons between taxa at the threshold of <0.05 using Welch's unpaired *t*-tests applying a Bonferroni correction, where A = Banda Islands vs. Tanimbar Islands, B = Banda Islands vs. Babar, C = Tanimbar Islands vs. Babar.

Population	Number of notes	Total length of strophe (s)	<b>Minimum frequency</b> (kHz)	Max. frequency (kHz)
<i>M. b. boiei</i>	7 ± 2 <sup>A,B</sup>	<b>2.1 ± 0.3</b> <sup>A,B</sup>	$3.8 \pm 0.4^{\text{B}}$	<b>8.4 ± 0.4</b> <sup>A,B</sup>
(Banda Islands) ( <i>n</i> = 6)	(5–11)	(1.7–2.5)	(3.3-4.2)	(8.1–9.1)
<i>M. b. annabellae</i>	4 ± 1 <sup>A,C</sup>	<b>0.7 ± 0.1</b> <sup>A,C</sup>	<b>3.5 ± 0.4</b> <sup>C</sup> (2.7–3.9)	<b>6.0 ± 0.6</b> <sup>A,C</sup>
(Tanimbar Islands) ( <i>n</i> = 8)	(3–5)	(0.5–0.8)		(5.2–6.8)
M. b. annabellae (Babar) ( $n = 7$ )	<b>17 ± 3</b> <sup>B,C</sup> (13–23)	<b>1.1 ± 0.2</b> <sup>B,C</sup> (0.9–1.4)	<b>2.8 ± 0.1</b> <sup>B,C</sup> (2.6–2.9)	$\begin{array}{c} 4.3 \pm 0.2^{B,C} \\ (4.2 - 4.8) \end{array}$

#### TABLE 3

Results of playback experiments (*n* = 152) on three populations of *Myzomela boiei* (see Methods). Values in **bold** represent response scores, calculated as the proportion of birds subjected to experiments that responded to playback of each song type. Total sample sizes in parentheses. SR = strong response, MR = moderate response, NR = no response. Shaded cells represent playback of allopatric song.

	Song played			
	Tanimbar Islands	Babar	Banda Islands	
Tanimbar Islands	<b>0.86</b>	<b>0.0</b>	<b>0.0</b>	
	12 SR, 6 MR, 3 NR	20 NR	1 NR	
	( <i>n</i> = 21)	( <i>n</i> = 20)	( <i>n</i> = 1)	
Babar	<b>0.0</b>	<b>0.95</b>	<b>0.0</b>	
	10 NR	17 SR, 4MR, 1 NR	1 NR	
	( <i>n</i> = 10)	( <i>n</i> = 22)	( <i>n</i> = 1)	
Banda Islands	<b>0.0</b>	<b>0.0</b>	<b>1.0</b>	
	20 NR	18 NR	21 SR, 18 MR	
	( <i>n</i> = 20)	( <i>n</i> = 18)	( <i>n</i> = 39)	

## Discussion

Morphological and vocal data reveal there to be substantial differences between the three insular populations of *M. boiei*. Applying a modern interpretation of the Biological Species Concept to our data, we agree with the very earliest taxonomic arrangement (Hartert 1901) for this group, and Eaton *et al.* (2021), i.e., that *M. boiei* should be considered a monotypic species confined to the Banda Sea Islands. Compared to both populations of *M.* [*b.*] *annabellae*, nominate *boiei* is considerably larger, has a much broader breastband and darker lower underparts. Vocally, *boiei* has a song type that is not recorded in either population of *annabellae* and is so divergent from the latter that differences cannot reasonably be dismissed as merely dialectical. In recent years, vocal data have been advocated and frequently used to elucidate taxonomic limits on the assumption they are indicative of reproductive isolation (e.g., Alström & Ranft 2003, Remsen 2005, Brambilla *et al.* 2008). Here, we test this assumption explicitly and find that Banda Islands birds are consistently unresponsive to playback of Tanimbar (*n* = 20) and Babar (*n* = 18) songs, indicating that the vocal differences between them probably have reproductive significance (Freeman & Montgomery 2017).

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,

Within Wallacean *Myzomela*, Prawiradilaga *et al.* (2017) described Rote Myzomela *M. irianawidodoae* as a species distinct from Sumba Myzomela *M. dammermani* by virtue of its narrow black breast-band (in males), larger size and unique vocalisations, a suite of characters almost identical to those being proposed here to separate *M. [b.] boiei* and *M. [b.] annabellae.* Similarly, Irham *et al.* (2020) described Alor Myzomela *M. prawiradilagae* as a species distinct from Crimson-hooded Myzomela *M. kuehni* of Wetar on account of comparatively subtle morphological and vocal differences. Similar lines of evidence were also used in the recent elevation of Bacan Myzomela *M. batjanensis* to species rank (del Hoyo & Collar 2016, Eaton *et al.* 2021, Berryman 2023).

44

For *M. boiei sensu stricto*, we recommend the English name 'Banda Islands Myzomela' to avoid confusion with the previous name for the entire group, 'Banda Myzomela'. The species has been recorded throughout the Banda Islands (PS & AJS pers. obs.; records on www.ebird.org as of 2024).

It is also apparent from our data that the two populations of *M. annabellae* differ to an extent that merits taxonomic recognition. In particular, the highly divergent vocalisations of the two populations (which playback data suggest are of likely reproductive significance) are suggestive of cryptic species-level divergence for reasons given above as justification for the separation of *M. boiei* and *M. annabellae*. With the Tanimbar Islands listed as the type locality of *annabellae* (Sclater 1883), and no name available for the Babar population, we name it:

### Myzomela babarensis sp. nov.

*Holotype*.—American Museum of Natural History, New York, AMNH 692701, collected by Heinrich Kühn, at Tepa, Babber [Babar] (07°52′06.3″S, 129°35′43.7″E), Indonesia, on 24 August 1905.

*Paratypes.*—All specimens collected by H. Kühn at Tepa, Babber [Babar]: AMNH 692704 (adult male) on 17 August 1905; AMNH 692700 (adult male) and AMNH 692705 (immature male) on 23 August 1905; AMNH 692707 and AMNH 692708 (both adult females) on 18 August 1905.

**Diagnosis**.—Compared to *M. boiei sensu stricto*, male *M. babarensis* differs in having a much narrower black breast-band that is confined to the upper breast (vs. extending onto the lower breast in *M. b. boiei*; Figs. 3–4). The lower underparts (especially the vent and flanks) of *M. boiei* are dusky, but consistently much paler cream-white in the nine specimens of *M. babarensis* examined. In plumage, females of the two populations appear to be identical. *M. boiei s. s.* is larger in wing, bill and tarsus length (Table 1) than *M. babarensis*. Morphologically, *M. babarensis* is similar to *M. annabellae* (restricted here to the Tanimbar Islands) and only very subtly identifiable. Male *M. babarensis* has a larger wing, bill and tail with no overlap (Table 1 and Fig. 2), and the available specimens (n = 5 for *M. annabellae*) appear to consistently have more extensive scarlet-red on the upperparts, especially on the uppertail-coverts. Female plumages appear inseparable. All three species differ radically in song (Table 2, Fig. 5 and accompanying descriptions) and playback experiments show them to be unresponsive to one another's song (Table 3).

Red-headed Myzomela *M. erythrocephala* is much larger (five males chosen randomly at AMNH and measured by AJB had mean wing length 58.3 mm [range 55.8–59.6 mm], bill length to skull 15.8 mm [15.4–16.3 mm]), has paler upperparts, more even smoky grey underparts (lacking the strong contrast of the black breast-band) and scarlet on the upperparts confined to the lower back and rump. *M. kuehni* lacks the black breast-band entirely and instead has the scarlet-red of the face extending to the upper breast; its upperparts are grey (not blackish) with scarlet confined to the rump and females are rather

© 2025 The Authors; *This is an open-access article distributed under the terms of the* 

Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,

ISSN-2513-9894 (Online) like males (thus it lacks the striking sexual dimorphism of *M. babarensis*). The recently described *M. prawiradilagae* (Irham *et al.* 2020) differs in the same respect as the previous species, although its red hood is less extensive. *M. dammermani* has much more extensive black on its underparts (reaching the upper belly) and a dusky (not whitish) lower belly and vent. All the above-mentioned species also differ significantly in vocalisations with no song type that overlaps with the apparently stereotypical vocalisations of *M. babarensis* (all authors pers. obs.; also see Prawiradilaga *et al.* 2017: 82).

45

*Description of holotype.*—Capitalised colour names and codes correspond to Smithe (1976). Head Geranium (12) except Jet Black (89) lores extending to the base of the maxilla. Mantle and back feathers mostly Light Neutral Gray (85) with broad black tips. Some feathers grey basally, black in their centres, and broadly tipped Geranium (12), particularly on the rump and uppertail-coverts, giving the appearance of a broken red stripe down the back. Upper breast and lower neck Jet Black (89) (forming collar with mantle), meeting narrow area of mid and lower breast, which is Light Neutral Gray (85) mixed with some feathers that are closest to Pale Horn Color (92), especially in centre. Lower underparts Pale Horn Color (but slightly paler) in the centre, and nearly white on the flanks and vent. Remiges closest to Vandyke Brown (121) but marginally darker; inner primaries and secondaries have very narrow Yellowish Olive-Green (50) outer margins. Upperwing-coverts Vandyke Brown; underwing-coverts whitish. Undersurface of remiges much paler, with broad whitish inner margins to the secondaries and pp1–2. Rectrices close to Hair Brown (119A) but a little darker. Bare parts all dark post-mortem; iris, feet and bill recorded on label as 'black', 'blackish' and 'black' respectively.

*Measurements of holotype*.—Wing 52.7 mm, tail 43.6 mm, bill (to skull) 13.5 mm, bill width (at nostril) 2.4 mm, bill depth (at nostril) 2.4 mm, tarsus 14.9 mm.

*Variation in paratypes.*—Among males, AMNH 692704 agrees with AMNH 692701 but has a slightly more extensive black collar extending onto the mid-breast (though not in extent matching any of the eight AMNH specimens of *M.* [*b.*] *boiei*). Some more red feathers on back create a more complete stripe on the back. AMNH 692700 is like 692704 but for some admixed scarlet feathers on the black upper breast. Immature male (AMNH 692705) most like adult female AMNH 692707 (see below) but has more extensive red feathers on face, reaching almost to the crown and a few feathers behind the eye. A few scattered back feathers are tipped Geranium (like adult males, but not as extensive).

AMNH 692707 (adult female) has a few Geranium (12) feathers on forehead/at base of bill, as well as on the upper throat and malar area. Crown, nape and ear-coverts Dark Neutral Gray (83) but some feathers have very inconspicuous Grayish Olive (43) tips. Mantle, back, rump and uppertail-coverts Dark Drab (119B). Lower throat and upper breast Dark Neutral Gray (83) with much paler Pale Neutral Gray (86) tips (some even paler, almost whitish), creating an overall rather mottled and messy appearance. Rest of underpart feathers whitish or Pale Horn Color (92). Primaries Hair Brown (199A) or slightly paler and becoming progressively paler inwards, thus secondaries close in shade to Army Brown (219B) (albeit slightly darker). Inner primaries and secondaries have narrow Yellowish Olive-Green (50) outer margins. Upperwing-coverts Army Brown (219B); underwing-coverts whitish. Undersurface of remiges much paler, with broad whitish inner margins to the secondaries and pp1-2. Rectrices Army Brown. Bill and legs dark postmortem, but feet and claws somewhat paler. Iris, legs and bill recorded on label as 'blackish, 'olivaceous-grey' and 'black' respectively. Variation among females: AMNH 692708 almost identical to AMNH 692707 but red less extensive on face (restricted to chin, malar area and base of maxilla), suggesting this character is probably variable in adult females, as it seems to be in other female Wallacean Myzomela.

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



ISSN-2513-9894 (Online) *Measurements of paratypes.*—AMNH 692704 (adult male) wing 50.6 mm, tail 39.7 mm, bill (to skull) 13.3 mm, bill width (at nostril) 2.3 mm, bill depth (at nostril) 2.2 mm, tarsus 14.5 mm; AMNH 692700 (adult male) wing 51.6 mm, tail 39.7 mm, bill (to skull) 13.5 mm, bill width (at nostril) 2.2 mm, bill depth (at nostril) 2.3 mm, tarsus 14.2 mm; AMNH 692705 (immature male) wing 52.1 mm, tail 38.6 mm, bill (to skull) 13.9 mm, bill width (at nostril) 2.3 mm, bill depth (at nostril) 2.3 mm, bill depth (at nostril) 2.4 mm, tarsus 15.0 mm; AMNH 692707 (adult female) wing 48.6 mm, tail 38.8 mm, bill (to skull) 12.6 mm, bill width (at nostril) 2.0 mm, bill depth (at nostril) 2.1 mm, tarsus 13.1 mm; AMNH 692708 (adult female) wing 45.6 mm, tail 33.9 mm (probably not fully grown), bill (to skull) 13.0 mm, bill width (at nostril) 2.2 mm, bill depth (at nostril) 2.1 mm, tarsus 13.8 mm.

46

*Geographic distribution*. – Endemic to Babar, Indonesia, perhaps including the island's five small satellites, although these have not been explored ornithologically.

*Etymology*.—The species is named *babarensis* for the island of Babar, to which it is endemic. We propose the English name 'Babar Myzomela' (and 'Tanimbar Myzomela' for *M. annabellae s. s.*).

Taxonomic rank.-Following a modern interpretation of the Biological Species Concept, we advocate species rank for M. babarensis. From M. boiei s. s., it is highly distinctive in morphometrics, plumage and vocalisations to a degree that in our view exceeds the differences used to justify the separation of other Wallacean Myzomela (e.g. del Hoyo & Collar 2016, Prawiradilaga et al. 2017, Irham et al. 2020). Specifically, the differences in size and underpart pattern are very similar to those that Prawiradilaga et al. (2017) used to argue that M. irianawidodoae is specifically distinct from M. dammermani. From M. annabellae s. s., M. babarensis is only marginally differentiated in morphometrics and plumage but the differences in vocalisations far exceed many other Myzomela species pairs. In an explicit test of the significance of this, we found M. babarensis to be unresponsive to playback of annabellae song, suggesting these differences represent a mechanism of pre-mating reproductive isolation. Such experiments have often been used to justify species rank (e.g. Freeman & Montgomery 2017). While there are no published molecular data available to investigate genetic differences between the three populations-the most comprehensive genetic sampling of Myzomela to date, provided by Marki et al. (2017), sampled only M. *boiei s. s.*—we do not consider this an obstacle to advocating species rank for the three taxa given the strong reproductive barriers their divergent songs represent. Moreover, genetic distances between Myzomela species are often comparatively small (Marki et al. 2017, Irham et al. 2020).

*Conservation status.*—*M. boiei s. l.* is currently listed as Least Concern on the IUCN Red List (BirdLife International 2024b). While the proposed division of *M. boiei* into three range-restricted species might ostensibly suggest that each could be at a heightened risk of extinction, all populations are highly adaptable to habitat degradation and are common within their respective ranges (Johnstone & Sudaryanti 1995, Bishop & Brickle 1998, Trainor & Verbelen 2013, Eaton *et al.* 2021; all authors pers. obs.). *M. babarensis* occurs in all manner of wooded habitats, including 'degraded agricultural land' (Trainor & Verbelen 2013; JAE pers. obs.), so its population is probably largely unaffected by ongoing forest degradation on Babar. We suggest that *M. boiei, M. annabellae* and M. *babarensis* are best considered Least Concern.

#### Acknowledgements

We thank all those who made available their sound-recordings for analysis, in particular Mike Catsis, Frank Lambert, Mike Nelson, Colin Trainor and Philippe Verbelen. AJB thanks P. Sweet and S. R. Bello at AMNH, and A. Bond and M. Adams (NHMUK) for facilitating work on the specimens in their care. M. Päckert and F. Albrecht at SMTD kindly sent photographs of relevant material. We are grateful to Colin Trainor and

© 2025 The Authors; This is an open-access article distributed under the terms of the

ISSN-2513-9894 (Online)

Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. Downloaded From: https://complete.bioone.org/journals/Bulletin-of-the-British-Ornithologists'-Club on 30 May 2025 Terms of Use: https://complete.bioone.org/terms-of-use Philippe Verbelen for their helpful comments as reviewers, and to Guy Kirwan for his help and guidance throughout the preparation of this manuscript.

References:

- Alström, P. & Ranft, R. 2003. The use of sounds in avian systematics and the importance of bird sound archives. *Bull. Brit. Orn. Cl.* 123: 114–135.
- Berryman, A. J. 2022. Notes on the plumages, vocalisations, ecology and conservation of the Vulnerable Bacan Myzomela *Myzomela batjanensis*. *BirdingASIA* 38: 58–64.
- Berryman, A. J. & Eaton, J. A. 2020. Vocalisations and taxonomy of the Sulawesi Leaf-warbler *Phylloscopus sarasinorum* complex, including discussion of a novel undescribed taxon from Selayar, Indonesia. *Forktail* 36: 90–96.
- BirdLife International. 2024a. Country profile: Indonesia. https://datazone.birdlife.org/country/ indonesia (accessed 11 April 2024).
- BirdLife International. 2024b. Species factsheet: Banda Myzomela *Myzomela boiei*. https://datazone.birdlife. org/species/factsheet/banda-myzomela-myzomela-boiei (accessed 20 July 2024).
- Bishop, D. & Brickle, N. 1998. An annotated checklist of the birds of the Tanimbar Islands. Kukila 10: 115–150.
- Brambilla, M., Janni, O., Guidali, F. & Sorace, A. 2008. Song perception among incipient species as a mechanism for reproductive isolation. J. Evol. Biol. 21: 651–657.
- Clements, J. F., Rasmussen, P. C., Schulenberg, T. S., Iliff, M. J., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Spencer, A., Billerman, S. M., Sullivan, B. L., Smith, M. & Wood, C. L. 2024. The eBird/Clements checklist of birds of the world: v2024. http://www.birds.cornell.edu/clementschecklist/download/ (accessed 26 November 2024).

Collar, N. J. 2003. How many bird species are there in Asia? Bull. Oriental Bird Cl. 38: 20-30.

- Dickinson, E. C. & Christidis, L. (eds.) 2014. *The Howard & Moore complete checklist of the birds of the world*, vol. 2. Fourth edn. Aves Press, Eastbourne.
- Eaton, J. & Hutchinson, R. 2011. Banda Sea cruise, 18 October-6 November 2011. https://tinyurl.com/ btabanda11.
- Eaton, J. A., van Balen, B., Brickle, N. W. & Rheindt, F. E. 2016. Birds of the Indonesian archipelago: Greater Sundas and Wallacea. First edn. Lynx Edicions, Barcelona.
- Eaton, J. A., van Balen, B., Brickle, N. W. & Rheindt, F. E. 2021. Birds of the Indonesian archipelago: Greater Sundas and Wallacea. Second edn. Lynx Edicions, Barcelona.
- Finsch, O. 1901. Systematische uebersicht der Vögel der südwest-inseln. Notes Leyden Mus. 22: 225–309.
- Freeman, B. & Montgomery, G. 2017. Using song playback experiments to measure species recognition between geographically isolated populations: a comparison with acoustic trait analyses. *Auk* 134: 857–870.
- Gill, F., Donsker, D. & Rasmussen, P. (eds.) 2024. IOC world bird list. Version 14.2. doi:10.14344/IOC.ML.14.2 (accessed 26 November 2024).
- Gwee, C. Y., Eaton, J. A., Garg, K. M., Alström, P., van Balen, S. (B.), Hutchinson, R. O., Prawiradilaga, D. M., Manh Hung Le & Rheindt, F. E. 2019. Cryptic diversity in *Cyornis* (Aves: Muscicapidae) jungle-flycatchers flagged by simple bioacoustic approaches. *Zool. J. Linn. Soc.* 186: 725–741.
- Hartert, E. 1900. The birds of Dammer Island in the Banda Sea. Novit. Zool. 7: 12–24.
- Hartert, E. 1901. On a collection of birds from the Timor Laut islands. Novit. Zool. 8: 163–176.
- Hartert, E. 1904. On the birds of the South-west Islands of Wetter, Roma, Kisser, Letti and Moa. *Novit. Zool.* 11: 174–221.
- Hartert, E. 1906. On the birds of the island of Babber. Novit. Zool. 13: 288-302.
- Higgins, P. J., Peter, J. M. & Steele, W. K. (eds.) 2001. Handbook of Australian, New Zealand and Antarctic birds, vol. 5. Oxford Univ. Press, Melbourne.
- del Hoyo, J. & Collar, N. J. 2016. HBW and BirdLife International illustrated checklist of the birds of the world, vol.
  2. Lynx Edicions, Barcelona.
- Inskipp, T., Lindsey, N. & Duckworth, W. 1996. An annotated checklist of the birds of the Oriental region. Oriental Bird Club, Sandy.
- Irham, M., Ashari, H., Suparno, Trainor, C. R., Verbelen, P., Wu, M. Y. & Rheindt, F. E. 2020. A new *Myzomela* honeyeater (Meliphagidae) from the highlands of Alor Island, Indonesia. *J. Orn.* 161: 313–324.
- Irham, M., Haryoko, T., Shakya, S. B., Mitchell, S. L., Burner, R. C., Bocos, C., Eaton, J. A., Rheindt, F. E., Suparno, S., Sheldon, F. H. & Prawiradilaga, D. M. 2022. Description of two new bird species from the Meratus Mountains of southeast Borneo, Indonesia. J. Orn. 163: 575–588.
- Irham, M., Prawiradilaga, D. M., Menner, J. K., O'Connell, D. P., Kelly, D. J., Analuddin, K., Karya, A., Meads, M., Marples, N. M. & Rheindt, F. E. 2023. A distinct new species of *Zosterops* white-eye from the Sulawesi region, Indonesia. *Ibis* 165: 808–816.
- Johnstone, R. E. & Sudaryanti. 1995. The birds of Banda Neira, Moluccas, Indonesia. West. Austr. Natur. 20: 15–19.

© 2025 The Authors; This is an open-access article distributed under the terms of the Creative Commons Attribution-NonCommercial Licence, which permits unrestricted use,



Marki, P. Z., Jønsson, K. A., Irestedt, M., Nguyen, J. M. T., Rahbek, C. & Fjeldså, J. 2017. Supermatrix phylogeny and biogeography of the Australasian Meliphagides radiation (Aves: Passeriformes). *Mol. Phylo. & Evol.* 107: 516–529.

48

- Müller, S. & Schlegel, H. 1843. Bijdragen tot de Natuurlijke geschiedenis der Honigvogels (Nectariniae) van den Indischen Archipel. Pp. 53–71 in Temminck, C. J. (ed.) Verhandelingen over de natuurlijke geschiedenis der Nederlandsche Overzeesche Bezittingen, vol. 1, Zoölogie, pt. 12. Natuurkundige Commissie voor Nederlandsch-Indie, Leiden.
- Prawiradilaga, D. M., Baveja, P., Suparno, Ashari, H., Ng, N. S. R., Gwee, C. Y., Verbelen, P. & Rheindt, F. E. 2017. A colourful new species of *Myzomela* honeyeater from Rote Island in eastern Indonesia. *Treubia* 44: 77–100.
- Remsen, J. V. 2005. Pattern, process, and rigor meet classification. Auk 122: 403-413.
- Rheindt, F. E. & Hutchinson, R. O. 2007. A photoshot odyssey through the confused avian taxonomy of Seram and Buru (southern Moluccas). *BirdingASIA* 7: 18–38.
- Rheindt, F. E., Prawiradilaga, D. M., Ashari, H., Suparno, Gwee, C. Y., Lee, G. W. X., Wu, M. Y. & Ng, N. S. R. 2020. A lost world in Wallacea: description of a montane archipelagic avifauna. *Science* 367: 167–170.
- Schodde, R. & Mason, I. J. 1999. The directory of Australian birds: a taxonomic and zoogeographic atlas of the biodiversity of birds in Australia and its territories, vol. 1. CSIRO Publishing, Collingwood, VIC.
- Sclater, P. L. 1883. Additional notes on birds collected in the Timor-Laut, or Tenimbar, group of islands by Mr. Henry O. Forbes. Proc. Zool. Soc. Lond. 1883: 194–200, pls. 26–28.
- Smithe, F. B. 1976. Naturalist's color guide. Amer. Mus. Nat. Hist., New York.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. 1998. Endemic Bird Areas of the world: priorities for biodiversity conservation. BirdLife International, Cambridge, UK.
- Trainor, C. R. & Verbelen, P. 2013. New distributional records from forgotten Banda Sea islands: the birds of Babar, Romang, Sermata, Leti and Kisar, Maluku, Indonesia. *Bull. Brit. Orn. Cl.* 133: 272–315.
- White, C. M. N. & Bruce, M. D. 1986. The birds of Wallacea: an annotated check-list. BOU Check-list No. 7. British Ornithologists' Union, London.
- Wolters, H. E. 1982. Die Vogelarten der Erde. Paul Parey, Hamburg & Berlin.
- Yue, A. Y., Ng, E. Y. X., Eaton, J. A. & Rheindt, F. E. 2020. Species limits in the Elegant Pitta (*Pitta elegans*) complex from Wallacea based on bioacoustic and morphometric analysis. *Avian Res.* 11: 42.
- Addresses: Alex J. Berryman, BirdLife International, David Attenborough Building, Cambridge, CB2 3QZ, UK, e-mail: alex.berryman@birdlife.org. Andrew J. Spencer, Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY, 14850, USA, e-mail: ajs535@cornell.edu. Puja Sharma, A-13 New Friends Colony, New Delhi, 110025, India, e-mail: pujasharma1@gmail.com. James A. Eaton, A-3A-5, Casa Indah, Persiaran Surian, Petaling Jaya, 47410, Malaysia, e-mail: jameseaton@birdtourasia.com

#### Appendix 1

All specimens measured for this study.

*M. b. boiei* (Banda Islands).—Males (*n* = 11): AMNH 692711, 692712, 692713, 692714, 692715, 692716, 692717, 692721; NHMUK 1873.5.12.896, 1936.4.20.76, 1936.4.20.77. Females (*n* = 3): AMNH 692718, 692719, 692720.

*M. b. annabellae* (Tanimbar Islands).—Males (*n* = 3): AMNH 692709, 692710; NHMUK 1883.5.30.70 (holotype).

*M. b. annabellae* (Babar).—Males (*n* = 9): AMNH 692697, 692698, 692699, 692700, 692701, 692702, 692702, 692704, AMNH unregistered. Females (*n* = 2): AMNH 692707, 692708.

#### Appendix 2

All sound recordings of song measured as part of this study. ML = Macaulay Library; XC = Xeno-canto. *M. b. boiei* (Banda Islands).—ML 616087419, ML 616087421, ML 616087425, ML 616087427, ML 616087531, ML 616087531.

*M. b. annabellae* (Tanimbar Islands).—ML 203925841, ML 613342321, ML 613342331, ML 613342338, ML 613342355, XC 205153, XC 205151, XC 205085.

*M. b. annabellae* (Babar).-ML 609070464, ML 609070462, XC 205056, XC 138359, XC 138360, XC 949226, XC 949225.

