

A new species of lowland tailorbird (Passeriformes: Cisticolidae: *Orthotomus*) from the Mekong floodplain of Cambodia

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Based on distinctive morphological and vocal characters we describe a new species of lowland tailorbird *Orthotomus* from dense humid lowland scrub in the floodplain of the Mekong, Tonle Sap and Bassac rivers of Cambodia. Genetic data place it in the *O. atrogularis*–*O. ruficeps*–*O. sepium* clade. All data suggest that the new species is most closely related to *O. atrogularis*, from which genetic differences are apparently of a level usually associated with subspecies. However the two taxa behave as biological species, existing locally in sympatry and even exceptionally in syntopy, without apparent hybridisation. The species is known so far from a small area within which its habitat is declining in area and quality. However, although birds are found in a number of small habitat fragments (including within the city limits of Phnom Penh), most individuals probably occupy one large contiguous area of habitat in the Tonle Sap floodplain. We therefore recommend it is classified as Near Threatened on the IUCN Red List. The new species is abundant in suitable habitat within its small range. Further work is required to understand more clearly the distribution and ecology of this species and in particular its evolutionary relationship with *O. atrogularis*.

INTRODUCTION

After a hiatus of over half a century owing to the intense human conflicts in the area, the last two decades have witnessed the discovery of a flush of novel bird taxa in Indochina. These recent discoveries have been facilitated by better sampling of remote micro-habitats and to a much lesser degree the greater use of non-morphological characters in delimiting species. Most of these discoveries concerned babblers (Timaliidae) from isolated montane areas in Vietnam (Eames *et al.* 1994, Eames *et al.* 1999a,b, Eames & Eames 2001, Eames 2002). A smaller wave of discoveries involving a diverse range of taxa took place in forested limestone karst in Lao PDR, Vietnam and adjacent areas of China (Zhou Fang & Jiang Aiwu 2008, Woxvold *et al.* 2009, Alström *et al.* 2010). Only one new species, Mekong Wagtail *Motacilla samveasnae*, was named from Cambodian specimens, but it also occurs in Lao PDR, Thailand and Vietnam in ‘channel mosaic’ habitat on the Mekong

and its major tributaries (Duckworth *et al.* 2001, Le Trong Trai & Craik 2008). Here we describe a new species of lowland tailorbird *Orthotomus*, confined to low elevation humid evergreen scrub in the floodplain of the Mekong and associated large rivers, in Cambodia.

THE NEW TAILORBIRD

During routine sampling of birds for avian influenza in 2009, four individual tailorbirds *Orthotomus* sp. were mist-netted and photographed in the hand: one on 28 and another on 29 January 2009 in a patch of scrub near a pond at Kraing Check, Kandal province (11°41'53.36"N 104°46'38.93"E) (J. Reside per F. Goes *in litt.* 2012), one on 24 February 2009 and another on 12 March 2009 near to Phnom Tamao Zoo, Takeo province (11°17'56"N 104°50'22"E), in 3–5 m high scrub near rice fields (HN, A. Yang and P. Joyner *in litt.* 2012). Based on photographs and inferences

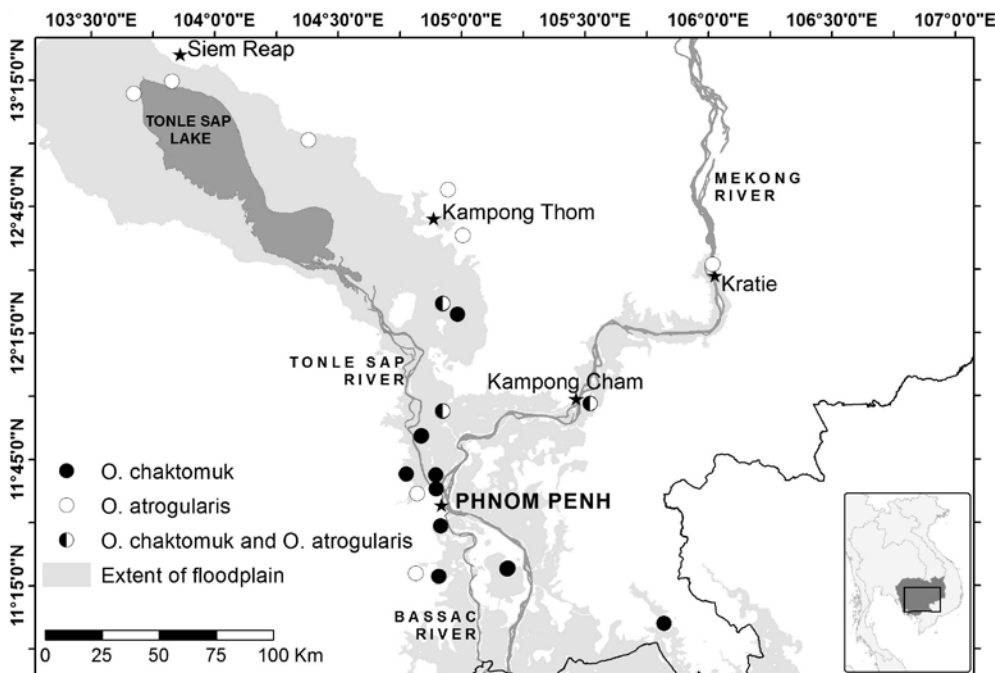


Figure 1. Distribution of records of *Orthotomus chaktomuk* and *O. atrogularis* within and close to the floodplain of the Mekong, Tonle Sap and Bassac rivers.

drawn from incorrect location data (which misleadingly indicated that the birds had been caught close to the coast) these individuals were incorrectly identified as Ashy Tailorbird *O. ruficeps*; the possibility of their representing aberrant Dark-necked Tailorbird *O. atrogularis* was considered and rejected based on general plumage similarity to *O. ruficeps* (F. Goes verbally 2012).

On 29 January 2012, HN found a similar bird at Prek Ksach, in a partially flooded construction site c.15 km from Phnom Penh (11°41'37.14"N 104°53'43.79"E) and, owing to similarity to the 2009 birds, assigned it to *O. ruficeps*. In early June 2012, photographs by AJIJ of an *Orthotomus* sp. from this site raised the interest of SPM. Subsequent field observations by SPM, AJIJ and T. D. Evans and discussion with J. W. Duckworth, P. D. Round, CMP and C. Robson indicated to SPM that these birds might not be *O. ruficeps*, but could perhaps represent an undescribed taxon. On 23 June 2012, SPM, HN and AJIJ searched for additional individuals at Prek Ksach and located five single males and two pairs. Between 23 June 2012 and 20 April 2013, intensive searches revealed at least 100 individuals at nine additional locations (Figure 1, Table SOM 1 [supplementary online material—see page 14]). Seven morphologically typical *O. atrogularis* comprising six males and one female were seen at five floodplain locations at or within 10 km of locations where birds of the new taxon were found (Figure 1, Table SOM 1).

From photographs SPM re-identified all of the individuals mist-netted in 2009 as conforming to the new taxon, thus temporarily removing *O. ruficeps* from the list of birds recorded in Cambodia. Typical *O. ruficeps* has since been recorded in mangrove forest in coastal Cambodia close to the border with Vietnam (Mahood & Martin 2013).

In August 2012 two adult males, one immature male and two immature females (aged by plumage, sexed internally) were collected for formal description (below). SPM was later able to compare these specimens directly with the *Orthotomus* material held at the Natural History Museum, Tring, UK (NHMUK) including a syntype (NHMUK 1886.10.1.1830) of *O. atrogularis nitidus* (the subspecies in Cambodia) and the holotype of Olive-backed Tailorbird *O. sepium* (NHMUK 1880.1.1.4473), and also examined specimens at Naturalis Biodiversity Centre, Leiden, Netherlands (RMNH) including the holotype of *O. ruficeps cineraceus* (RMNH 137559). (The disjunct population of *O. ruficeps* in coastal southern Vietnam and Cambodia has not been assigned to a subspecies; however, *O. r. cineraceus* is the subspecies recorded in mainland Asia: Madge 2006). All other *Orthotomus* taxa differed so extensively from the



Plate 1. Dorsal, ventral and lateral views of the holotype of *O. chaktomuk*. Harry Taylor © Natural History Museum, London.

new form that detailed comparison would be superfluous. A detailed list of all specimens examined is provided in Table SOM 2.

The new taxon shows significant morphological differences from its close relatives and is sympatric with two lowland tailorbird species, *O. atrogularis* and Common Tailorbird *O. sutorius*, without signs of intergradation. We therefore consider that it represents a new species, which we name:

***Orthotomus chaktomuk*, sp. nov.**
Cambodian Tailorbird

<http://zoobank.org/urn:lsid:zoobank.org:act:23E9A09C-AD9C-4346-A594-F187DAFB6013>

Holotype and paratypes

Study skins deposited in NHMUK (Table 1, Plate 1, Plate 2a–c) were collected by JCE and SPM at Bateay District, Kompong Cham

Table 1. Mensural and other relevant data of holotype and paratypes (in mm, except mass in g).

	Sex	Age	Culmen	Tarsus	Wing	Tail	Mass	Testes length	State of wing moult	Collection date
Holotype NHMUK reg. no. 2012.9.1 LSUMNS tissue accession no. B77286	M	ad	13	19	47	42	8	4.5, 2	P1–5 (R), P2–6 (L), tertials, greater and median coverts	8 August 2012
Paratype NHMUK reg. no. 2012.9.2 LSUMNS tissue accession no. B77287	M	ad	14	19.5	46	41	7	5, 3.5	P1–6 (R), P1–6 (L), tertials, greater and median coverts	9 August 2012
Paratype NHMUK reg. no. 2012.9.3 LSUMNS tissue accession no. B77288	M	1yr	14.5	19	45	36	8	4, 0.5	P1–6 (R), P1–6 (L), tertials, greater and median coverts	9 August 2012
Paratype NHMUK reg. no. 2012.9.4 LSUMNS tissue accession no. B77289	F	1yr	13	18	41	35.5	6.5	n/a	P2–3 (R), P2–3 (L), tertials and median coverts	9 August 2012
Paratype NHMUK reg. no. 2012.9.5 LSUMNS tissue accession no. B77290	F	1yr	12	17	42	35.5	6	n/a	P1–3 (R), P1–3 (L), tertials, greater and median coverts	8 August 2012

M, Male; F, Female; ad, adult; 1yr, first calendar year. State of wing moult lists feather tracts recently replaced; P, primaries; R, right wing; L, left wing.



Plate 2. Specimens of *O. chaktomuk*: (a) dorsal, (b) ventral and (c) lateral views of the holotype and four paratypes (from left to right NHMUK 2012.9.1, 2012.9.2, 2012.9.3, 2012.9.4, 2012.9.5). Harry Taylor © Natural History Museum, London.

province, Cambodia (11°56'53.94"N 104°56'50.94"E), c.43 km north of Phnom Penh at c.15 m elevation on 8 and 9 August 2012, and prepared by JCE. Tissue samples from the same individuals were deposited in Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana, USA (Table 1). Holotype (NHMUK 2012.9.1): adult male; in active wing moult; one large testis (left testis 4.5 mm length, right testis 2 mm length). Paratypes aged by plumage: one adult male (NHMUK 2012.9.2); one immature male (NHMUK 2012.9.3) with unmoulted rectrices olive-green fringed; one immature female (NHMUK 2012.9.4) with some retained greater coverts fringed olive-green indicating immaturity, all other rectrices as adult;

and one immature female (NHMUK 2012.9.5) with unmoulted rectrices as immature male.

Diagnosis of species

Head: in male entirely rich cinnamon-rufous crown and contrasting white cheeks, very similar to *O. atrogularis*, differing from *O. ruficeps* and *O. sepium* in cheek colour (Table 2, Plate 3a–c). Rufous of crown less extensive in female. **Upperparts and wings:** mid-grey in adult, superficially similar to those of *O. sepium* but lacking olive tones, strikingly different from *O. atrogularis* which is yellowish-green (Table 2, Plate 3a, c); tail with dark grey subterminal band and whitish tips when fresh. **Underparts:** pale grey ground colour

Table 2. Qualitative summary of plumage of *Orthotomus chaktomuk* and closely related species (all adult male).

Species	Crown	Cheeks	Mantle and rump		Wing	Chin	Throat	Breast	Belly	Vent	Thighs	Tail
			Malar stripe									
<i>O. chaktomuk</i>	Rich cinnamon-rufous	Whitish	White, black speckled	Mid-grey	Mid-grey	Dark-grey with white speckling	Dark-grey with white speckling	Mid-grey with white speckling	Light-grey, darker on flanks	Greyish-white	Whitish-cinnamon	Mid-grey with blackish subterminal band and whitish tips
<i>O. a. nitidus</i>	Dull brick-red	Whitish	White, black speckled	Bright yellow-olive	Bright yellow-olive	Black with white speckling	Black with white speckling	Whitish, black streaking on upper-breast	White with greenish-yellow flanks	Bright sulphur yellow	Bright yellowish-orange	Bright yellowish-green
<i>O. r. cineraceus</i>	Bright orange-rufous	Orange-rufous	Orange-rufous	Dark brownish-grey	Dull olive-brown	Bright orange	Mid-grey	Pale-grey	Whitish-grey	White	Bright orange-rufous	Dull olive-brown, whitish terminal tips
<i>O. s. sepium</i>	Fore-crown rufous, central mid- and hind- crown olive-rufous	Cinnamon-rufous	Cinnamon-rufous	Brownish-olive	Dull brown with dull olive fringing	Pale orange-rufous	Dark olive-grey	Greyish-olive	Pale greyish-olive	Whitish-grey	Pale cinnamon-rufous	Pale olive-brown with whitish terminal tips



Plate 3. Specimens of the holotype of *Orthotomus chaktomuk* and closely related species (all males): (a) dorsal, (b) ventral and (c) lateral views (from left to right of *O. chaktomuk*, *O. sepium sepium*, *O. ruficeps cineraceus* and *O. atrogularis nitidus*). Harry Taylor © Natural History Museum, London.

with profuse blackish throat-streaking in males (largely absent in females) with white drop-shaped marks, extensive mid-grey on flanks, and white vent; underparts of both sexes superficially similar to those of respective sexes of *O. atrogularis* owing to throat-streaking, but greyer on flanks and vent white, *O. ruficeps* and *O. sepium* lacking throat-streaking in both sexes (Table 2, Plate 3b, c); further distinguished from other members of the genus by whitish-cinnamon thighs. **Vocalisations:** loud, lengthy, complex and highly varied. Very similar to *O. atrogularis*. Compared to *O. atrogularis*, phrases are given at a quicker pace and the gaps between phrases are shorter. Subjectively, these characteristics mean that the vocalisations of *O. chaktomuk* sound faster and more complicated than those of *O. atrogularis*.

Sexing and ageing

Based on field observations (Plate 4a–k, Media Files SOM 1–3) and specimens (Plate 2a–c), female *O. chaktomuk* can be distinguished from males by paler cinnamon-rufous on crown, which is restricted to forecrown and sides of mid-crown (in lateral view this appears as a short cinnamon-rufous supercilium), paler grey upperparts and wings and whitish underparts with usually faint dark streaking. The latter is usually evident only at the edges of the throat/upper breast, although some (possibly older birds) show stronger and more extensive streaking on throat and breast. Even in these extreme individuals, the degree of female streaking does not approach that in males (Plate 4a–g). All three immature paratypes show shorter tails than adults (Table 1). Immature birds possess bright yellowish-olive fringing to the wing-feathers (Plate 4h), which are moulted during August and replaced with grey adult-type feathers (Plate 4i–j). Immatures are browner (slightly olive) above and paler below, with reduced streaking (Plate 4h–j). Wing-feathers of subadults appear as in adults, except sometimes they retain yellowish-olive-fringed greater coverts (Plate 4k). Overall, subadults resemble adults, but are paler and less heavily marked below. In adults, there is individual variation in colour tone of grey feathering above and below, and intensity of throat-streaking (e.g. Media Files SOM 1–3). It is unknown if this is age-related.

Description of species

The detailed description below was completed in the NHMUK based primarily on the prepared specimens (Plates 1–2), supplemented by information from individuals observed and photographed in the field (Plate 4). It refers to the holotype unless otherwise stated. Although moult of body feathers was almost complete when specimens were collected, all adult specimens retained a few head, throat or breast feathers in pin. The holotype and paratypes were in wing moult. Moult of wing feathers is complete by late August and followed immediately by moult and replacement of tail feathers, which were very worn in all specimens. Subjective colour assessments of plumage are, where possible, followed by a formal colour classification taken from Smithe (1975).

Head and face

Crown from forehead to nape, lores, and feathers on orbital ring and just behind eye rich cinnamon-rufous (136 Raw Sienna) (slightly richer-coloured in the adult male paratype); hindcrown slightly darker and more brownish (23 Raw Umber). Crown feathers in moult with newer feathers slightly richer rufous. On the immature female paratypes the crown is less richly coloured than that of the holotype (240 Kingfisher Rufous) and the cinnamon-rufous lores and feathering on the orbital ring and immediately behind the eye are replaced by rufous-buff (118 Warm Buff). The rufous crown feathering extends from the bill only as far back as the anterior of the mid-crown where dark-grey feathers predominate, imparting an overall greyish-brown colour (129 Dark Brownish Olive) to the hindcrown.



Plate 4. *Orthotomus chaktomuk* (a–b) adult males in fresh plumage, 21 November 2012 (J. A. Eaton); (c–d) adult male in active moult (holotype), 8 August 2012 (NHMUK 2012.9.1; J. C. Eames); (e) adult male in worn plumage, 29 July 2012 (A. J. I. John); (f) adult female in fresh plumage, 21 November 2012 (J. A. Eaton); (g) adult female in worn plumage, 29 July 2012 (A. J. I. John); (h) immature male pre-moult, 16 July 2012 (A. J. I. John); (i) immature male in active moult, 29 July 2012 (A. J. I. John); (j) immature female in active moult, 8 August 2012 (NHMUK 2012.9.5; J. C. Eames); (k) subadult female in active moult, 9 August 2012 (NHMUK 2012.9.4; J. C. Eames).

Five blackish rictal bristles per side, anterior two c.3 mm, twice the length of posterior three. Ear-coverts, cheeks and moustachial stripe almost white contrasting strongly with crown and underparts; however, feathers have buff (124 Buff) tips imparting an off-white wash. Feathers of submoustachial stripe and malar stripe white with very dark grey (82 Blackish Neutral Gray) bases and sometimes tips and fringes; white predominates, giving an impression of white speckling on a blackish base and contrasting strongly with the whitish cheeks. The malar stripe on the immature paratypes is quite different to that of the adult male specimens. It is made up of white feathers with pale grey central portions (85 Light Neutral Gray) and therefore contrasts little with the cheeks.

Upperparts

Boundary between hindcrown and upper neck abrupt. Upper neck, mantle and rump concolorous mid-grey (84 Medium Neutral Gray), slightly blue-toned approaching 78 Plumbeous (all feathers fresh and body moult apparently completed). Feathers on mantle and particularly rump relatively long and filamentous.

Wings

Wings of all prepared specimens in active moult (Table 1). On all specimens, fresh adult feathers are slightly darker grey (83 Dark Neutral Gray) than mantle, tinged very slightly brownish with mid-grey (84 Medium Neutral Gray) fringing (slightly broader on outer webs). Fresh primaries with off-white inner webs; worn adult rectrices buffy-brown (239 Ground Cinnamon) lacking fringing or pale webs. Underside of remiges dull silver-grey (84 Medium Neutral Gray). Underwing-coverts paler grey (85 Light Neutral Gray). Alula and axillaries contrasting white. Unmoulted rectrices of the immature male paratype and immature female paratypes differ strikingly from those of adult male specimens in being fringed bright olive-green (50 Yellowish Olive-Green).

Tail

Slightly rounded, outermost pair of rectrices 7 mm shorter than central pair. Tail of holotype very worn, buffy-brown (239 Ground Cinnamon), dorsal side slightly darker than ventral but heavily worn. Whitish-buff terminal tips just visible on all but central rectrices. Tail of immature female paratype (NHMUK 2012.9.4) less worn than that of the holotype (and other paratypes) and is dark greyish-brown (21 Fuscous) with broader whitish tips than those shown by other specimens. Field observations indicate that fresh tail feathers are mid-grey (similar in colouration to fresh wing feathers and therefore probably 83 Dark Neutral Gray or 84 Medium Neutral Gray) with a blackish-grey subterminal band (c.1 cm wide) and whitish tips.

Underparts

The holotype shows white chin feathers with very dark grey (82 Blackish Neutral Gray) bases, tips and fringes, therefore darker overall than feathers on malar stripe, the latter overhanging those on throat. In the holotype, feathers of throat in an advanced stage of moult, some feathers in pin visible. Throat similar in colouration to chin although with much less white; feathers almost entirely solid dark grey (82 Blackish Neutral Gray) gradually becoming darker towards the breast (83 Dark Neutral Gray) with some white tips throughout. On the breast some dark grey feathers (83 Dark Neutral Gray) possess contrasting white rachis and base of barbs on distal two-thirds of feather, creating a pattern of whitish drops on a mid-grey background. On the edges of the breast, solid mid-grey (84 Medium Neutral Gray) feathers predominate. On the adult male paratype (NHMUK 2012.9.2), the whitish drop-shaped marks on the breast are better developed than on the holotype and extend onto the throat, perhaps because the darker fringes are more worn. Field observations indicate that there is variation in

the extent and intensity of dark throat-streaking in males (Media files SOM 1–2). The boundary between breast and belly is gradual; feathers tend towards lighter grey on belly (86 Pale Neutral Grey) and flanks (85 Light Neutral Gray). Flank feathers are relatively long. Vent greyish-white (paler than 86 Pale Neutral Gray). Thighs whitish-cinnamon (6 Salmon).

The underparts of the immature male paratype (NHMUK 2012.9.3) differ from those of the adult male holotype in being paler with reduced dark grey on the throat and upper breast. There is an almost complete lack of dark tones on the throat, and the very dark grey (82 Blackish Neutral Gray) area on the throat is much smaller and barely extends onto the breast. On the throat and breast, feathers with white shafts and distal portions are more abundant than on the holotype, giving the throat a more speckled appearance. On the breast, solid white and pale grey feathers predominate such that the overall colour is whitish-grey (86 Pale Neutral Gray) rapidly grading to off-white on the belly. Flank feathers of the immature male are slightly whiter than those of the holotype. The underparts of the immature female paratypes are even paler than those of the immature male and almost completely lack dark tones. In those two specimens the chin and throat are white. Although there is a small area of mid-grey (84 Medium Neutral Gray) on the sides of the upper breast and the flank feathers are pale grey (86 Pale Neutral Gray or 85 Light Neutral Gray), the underparts are otherwise off-white.

Bare parts

Upper mandible dark horn, lower mandible pink horn, paler and pinker at base (more extensively pink on adult male paratype). Bill slender. Culmen decurved close to tip, not strongly carinated, tip very slightly hooked. Gonyx convex. Tarsus and toes pinkish (slightly darker in adult male paratype, paler in immature male paratype); soles of the feet pale pink. Claws pale brownish pink, becoming paler towards tips. On female paratypes tarsi, feet, soles and lower mandibles are paler than those of the holotype. Iris orange-brown. Inside of mouth pale pink.

Description of vocalisations

For clarity we use the following terminology to describe vocalisations: note – a single song element; strophe – a continuous flow of notes, separated from other strophes by silent pauses; phrase – one or more strophes given in quick succession; and song – one or more phrases given in quick succession; strophe pace – number of notes per strophe/strophe length; phrase pace (for phrases with more than one strophe) – phrase duration/strophes per phrase. Note that recordings varied in length and quality, so only those with good quality strophes were analysed.

Male *O. chaktomuk* songs are lengthy, often lasting more than one minute (Figure S1o–s, S1u, Media Files SOM 1–6). They consist of multiple phrases repeated at intervals of 0.42–4.30 seconds, typically much shorter than the maximum interval (mean: 1.7 seconds). Phrases are made up of 2–5 strophes, which are given at 0.12–0.95 second intervals. Males occasionally switch to a different strophe type mid-way through a song, although not within the same phrase. Strophes are also sometimes given singly. Strophes are trilled, consist of 3–18 notes and typically last 0.17–0.49 seconds (Table 3). Twelve distinct male strophe types are known, ranging from up, down or 'overslurred' (the latter referring to sequences of notes that rise and then fall) trills (often with a louder initial or terminal note) to a mix of trilled notes and upslurs, downslurs or 'overslurs' (Table 3, Figure S1a–l, Media Files SOM 1–6). Within strophe type, number of notes varies slightly (Table 4).

Female *O. chaktomuk* vocalisations are typically emitted whilst the male is vocalising, but are sometimes given between male vocalisations (Figure S1o–s, S1u, Media File S1–6). Females give a stereotyped trill at a higher frequency than male vocalisations (typically 5–16 notes lasting 0.24–0.84 seconds; Table 3, Figure

Table 3. Transliterations and univariate summary statistics of measurements of strophe characteristics of *Orthotomus chaktomuk*.

Figure no.	No. notes	Length (s)	Notes per second	Max freq. (Hz)	Min freq. (Hz)	Bandwidth (Hz)	Transliteration
Male							
S1a	5–6 (5.5, 0.7, 2)	0.35–0.42 (0.39, 0.05, 2)	0.35–0.42 (0.07, 0, 2)	4,616–5,026 (4,821, 290, 2)	2,291–2,394 (2,343, 73, 2)	2,325–2,632 (2,479, 217, 2)	<i>pi'pi'Pih</i>
S1b	9–12 (10.6, 1.0, 25)	0.30–0.41 (0.36, 0.03, 25)	0.03–0.04 (0.03, 0, 25)	3,780–4,657 (4,248, 293, 25)	1,485–1,957 (1,766, 136, 25)	1,991–3,037 (2,481, 334, 25)	<i>chu'u'u'u'u'u'URH</i>
S1c	7–8 (7.9, 0.2, 18)	0.31–0.38 (0.37, 0.02, 18)	0.04–0.05 (0.05, 0, 18)	3,864–4,308 (4,101, 143, 18)	1,402–1,778 (1,656, 106, 18)	2,154–2,906 (2,444, 201, 18)	<i>pu'u'u'u'u'u'RU</i>
S1d	12–14 (13.3, 0.8, 15)	0.38–0.47 (0.43, 0.03, 15)	0.03–0.03 (0.03, 0, 15)	3,658–4,206 (3,946, 156, 15)	1,504–2,667 (1,901, 316, 15)	1,368–2,668 (2,045, 294, 15)	<i>Tn'n'R'R'R'R'R'R'R'</i>
S1e	10–18 (14.3, 2.7, 6)	0.28–0.40 (0.32, 0.04, 6)	0.02–0.03 (0.02, 0, 6)	4,306–4,545 (4,393, 102, 6)	1,547–1,886 (1,700, 117, 6)	2,602–2,998 (2,694, 154, 6)	<i>EEEEE\EEU</i>
S1f	9–12 (10.6, 0.9, 8)	0.27–0.35 (0.31, 0.03, 8)	0.03–0.03 (0.03, 0, 8)	4,836–5,609 (5,271, 112, 8)	1,499–1,838 (1,705, 112, 8)	3,192–4,110 (3,566, 297, 8)	<i>PleeE\RRiet</i>
S1g	10–16 (12.1, 1.7, 54)	0.33–0.49 (0.39, 0.03, 54)	0.03–0.04 (0.03, 0, 54)	2,839–4,286 (3,779, 394, 54)	1,282–1,890 (1,608, 119, 54)	1,183–3,004 (2,171, 395, 54)	<i>PTeur'n'n'n'n'n'</i>
S1h	10–13 (11.1, 0.9, 7)	0.23–0.29 (0.26, 0.02, 7)	0.02–0.02 (0.02, 0, 7)	4,387–4,758 (4,474, 133, 7)	1,653–2,126 (1,866, 196, 7)	2,261–2,902 (2,608, 258, 7)	<i>CHEEE\UP</i>
S1i	13–15 (14.0, 0.9, 8)	0.29–0.36 (0.32, 0.03, 8)	0.02–0.02 (0.02, 0, 8)	5,669–6,311 (6,011, 201, 8)	1,451–1,991 (1,687, 178, 8)	3,880–4,725 (4,324, 337, 8)	<i>ree/\uET!</i>
S1j	3–4 (3.5, 0.5, 33)	0.17–0.24 (0.21, 0.02, 33)	0.05–0.06 (0.06, 0, 33)	3,830–4,821 (4,455, 239, 33)	1,128–2,120 (1,610, 259, 33)	2,394–3,522 (2,844, 252, 33)	<i>P'p'Biu</i>
S1k	3–3 (3.0, 0, 5)	0.22–0.23 (0.23, 0.01, 5)	0.07–0.08 (0.08, 0, 5)	4,616–5,026 (4,828, 153, 5)	1,881–2,017 (1,963, 52, 5)	2,633–3,043 (2,865, 152, 5)	<i>pi'pi'pui</i>
S1l	3–4 (3.1, 0.3, 18)	0.19–0.27 (0.20, 0.02, 18)	0.06–0.07 (0.07, 0, 18)	3,680–4,240 (4,097, 135, 18)	1,573–1,949 (1,742, 115, 18)	1,731–2,633 (2,355, 196, 18)	<i>bi'bi'bBit</i>
Female							
S1m	5–16 (9.4, 3.4, 25)	0.24–0.84 (0.48, 0.18, 25)	0.05–0.05 (0.05, 0, 25)	4,725–5,805 (5,038, 260, 25)	2,086–3,544 (2,673, 398, 25)	1,485–3,213 (2,365, 421, 25)	<i>Tcni'iiiiiiiiiii</i>
S1n	1–1 (1, 0, 17)	0.07–0.23 (0.15, 0.07, 17)	0.07–0.23 (0.15, 0.07, 17)	4,484–6,243 (5,176, 409, 17)	2,460–4,252 (3,189, 376, 17)	1,553–2,354 (1,987, 280, 17)	<i>tew</i>

Analyses based on 12 recordings of male vocalisations from six pairs of *Orthotomus chaktomuk* in Kandal province, Cambodia, obtained as follows: (1) four pairs from c.40 km south-east of Phnom Penh (at or very close to 11°19'45.77"N 105°11'48.41"E); (2) one pair from c.15 km north of Phnom Penh (11°41'37.14"N 104°53'43.79"E); and (3) one pair from c.30 km north of Phnom Penh (11°50'18.24"N 104°49'26.55"E). Measurements taken in Raven Pro 1.4 (Raven 2012). Values given are: minimum–maximum (mean; sd; sample size). In vocal transcriptions, notation follows Rasmussen & Anderton (2005).

S1m, Media File S1–6). Females, and exceptionally males, sometimes produce a nasal squeak consisting of a single note with harmonics (Figure S1n, Media File S6). This vocalisation is usually given singly (Figure S1p), but occasionally more than one is repeated in quick succession; when many squeaks are given in sequence the first is usually longer than others (Figure S1t, Media File S6).

Etymology

The specific epithet '*chaktomuk*' is a Khmer word meaning 'four faces'. It is used in reference to the low-lying area at which the Tonle Sap, Bassac and Mekong rivers come together to form an 'X' centred on Phnom Penh, itself historically known as 'Krong Chaktomuk' (literally 'City of Four Faces'). Based on current knowledge, the global distribution of the new species is restricted to scrub within the dynamic floodplain created by the confluence of these waters. We use *chaktomuk* as a noun in apposition to the genus name, and it is thus invariable.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2012), and hence the new name contained herein is available under that Code from the electronic edition of this article. This published

work and the nomenclatural act it contains have been registered in ZooBank, the online registration system for the International Commission of Zoological Nomenclature. The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:F1778491-B6EE-4225-95B2-2843B32CBA08. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the digital repository *BioTaxa* (<http://biotaxa.org>).

ECOLOGY AND BEHAVIOUR

Habitat

All observations of *O. chaktomuk* were made on level ground in very dense humid evergreen scrub (multi-stemmed woody plants, 2–6 m tall), sometimes admixed with long grasses or trees (Plate 5), at elevations of 3–25 m above sea level. Trees occur exceptionally; where present they are typically scarce, the scrub forming a dense layer with occasional tree canopies emerging from it. *Orthotomus chaktomuk* has not been seen in forest (defined as a habitat where trees predominate) and is therefore assumed to be absent from it. At all locations where birds have been found, the scrub is located



Plate 5. Habitat at the type locality of *Orthotomus chaktomuk*. Simon P. Mahood.

within a floodplain and experiences seasonal or permanent (artificial) flooding. The presence of seasonally flooded scrub in any location is probably typically transitory, since in the absence of disturbance by people, large ungulates or hydrological processes it would presumably revert to seasonally flooded forest.

Orthotomus atrogularis is sometimes found in seasonally flooded scrub occupied by *O. chaktomuk* (Figure 1, Table SOM 1). Where the two species are syntopic, *O. atrogularis* is much the rarer. Typically *O. atrogularis* is found in the edge and canopy of taller forest habitats, showing a preference for disturbed and secondary forest because these offer an abundance of vines (Madge 2006, Wells 2007). In some parts of the Tonle Sap floodplain where *O. chaktomuk* is absent, *O. atrogularis* is common in seasonally flooded forest and scrub, presumably because this habitat also offers an abundance of edge surfaces. At the other end of the habitat continuum, *O. sutorius* replaces *O. chaktomuk* in open scrub and gardens, although at some locations the two species are syntopic, even vocalising from the same individual plants (SPM pers. obs.). *Orthotomus chaktomuk* possibly occupies a habitat intermediate between those of *O. atrogularis* and *O. sutorius*. However, as in other geographic areas where more than one lowland tailorbird species is present, habitat niches are difficult to define and distinguish. Ecological interactions and habitat associations of *O. chaktomuk* and other lowland tailorbirds are worthy of further research.

Birds sharing the habitat of *O. chaktomuk* include widespread species often associated with gardens, e.g. Yellow-vented Bulbul *Pycnonotus goiavier*, Pied Fantail *Rhipidura javanica*, Oriental Magpie Robin *Copsychus saularis*, sometimes *O. sutorius*, and species usually associated with dense lowland humid evergreen scrub, including Striped Tit Babbler *Macronous gularis*, Yellow-bellied Prinia *Prinia flaviventris*, Plain Prinia *Prinia inornata*, Olive-backed Sunbird *Cinnyris jugularis* and *O. atrogularis*. From October to April, Palearctic migrants (e.g. Dusky Warbler *Phylloscopus fuscatus* and Siberian Rubythroat *Luscinia calliope*) are abundant in this habitat. In locations where it occurs, *O. chaktomuk* often appears to be one of the most abundant bird species.

Behaviour

Owing to the structural characteristics of its habitat, *O. chaktomuk* is rarely seen without the aid of playback of vocalisations, and thus data on 'normal' behaviour are few. Almost all encounters have been with what appear to be adult male–female pairs, or adult male–female pairs with one subadult. Prior to moult, immature birds were seen singly, in male–female pairs of exclusively immature birds or in male–female pairs consisting of one immature and one adult bird.

Birds usually stay within dense vegetation, where they glean and sally-glean from live and dead leaves of multi-stemmed bushes and occasionally vines, from ground-level to canopy. *Orthotomus*

chaktomuk has not been observed foraging in trees. When vegetation is flooded, birds typically forage below the crown of the bush, on hanging branches just above the water. One individual that was lured out of dense scrub with the aid of playback foraged on long grass-stems, gleaning leaves of a vine that was growing amongst the grass. Individuals have been observed taking the following prey (once each): a small fly Diptera, a small spider Araneae, a small caterpillar Lepidoptera and a small katydid Tettigoniidae; all were consumed immediately.

In response to playback, birds that have approached the observer have been seen to sing, usually in a duet, while perched (usually on or near the top of vegetation, including trees; Media Files SOM 1–3) and occasionally in song flight. Singing is sometimes accompanied by rapid downwards tail-wagging. Sometimes, while singing in duet, perched birds droop and shiver their wings. Immature males gave a simpler, less developed song than adults.

During March and April only males responded strongly to playback of vocalisations; females typically did not respond, or did so only briefly. Because this was in stark contrast to behaviour at other times of year it is thought to indicate that females were on the nest. Although there are no data on the timing of breeding of lowland tailorbirds in Cambodia, in Thailand *O. atrogularis* pairs with dependent young have been recorded from July to early September (Round 2008). The nest and eggs of *O. chaktomuk* remain to be described.

Distribution

The distribution of *O. chaktomuk* is incompletely known. It is apparently constrained by the distribution of seasonally flooded dense scrub within the floodplain of the Tonle Sap, Mekong and Bassac rivers in Cambodia (Figure 1). However, based on current data it is absent from part of this floodplain. Searches at various locations in apparently suitable habitat in the Tonle Sap floodplain have thus far only found the species in the south-east (see Table SOM 1 for a list of all locations in the floodplain of the Mekong, Tonle Sap and Bassac rivers where searches for *O. chaktomuk* have been conducted). In the north of the Tonle Sap floodplain (where we have searched for and not found *O. chaktomuk*), *O. atrogularis* is abundant in habitat that is superficially structurally similar to habitat in the south-east, and it is unclear how far north and west along the lakeshore the distribution of *O. chaktomuk* extends. There is no biogeographic reason why *O. chaktomuk* should be absent from parts of the Tonle Sap floodplain, and the causes of its absence are unknown; *O. atrogularis* is scarce or absent at sites where *O. chaktomuk* was recorded (Table SOM 1).

Orthotomus chaktomuk was not found in seemingly appropriate small seasonally flooded scrub patches at the northern limit of the Mekong floodplain (12°36'27.52"N 106°01'36.06"E) in Kratie province (Table SOM 1, J. A. Eaton verbally 2012). Satellite data indicate that there is little, if any, suitable habitat for *O. chaktomuk* in the Mekong floodplain in Vietnam and it is currently unrecorded there (although no specific searches have been conducted). As might be expected, we have located only *O. atrogularis* in scrub habitats outside of the Mekong, Tonle Sap and Bassac floodplain (where these records were within 10 km of superficially suitable habitat for *O. chaktomuk* they are mapped on Figure 1). Based on current knowledge of its range, the distribution of *O. chaktomuk* covers less than c.10,000 km² (Figure 1); it therefore can be considered a restricted-range species (*sensu* Stattersfield *et al.* 1998).

Conservation

Orthotomus chaktomuk is restricted in distribution. Suitable habitat is patchy outside of the Tonle Sap floodplain and in the latter its distribution is poorly understood. Trends in loss, degradation and fragmentation of floodplain scrub are poorly documented and subject to considerable local variation (e.g. Packman *et al.* 2013).

However, most floodplain scrub in Cambodia occupies land suitable for rice cultivation and could be further threatened by changes in ongoing burning, fuel-wood collection, cattle grazing (all of which potentially have a dual role because they also serve to slow succession) and the spread of the invasive plant *Mimosa pigra*. Ironically, *O. chaktomuk* might now be dependent on human activity to keep suitable scrubby habitat from becoming forest, since other anthropogenic impacts—eradication of wild ungulates, replacement of domestic animals by machines, water flow/level control, and changes in agricultural practices such as fallows and cyclical abandonment—have greatly curtailed processes that maintained the scrub. The species occurs in one protected area, Baray Bengal Florican Conservation Area, although at that site habitat is managed to maximise the area of grassland. It has already been lost from one site (Kraing Check) where birds were netted in 2009: visits in late 2012 found no birds and all suitable habitat had been converted to aquaculture ponds.

We believe that *O. chaktomuk* should be classified as Near Threatened on the IUCN Red List because it approaches the thresholds for Vulnerable under criteria B1a+bi,ii,iii,iv (IUCN 2001). Its Extent of Occurrence is 9,385 km² and thus below the threshold for Vulnerable (<20,000 km²; criterion B1). Although most locations where it occurs are small and isolated it has been found in the Tonle Sap floodplain where there is a large area of apparently suitable habitat (although it apparently does not occupy all of it). Because of this, its habitat cannot be considered severely fragmented (subcriterion a). Nonetheless it is inferred to be undergoing a continuing decline (subcriterion b) in (i) extent of occurrence, (ii) area of occupancy, (iii) area, extent and/or quality of habitat, and (iv) number of locations or subpopulations. Its Area of Occupancy has not yet been evaluated owing to uncertainty regarding both the distribution of suitable habitat and its distribution within apparently suitable habitat. Notwithstanding this assessment, if the species is found to be more widely distributed in the Tonle Sap floodplain, then it would warrant downlisting to Least Concern.

Ongoing habitat loss is likely to be exacerbated by the impacts of hydropower development on the Mekong and its tributaries. Models of the effects of hydropower dams predict changes in the duration and size of the annual flood-pulse that will lead to a reduction in the extent of seasonally flooded habitats (Arias *et al.* 2012). Dam construction will also reduce fish populations (the primary protein source in rural Cambodia), cause changes in flood regime and lead to water shortages in the floodplain (Orr *et al.* 2012). These changes will probably lead to additional loss of floodplain scrub owing to expansion of agricultural land for rice production, fish ponds and grazing land for cattle. Construction has started on one mainstream lower Mekong dam (Xayaburi, in northern Lao PDR) and numerous tributary dams and 'pre-construction' works are thought to have begun on another (Don Sahong) in the far south of Lao PDR (International Rivers 2012); nine more mainstream dams are planned (Mekong River Commission 2011).

TAXONOMIC CONSIDERATIONS

Higher-level systematics

Assignment of the new species to the genus *Orthotomus* is straightforward based on its overall structure, plumage and habits, which typify this genus. Genetic analysis provide additional support for this arrangement, as DNA sequence comparisons (detailed below) included specimens of the type species for the genus: *O. sepium* Horsfield, 1821. *Orthotomus* was previously placed in an expanded Sylviidae (Sibley & Ahlquist 1990) until that family was shown to be paraphyletic and the genus was transferred to the Cisticolidae, along with the cisticolas (*Cisticola*), prinias (*Prinia*)

and a number of other genera (Alström *et al.* 2006). Within the Cisticolidae, *Orthotomus* occupies a clade with the genera *Heliolais*, *Prinia* and *Urorhipis* (Olsson *et al.* 2013). *Orthotomus* remained intact until molecular evidence led to the removal of four superficially similar species: the two African tailorbird species were transferred to the resurrected genus *Scepomycter* (Nguembock *et al.* 2007) and the Asian mountain tailorbirds, Mountain Tailorbird *Phyllergates cucullatus* and Rufous-headed Tailorbird *P. heterolaemus*, were shown to be not particularly closely related to 'lowland tailorbirds'—the most appropriate English group name for the remaining *Orthotomus* species (Alström *et al.* 2006, 2011). The *Orthotomus* comparisons by Sheldon *et al.* (2012), based on one mitochondrial and two nuclear DNA markers, suggested that *O. sutorius* is sister to the rest of the lowland tailorbirds, which comprise four relatively divergent clades: (1) Rufous-fronted Tailorbird *O. frontalis*, (2) Rufous-tailed Tailorbird *O. sericeus*, (3) *O. atrogularis*–*O. ruficeps*–*O. sepium*, and (4) the rest of the Philippine endemics.

Taxonomic implications from morphology

Lowland tailorbirds appear to be relatively conservative in the evolution of distinctive plumage. For example *O. atrogularis*, the widespread *O. sutorius* and the Philippine endemics Philippine Tailorbird *O. castaneiceps*, *O. frontalis* and Grey-backed Tailorbird *O. derbianus* share the same basic plumage pattern and colouration, but are not particularly closely related (Sheldon *et al.* 2012). Owing to this morphological congruence, various Philippine taxa were long considered part of *O. atrogularis* (Delacour & Mayr 1946). These were later split from that species and grouped under *O. castaneiceps* and *O. derbianus* (Dickinson *et al.* 1991, Kennedy *et al.* 2000). Collar (2011) considered that morphological data alone were insufficient to afford *O. castaneiceps chloronotus* species status to resolve the geographically vexing situation created by the specific recognition of *O. derbianus*. Equally, treatment of *O. frontalis* as a species (proposed by Madge 2006) was deemed untenable using morphological information alone (Collar 2011).

The plumage of *O. chaktomuk* is typical of the *O. atrogularis*–*O. ruficeps*–*O. sepium* clade. Within this grouping, all species are characterised by a rufous crown; white or rufous cheeks; grey, olive-grey or bright olive-green upperparts; and grey or whitish-grey underparts with or without heavy blackish throat-streaking (Table 2, Plate 3). Superficially, the head and underparts pattern and colouration of *O. chaktomuk* are similar to *O. atrogularis*, while colouration of the upperparts is more similar to *O. ruficeps*. However, *O. chaktomuk* shows a suite of plumage features that in combination are unique, and there are various additional subtle plumage differences between it and closely related species (Table 2, Plates 3, 4). Immatures of all species within the clade possess yellow-olive fringing on the wing-feathers; adult *O. atrogularis* exhibit the same colouration on the wings, tail and much of the upperparts. Examination of specimens suggests that this colouration is not as vivid in immature *O. ruficeps* and *O. sepium* as in *O. atrogularis* and *O. chaktomuk*.

In common with other lowland tailorbird species, those in the *O. atrogularis*–*O. ruficeps*–*O. sepium* clade show relatively minor geographic variation in morphology. All three species within the clade are polytypic. Although a detailed examination of morphological variation within these species was not completed, examples (including some type material) of multiple subspecies were examined (Table S2). Within each species, all examined specimens were superficially very similar. Morphological variation within *O. atrogularis* is most marked along the Sabah–Sarawak border area, in common with other species that share a similar distribution (e.g. White-rumped Shama *Copsychus malabaricus*). The most morphologically divergent taxon within *O. ruficeps*, *O. r. cagayanensis* of Cagayan Sula, Philippines, which is apparently

extensively brown or rufous-washed above with pale eyes (Madge 2006), was not examined. Within this context of limited geographic variation within species, any suggestion that *O. chaktomuk* should be considered a highly distinctive localised subspecies of *O. atrogularis* is untenable. Equally, there is no evidence that any lowland tailorbird species possesses regularly occurring colour morphs.

Biometrics of *O. chaktomuk* are similar to other species within the *O. atrogularis*–*O. ruficeps*–*O. sepium* clade (Table SOM 3). Using bill length/wing length as a proxy for size, there is an indication that *O. chaktomuk* is smaller than closely related species (Figure 2). This could not be confirmed statistically, because the sample size of *O. chaktomuk* is too small (Table SOM 3). In the field, *O. chaktomuk* appeared to have a shorter tail than local *O. atrogularis*. However, this could not be confirmed from the specimens collected of *O. chaktomuk*, because their tails are very worn.

The description of a new species provides an opportunity to test the quantitative criteria for species delineation proposed by Tobias *et al.* (2010). These criteria use a scoring system for morphological, vocal and ecological features to assess taxonomic rank. Even when applied only to morphological features, *O. chaktomuk* exceeds the threshold score (7) for species status when compared with *O. atrogularis*, *O. ruficeps* and *O. sepium*. It scores 8 against *O. ruficeps*: cheeks white rather than orange-rufous (3), throat and breast very dark grey with white speckling rather than unmarked pale grey (3), thighs whitish-cinnamon rather than orange-rufous (2). Its scores against *O. sepium* are similar. It scores 8 against *O. atrogularis*: upperparts mid-grey rather than bright yellowish-olive (3), vent white rather than yellow (3), thighs whitish-cinnamon rather than yellowish-orange (2).

Taxonomic implications from vocalisations

Vocal data reaffirm the close relationship between *O. chaktomuk* and *O. ruficeps*, *O. sepium* and *O. atrogularis*, in particular the last. *Orthotomus* vocalisations are difficult to define. Males and females often duet, or if three birds are present, all will vocalise simultaneously. Vocalisations of *O. chaktomuk* are typically lengthy, and those of males are extremely varied (Media File SOM 4–6). We do not think that we have documented the full vocal range of the species. In addition, comparisons with closely related species were hampered because it is doubtful that the full vocal repertoire of such species has been documented.

The vocalisations of species in the *O. chaktomuk*–*O. atrogularis*–*O. ruficeps*–*O. sepium* clade fall into two distinct types. Those of *O. ruficeps* and *O. sepium* are largely short, pure-tone whistles, while those of *O. chaktomuk* and *O. atrogularis* are restricted to short trills. To quantify the distinctiveness in songs of *O. chaktomuk* in relation to other species within the clade, we conducted a discriminant analysis (DA) on male vocalisations using XLStat (Addinsoft 2013). We randomly selected one song (defined as above) from each individual of *O. chaktomuk* from which we had obtained recordings (total five individuals) and randomly selected a similar number of songs from five individuals each of *O. a. nitidus* (the geographically closest subspecies of *O. atrogularis*), *O. ruficeps* and *O. sepium*. These included three recordings of *O. atrogularis* from Cambodia (including one from the floodplain of the Tonle Sap) and one recording from Vietnam made within 100 km of the border with Cambodia. (For a full list of recordings used in analyses see Table SOM 4.) Recordings were downloaded from www.xeno-canto.org and <http://avocet.zoology.msu.edu/>. From each recording we calculated mean values of the following variables: notes/strophe, length (in seconds) of longest note (one per strophe), strophe length (seconds), maximum and minimum fundamental frequencies (one each per strophe), number of strophes per phrase, length of interval between phrases (in seconds) and, for phrases with more than one strophe, interval between strophes and length of phrase (in seconds); we also calculated bandwidth (maximum

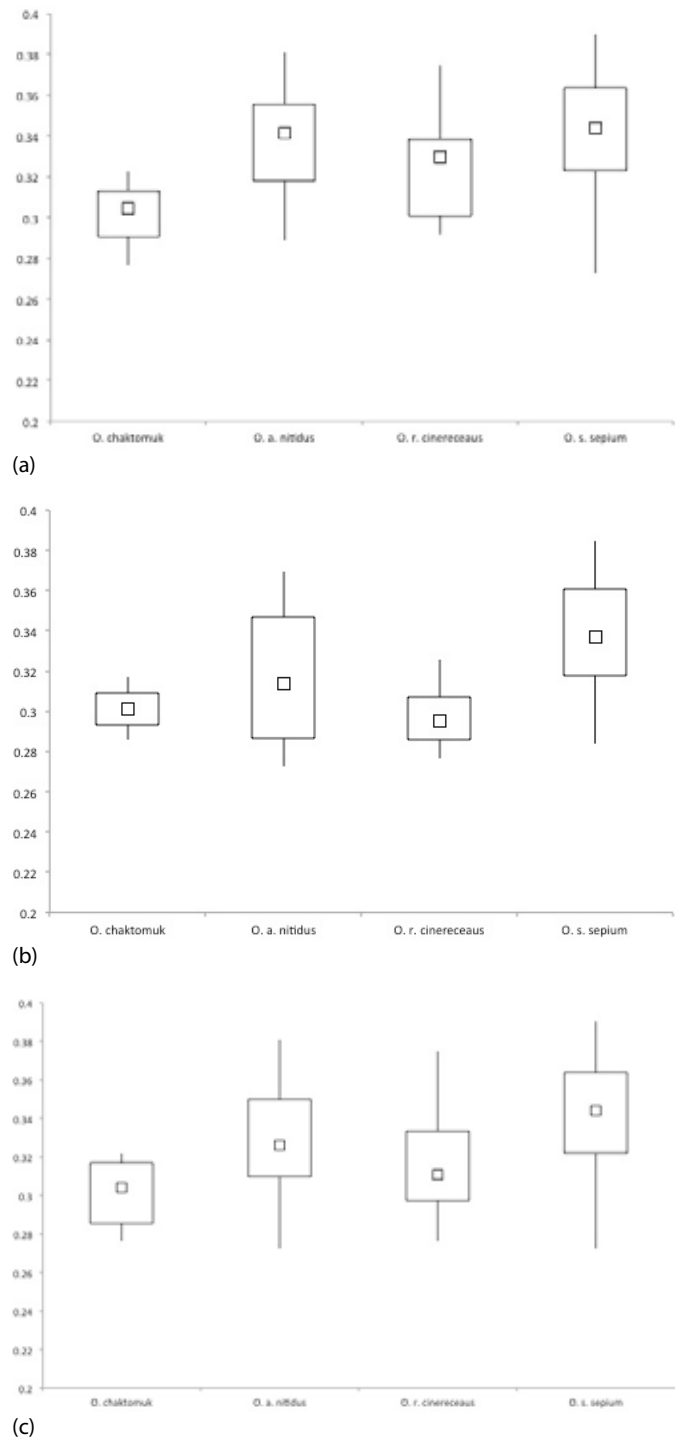


Figure 2. Box plots of bill-length (to skull) divided by wing-length of (a) males of *Orthotomus chaktomuk* ($n = 3$), *O. atrogularis nitidus* ($n = 15$), *O. ruficeps cinereaceus* ($n = 14$) and *O. sepium sepium* ($n = 20$); (b) females of *O. chaktomuk* ($n = 2$), *O. a. nitidus* ($n = 10$), *O. r. cinereaceus* ($n = 6$) and *O. s. sepium* ($n = 8$); (c) males and females of *O. chaktomuk* ($n = 5$), *O. a. nitidus* ($n = 25$), *O. r. cinereaceus* ($n = 20$) and *O. s. sepium* ($n = 28$). Small squares represent the median; box indicates 50% of samples; bars indicate maximum and minimum.

minus minimum fundamental frequency within a given strophe), strophe pace (number of notes per strophe/strophe length) and, for phrases with more than one strophe, phrase pace (phrase length/strophes per phrase).

Most of the analysed songs of *O. chaktomuk* and *O. atrogularis* clustered separately in multivariate vocal space and could be discriminated from each other and from the songs of *O. ruficeps* and *O. sepium* (Wilks's $\lambda = 0.005$, $F = 2.222$, $P = 0.047$; Figure 3).

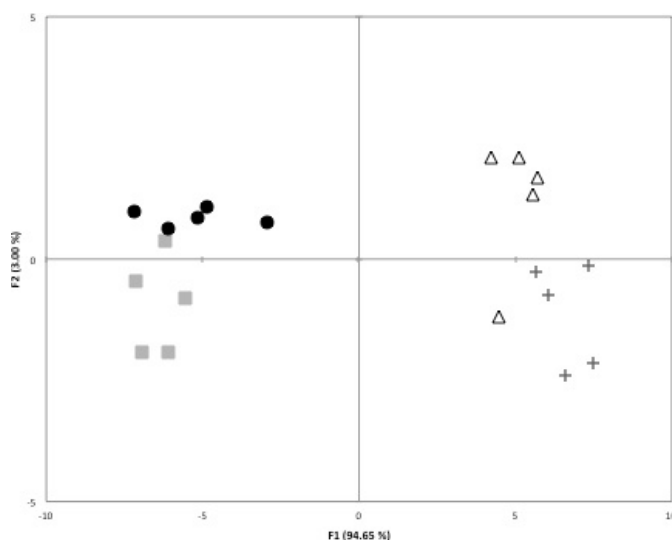


Figure 3. Multivariate vocal space of lowland tailorbirds in the *O. chaktomuk*–*O. atrogularis*–*O. ruficeps*–*O. sepium* clade from discriminant analyses based on 12 song traits. Scatter plot of the first two canonical functions that discriminated songs of *O. chaktomuk*, *O. atrogularis*, *O. ruficeps* and *O. sepium*. ● represent *O. chaktomuk*; ■, *O. atrogularis*; △, *O. ruficeps*; +, *O. sepium*.

Table 4. Results of discriminant analyses of songs of species in the *O. chaktomuk*–*O. atrogularis*–*O. ruficeps*–*O. sepium* clade, based on 12 acoustic variables, showing first three (of four) canonical functions.

Acoustic variable	Canonical function		
	1	2	3
Notes per strophe	-0.742	-0.196	-0.155
Strophe length (seconds)	0.221	0.265	-0.524
Strophe pace	0.721	0.331	-0.270
Maximum frequency	0.227	-0.147	-0.009
Minimum frequency	-0.021	-0.087	-0.183
Bandwidth	0.247	-0.105	0.112
Length of longest note (one per strophe)	0.873	0.187	-0.289
Strophes per phrase	-0.015	0.391	0.457
Inter-strophe interval (seconds)	-0.179	0.172	-0.006
Phrase length (seconds)	-0.103	0.507	0.156
Phrase pace	-0.131	0.405	-0.075
Inter-phrase interval (seconds)	-0.330	-0.152	-0.117
Eigenvalue	43.01	1.362	1.071
% variance explained	94.6	3.00	2.36

Overall, the analysis assigned songs to the correct species with 60% accuracy. Songs of *O. chaktomuk* were classified with 60% accuracy and songs of *O. atrogularis* were classified with 40% accuracy. Songs of *O. ruficeps* and *O. sepium* were classified with 40% and 100% accuracy, respectively. The discriminant analysis was mainly influenced by the length of the longest note, strophe pace and the number of notes per strophe (Table 4).

In accordance with their acoustic similarities, *O. chaktomuk* and *O. atrogularis* respond to playback of each other's vocalisations, indicating that inter-specific territoriality is common. There is individual variation in the magnitude of response, but this is poorly understood at present. Interspecific territoriality is a common trait in avian sister species whose ranges come into contact (e.g. Orians & Willson 1964, Murray 1971, Murray 1976). At locations where *O. chaktomuk* is sympatric with *O. sutorius*, the latter sometimes also responds to broadcast of vocalisations of the former by ascending the vegetation and singing.

Taxonomic implications from ecology

The apparently restricted distribution of *O. chaktomuk* differs from those of other *Orthotomus* species on the Asian mainland,

which are typically wide (Madge 2006). Lowland tailorbirds are thought to have originated in southern Asia or possibly Sundaland. They rapidly spread widely in Sundaland and the Philippines and, more recently, additional species have evolved in both island groups (Sheldon *et al.* 2012). The *O. chaktomuk*–*O. atrogularis*–*O. ruficeps*–*O. sepium* clade emerged relatively recently, and, in contrast to the clade containing Philippine endemics, exhibits lower species richness (four versus six species), presumably owing to the lack of opportunity for speciation in lowland populations in a continental mainland versus an oceanic island setting. Lowland passerines in mainland Asia typically have large distributions. Those with smaller distributions are largely confined to successional habitats in the floodplains of large rivers, such as Black-breasted Parrotbill *Paradoxornis flavirostris* and Marsh Babbler *Pellorneum palustre* (Rasmussen & Anderton 2005).

Tailorbird habitats are notoriously difficult to define (e.g. Mitra & Sheldon 1993), although lowland tailorbirds within the *O. chaktomuk*–*O. atrogularis*–*O. ruficeps*–*O. sepium* clade have slightly clearer habitat preferences. In this clade, greater specialisation is thought to have helped these younger species avoid competition with the pre-existing generalist species *O. sutorius* and *O. sericeus* (Sheldon *et al.* 2012). The habitat preferences of *O. chaktomuk* are thought to be somewhat intermediate between *O. atrogularis* and *O. sutorius*. In addition, *O. chaktomuk* is apparently confined to successional floodplain habitat. Vegetational patterns in what is now its distribution have been shaped by cyclical ice-ages and interglacials over the past two million years. During glacial maxima, the sea-level was much lower than today and southern Vietnam and Cambodia were connected by land to what is now Peninsular Malaysia by the now submerged Sunda Shelf (Sathiamurthy & Voris 2005). It is thought that there were four large river basins on the Sunda Shelf and these great river systems connected the freshwater riverine faunas of many of today's rivers (such as the Mekong) that are now restricted to Indochina, the Malay Peninsula or one of the greater Sunda Islands (Voris 2000). Floodplain habitats were therefore probably much more extensive during glacial maxima and it is possible that *O. chaktomuk* evolved on the Sunda Shelf. *Orthotomus chaktomuk* is now restricted to a much smaller area, constrained by the reduced availability of suitable habitat during an interglacial.

The known distribution of *O. chaktomuk* lies within the distribution of *O. atrogularis*. No parts of the distribution of *O. chaktomuk* are more than a few tens of kilometres from locations where *O. atrogularis* is found. The two species are locally syntopic (Figure 1, Table SOM 1); for instance, c.200 m from the type locality a pair of *O. atrogularis* was observed in the same bush as a single *O. chaktomuk* (SPM, AJIJ, HC pers. obs.; photographed). Although nearly 50 *O. chaktomuk*–*O. chaktomuk* male–female associations have been observed, neither mixed pairs nor birds that are phenotypically identifiable as hybrids have been detected.

Taxonomic implications from molecular analyses

Within the genus *Orthotomus*, superficial morphological and vocal similarities between taxa have frequently clouded their taxonomic status. In this context, molecular techniques can provide a useful tool to infer relationships between taxa. To determine the position of *O. chaktomuk* in the molecular phylogeny of *Orthotomus* we compared DNA sequences of mitochondrial ND2 and nuclear MUSK and TGFβ2 genes of the type specimens with all other species of lowland tailorbird (Sheldon *et al.* 2012) (see Table SOM 5 for details of all specimens used in the genetic analyses). Tissues from the five *O. chaktomuk* specimens (Table 1) were preserved in 95% ethanol and stored in the University of Kansas Natural History Museum (KUNHM) and Louisiana State University Museum of Natural Science (LSUMNS) tissue collections. DNA was extracted and sequenced following the protocol described in Sheldon *et al.* (2012), and the sequences deposited in GenBank: accession numbers

KF015230–KF015247. The total number of DNA nucleotides was 1,041 of ND2, 614 of MUSK, and 613 of TGF β 2. Separate and concatenated Bayesian phylogenetic analyses of these sequences using MrBayes ver. 3.2.1 (Ronquist *et al.* 2012) as in Sheldon *et al.* (2012) placed the novel taxon in a clade with *O. atrogularis*, *O. ruficeps* and *O. sepium*; all trees except TGF β 2 placed *O. atrogularis* and *O. chaktomuk* as sisters (Figure 4). This arrangement concurs with morphological and vocal analyses.

The ND2 sequences of the four taxa had 90 variable and 78 parsimony informative sites. Between the one sample of *O. atrogularis* and the five samples of *O. chaktomuk* were 22 variable sites of which 12 consistently differed. The ND2 p-distance from *O. chaktomuk* to *O. atrogularis* averaged 1.3% (range 1.1%–1.4%), to *O. ruficeps* 5.0% (4.6%–5.2%), and to *O. sepium* 6.5% (6.3%–6.8%). Variation in the MUSK and TGF β 2 sequences between *O. chaktomuk* and *O. atrogularis* was negligible (three and six sites, respectively). These genetic data are insufficient to resolve the relationship between *O. chaktomuk* and *O. atrogularis* owing to the small number of samples of *O. atrogularis* compared (one) and because that sample was not of the subspecies sympatric with *O. chaktomuk*. Instead, the *O. atrogularis* sample was of the nominate subspecies collected in Sarawak, which is restricted to the Sundaic region (except Sabah, north Borneo). The genetic divergence between *O. chaktomuk* and the *O. atrogularis* sample (1.3%) is small and broadly comparable to that between other lowland taxon-pairs on Borneo and mainland Asia that are considered subspecies, although there is considerable inter-species variation in genetic distances (e.g. Lim *et al.* 2010, Sheldon *et al.* 2012). A phylogeographic study including samples from all subspecies and biogeographically relevant populations of *O. ruficeps*, *O. atrogularis* and *O. chaktomuk* is required to clarify their evolutionary relationships.

Relationship of *Orthotomus chaktomuk* to species within *Orthotomus*

Orthotomus chaktomuk is locally syntopic (Figure 1, Table SOM 1) with the only species from which it shows apparently relatively low genetic divergence, *O. atrogularis*. We have found no evidence of hybridisation, and the taxa satisfy the precepts of the biological species concept because they behave like separate species when they come into contact (e.g. Mayr 1963, 1999). Classification of the new taxon as a subspecies or highly localised colour morph of *O. atrogularis* is therefore untenable. Because *O. chaktomuk* is on a distinct evolutionary trajectory it also satisfies the phylogenetic species concept (Cracraft 1989).

Although reported genetic divergence among sister species is typically lower in temperate regions than in the tropics this may be an artefact of incomplete sampling and incorrect taxonomy (Tobias *et al.* 2008, Sangster 2009). Recent studies are overturning the trend for lumping distinctive taxa into polytypic species and revealing cryptic diversity in widespread species (e.g. Collar 2006, 2011, Rheindt & Eaton 2010, Leader 2011, Moltesen *et al.* 2012, Rasmussen *et al.* 2012). By taking an integrated approach to taxonomy (as here), sister species are being recognised in tropical regions that differ in sampled regions of nuclear DNA by levels that are in line with those used in temperate regions (e.g. Irestedt *et al.* 2013).

There are a number of plausible explanations for the apparently low genetic divergence between *O. chaktomuk* and *O. atrogularis*. The molecular phylogenies suggest that *O. chaktomuk* might be a relatively young lineage. Its diagnostic phenotypic traits that apparently prevent modern hybridisation might be encoded by a small number of genes that evolved rapidly under sexual selection (cf. Uy *et al.* 2009). This process might have occurred too rapidly for significant additional genetic differences to accumulate in parts of the genome not under intense selection or which are selected for other purposes (as are mitochondrial genes). If *O. chaktomuk*

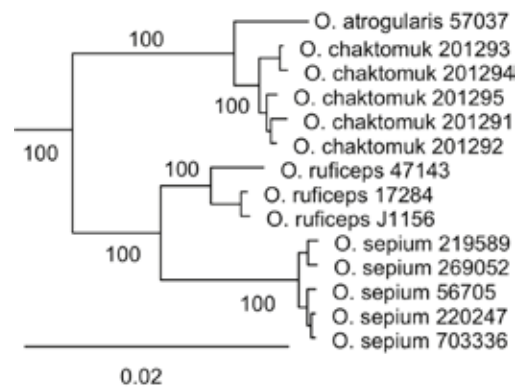


Figure 4. The *Orthotomus chaktomuk*, *O. atrogularis*, *O. ruficeps*, and *O. sepium* clade extracted from the entire *Orthotomus* phylogeny, which was constructed from concatenated DNA sequences of ND2, MUSK, and TGF β 2 via Bayesian phylogenetic inference as described in Sheldon *et al.* (2012). Numbers along branches indicate Bayesian posterior probabilities. The topology is the same as ND2 and MUSK trees by themselves.

is indeed a Sunda Shelf species, now confined to relict habitat in Indochina, then it might have been derived from Sundaic *O. atrogularis* rather than mainland populations. If this were the case then it might be expected to show greater genetic divergence from mainland *O. atrogularis* to which it is now locally syntopic than to the Sundaic nominate used here in the genetic analyses. An alternative explanation is that the apparent low genetic divergence between the species is a result of genetic introgression sometime during the last two million years (Rheindt & Edwards 2011). Periods of peak sea-level might be the most plausible time for genetic introgression to have occurred. A higher sea-level might have constrained suitable habitat for *O. chaktomuk* into a narrow band between the distributions of *O. ruficeps* and *O. atrogularis*. This process perhaps drove *O. chaktomuk* through a population bottleneck and increased the chances of hybridisation with *O. atrogularis*, leading to genetic introgression. If a comprehensive study of relationships within the *O. chaktomuk*–*O. atrogularis*–*O. ruficeps*–*O. sepium* clade reveals that *O. chaktomuk* is more closely related to *O. a. nitidus* than to Sundaic taxa, then this is perhaps a more likely explanation for the low genetic divergence.

Final remarks

The modern discovery of an undescribed bird species close to sea-level within the limits of a large city in a populous country is extraordinary, but not unprecedented (cf. *Stymphalornis sp. nov.*, an as-yet undescribed taxon restricted to marshes close to São Paulo, Brazil, discovered in 2005: Reinert *et al.* 2007). At least three interacting factors probably account for *O. chaktomuk* having gone unnoticed for so long. It inhabits a very small geographic range, and within this it is restricted to a very specific habitat type: dense floodplain scrub. This habitat is of little interest to birdwatchers and ornithologists because the other species that it supports are some of the most widespread and abundant birds in tropical South-East Asia. Even if its habitat were to attract more attention, the denseness of the habitat and the species's skulking habits would more often than not render it invisible to the casual would-be observer.

Vocalisations of *O. chaktomuk* are similar to those of *O. atrogularis*, which has a perplexing array of vocalisations with which birdwatchers rarely attempt to familiarise themselves fully. *Orthotomus atrogularis* is a common species within suitable habitat across a fairly broad range, and therefore there is little *a priori* reason for a birdwatcher or ornithologist to invest effort in trying to see a hidden, vocalising tailorbird in dense scrub in mainland South-East Asia. Moreover, collecting effort in Cambodia has been low: we have been able to trace only two *O. atrogularis* and one *O. sutorius* specimens (NHMUK 1928.6.26.1210, Eames & Ericson

1996) (the identification of all these specimens has been verified by the primary author, either first-hand or using photographs). Modern birdwatching effort in Cambodia is also limited and very localised. The factors discussed above also help explain why the first four individuals known were all mist-net captures. Their misidentification can be accounted for by the species's superficial similarity to other species, observer inexperience and the sheer unlikelihood of alternative options (cf. Woxvold *et al.* 2009). The discovery of *O. chaktomuk* indicates that new species of bird may still be found in familiar and unexpected locations.

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REFERENCES

- Addinssoft (2013) *XLStat*. Available at: <http://www.xlstat.com/en/>.
- Alström, P., Ericson, P. G. P., Olsson, U. & Sundberg, P. (2006) Phylogeny and classification of the avian superfamily Sylvioidea. *Mol. Phylog. Evol.* 38: 381–397.
- Alström, P., Davidson, P., Duckworth, J. W., Eames, J. C., Le Trong Trai, Nguyen Cu, Olsson, U., Robson, C. & Timmins, R. J. (2010) Description of a new species of *Phylloscopus* warbler from Vietnam and Laos. *Ibis* 152: 145–168.
- Alström, P., Hohna, S., Gelang, M., Ericson, P. G. P. & Olsson, U. (2011) Non-monophyly and intricate morphological evolution within the avian family Cettiidae revealed by multilocus analysis of a taxonomically densely sampled dataset. *BMC Evol. Biol.* 11: 352.
- Arias, M. E., Cochrane, T. A., Piman, T., Kumm, M., Caruso, B. S. & Killeen, T. J. (2012) Quantifying changes in flooding and habitats in the Tonle Sap Lake (Cambodia) caused by water infrastructure development and climate change in the Mekong Basin. *J. Env. Mgmt.* 112: 53–66.
- Cracraft, J. (1989) Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59 in D. Otte & J. A. Endler, eds. *Speciation and its consequences*. Sunderland, MA: Sinauer Associates.
- Collar, N. J. (2006) A partial revision of the Asian babblers (Timaliidae). *Forktail* 22: 85–112.
- Collar, N. J. (2011) Species limits in some Philippine birds including the Greater Flameback *Chrysocolaptes lucidus*. *Forktail* 27: 29–38.
- Delacour, J. & Mayr, E. (1946) *Birds of the Philippines*. New York: Macmillan.
- Dickinson, E. C., Kennedy, R. S. & Parkes, K. C. (1991) *The birds of the Philippines: an annotated check-list*. Tring, UK: British Ornithologists' Union (Checklist 12).
- Duckworth, J. W., Alström, P., Davidson, P., Evans, T. D., Poole, C. M., Setha, T. & Timmins, R. J. (2001) A new species of wagtail from the lower Mekong basin. *Bull. Brit. Orn. Club* 121: 112–142.
- Eames, J. C. (2002) Eleven new subspecies of babbler (Timaliinae) from Kon Tum province, Vietnam. *Bull. Brit. Orn. Club* 122: 109–141.
- Eames, J. C. & Eames, C. (2001) A new species of laughingthrush *Garrulax* Passeriformes: Sylviinae: (Garrulacinae) from the central highlands of Vietnam. *Bull. Brit. Orn. Club* 121: 10–23.
- Eames, J. C. & Ericson, P. G. P. (1996) The Bjorkegren expeditions to French Indochina: a collection of birds from Vietnam and Cambodia. *Nat. Hist. Bull. Siam Soc.* 44: 75–111.
- Eames, J. C., Robson, C. R. & Nguyen Cu (1994) A new subspecies of Spectacled Fulvetta *Alcippe ruficapilla* from Vietnam. *Forktail* 10: 141–158.
- Eames, J. C., Le Trong Trai, Nguyen Cu & Eve, R. (1999a) New species of barwing *Actinodura* (Passeriformes: Sylviinae: Timaliini) from the Western Highlands of Vietnam. *Ibis* 141: 1–10.
- Eames, J. C., Le Trong Trai & Nguyen Cu (1999b) A new species of laughingthrush *Garrulax* Passeriformes: Sylviinae: (Garrulacinae) from the Western Highlands of Vietnam. *Bull. Brit. Orn. Club* 119: 4–15.
- International Commission on Zoological Nomenclature (2012) Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *ZooKeys* 219: 1–10.
- International Rivers (2012) Laos begins work on a second Mekong river dam. Available at: <http://www.internationalrivers.org>.
- Irestedt, M., Fabre, P.-H., Henrique, B.-F., Jønsson, K. A., Roselaar, C. S., Sangster, G. & Ericson, P. G. P. (2013) The spatio-temporal colonization and diversification across the Indo-Pacific by a 'great speciator' (Aves, *Erythropitta erythrogaster*). *Proc. Roy. Soc. Lond. B.* 280: DOI:dx.doi.org/10.1098/rspb.2013.0309.
- IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. Gland, Switzerland & Cambridge, UK: IUCN Species Survival Commission.
- Kennedy, R. S., Gonzales, P. C., Dickinson, E. C., Miranda, H. C. & Fisher, T. H. (2000) *A guide to the birds of the Philippines*. Oxford: Oxford University Press.
- Le Trong Trai & Craik, R. C. (2008) Mekong Wagtail *Motacilla samveasnae* — resident breeder in Vietnam? *BirdingASIA* 8: 68–69.
- Leader, P. J. (2011) Taxonomy of the Pacific Swift *Apus pacificus* Latham, 1802, complex. *Bull. Brit. Orn. Club* 131: 81–93.
- Lim, H. C., Zou, F., Taylor, S. S., Marks, B. D., Moyle, R. G., Voelker, G. & Sheldon, F. H. (2010) Phylogeny of magpie-robins and shamas (Aves: Turdidae: *Copsychus* and *Trichixos*): implications for island biogeography in Southeast Asia. *J. Biogeog.* 37: 1894–1906.
- Madge, S. C. (2006) Family Cisticolidae (Cisticolas and allies) [*Orthotomus* accounts]. Pp. 422–427 in J. del Hoyo, A. Elliott & D. A. Christie, eds., *Handbook of the birds of the world*, 11. Barcelona: Lynx Edicions.
- Mahood, S. P. & Martin, R. W. (2013) Ashy Tailorbird *Orthotomus ruficeps*: the first records for Cambodia. *BirdingASIA* 19: 121–122.
- Mayr, E. (1963) *Animal species and evolution*. Cambridge, MA: Belknap Press of Harvard University Press.
- Mayr, E. (1999) *Systematics and the origin of species, from the viewpoint of a zoologist*. Cambridge, MA: Harvard University Press.
- Mekong River Commission (2011) *Planning atlas of the lower Mekong River basin*. Phnom Penh and Vientiane: Mekong River Commission.
- Mitra, S. & Sheldon, F. H. (1993) Use of an exotic tree plantation by Bornean lowland forest birds. *Auk* 110: 529–540.
- Moltesen, M., Irestedt, M., Fjeldså, J., Ericson, P. G. P. & Jønsson, K. A. (2012) Molecular phylogeny of Chloropsidae and Irenidae – cryptic species and biogeography. *Mol. Phylog. Evol.* 65: 903–914.
- Murray, B. J., Jr. (1971) The ecological consequences of interspecific territorial behaviour in birds. *Ecology* 52: 414–423.

- Murray, B. J., Jr. (1976) A critique of interspecific territoriality and character convergence. *Condor* 78: 518–525.
- Nguembock, B., Fjelså, J., Tillier, A. & Pasquet, E. (2007) A phylogeny for the Cisticolidae (Aves: Passeriformes) based on nuclear and mitochondrial DNA sequence data, and a re-interpretation of a unique nest-building specialisation. *Mol. Phylog. Evol.* 42: 272–286.
- Olsson, U., Irestedt, M., Sangster, G., Ericson, P. G. P. & Alström, P. (2013) Systematic revision of the avian family Cisticolidae based on a multi-locus phylogeny of all genera. *Mol. Phylog. Evol.* 66: 790–799.
- Orians, G. H. & Willson, M. F. (1964) Interspecific territories of birds. *Ecology* 45: 736–745.
- Orr, S., Pittock, J., Chapagain, A. & Dumaresq, D. (2012) Dams on the Mekong River: lost fish protein and the implications for land and water resources. *Glob. Env. Change* 22: 925–932.
- Packman, C. E., Gray, T. N. E., Collar, N. J., Evans, T. D., van Zalinge, R. N., Son Virak, Lovett, A. A. & Dolman, P. M. (2013) Rapid loss of Cambodia's grasslands. *Conserv. Biol.* 27: 245–247.
- Rasmussen, P. C. & Anderton, J. C. (2005) *Birds of South Asia: the Ripley guide*. Washington D.C. and Barcelona: Smithsonian Institution and Lynx Edicions.
- Rasmussen, P. C., Allen, D. N. S., Collar, N. J., DeMeulemeester, B., Hutchinson, R. O., Jakosalem, P. G. C., Kennedy, R. S., Lambert, F. R. & Paguntalan, L. M. (2012) Vocal divergence and new species in the Philippine Hawk Owl *Ninox philippensis* complex. *Forktail* 28: 1–20.
- Raven (2012) *Raven interactive sound analysis software*. Available at <http://www.birds.cornell.edu/brp/raven/RavenVersions.html#Raven14>.
- Reinert, B. L., Bornschein, M. R. & Firkowski, C. (2007) Distribuição, tamanho populacional, hábitat e conservação do bicudinho-do-brejo *Stymphalornis acutirostris* Bornschein, Reinert e Teixeira, 1995 (Thamnophilidae). *Rev. Bras. Ecol.* 15: 493–519.
- Rheindt, F. E. & Eaton, J. A. (2010) Biological species limits in the banded pitta *Pitta guajana*. *Forktail* 26: 86–91.
- Rheindt, F. E. & Edwards, S. V. (2011) Genetic introgression: an integral but neglected component of speciation in birds. *Auk* 128: 620–632.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542.
- Round, P. D. (2008) *Birds of the Bangkok area*. Bangkok: White Lotus Company.
- Sangster, G. (2009) Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. *Proc. Roy. Soc. Lond. B.* 276: 3185–3191.
- Sathiamurthy, E. & Voris, H. K. (2006) Maps of the Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Nat. Hist. J. Chulalonghorn Univ.* Supplement 2: 1–44.
- Sheldon, F. H., Oliveros, C. H., Taylor, S. T., McKay, B., Lim, H. C., Rahman, M. A., Mays, H. & Moyle, R. G. (2012) Molecular phylogeny and insular biogeography of the lowland tailorbirds of Southeast Asia (Cisticolidae: *Orthotomus*). *Mol. Phylog. Evol.* 65: 54–63.
- Sibley, C. G. & Ahlquist, J. E. (1990) *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Smithe, F. B. (1975) *Naturalist's color guide*. New York: American Museum of Natural History.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. (1998) *Endemic Bird Areas of the world: priorities for biodiversity conservation*. Cambridge UK: BirdLife International.
- Tobias, J. A., Bates, J. M., Hackett, S. J. & Seddon, N. (2008) Comment on the latitudinal gradient in recent speciation and extinction rate of birds and mammals. *Science* 319: 901.
- Tobias, J. A., Seddon, N., Spottiswoode, C. N., Pilgrim, J. D., Fishpool, L. D. C. & Collar, N. J. (2010) Quantitative criteria for species delineation. *Ibis* 152: 724–746.
- Uy, J. A. C., Moyle, R. G., Filardi, C. E. & Cheviron, Z. A. (2009) Difference in plumage color used in species recognition between incipient species is linked to a single amino acid substitution in the melanocortin-1 receptor. *Amer. Nat.* 174: 244–254.
- Voris, H. K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *J. Biogeog.* 27: 1153–1167.
- Wells, D. R. (2007) *The birds of the Thai-Malay Peninsula*, 2. London: Christopher Helm.
- Woxvold, I. A., Duckworth, J. W. & Timmins, R. J. (2009) An unusual new bulbul (Passeriformes: Pycnontidae) from the limestone karst of Lao PDR. *Forktail* 25: 1–12.
- Zhou Fang & Jiang Aiwu (2008) A new species of babbler (Timaliidae: *Stachyris*) from the Sino-Vietnamese border region of China. *Auk* 125: 420–424.

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Tables SOM 1 to SOM 5

Figure SOM 1

Media Files SOM 1 to SOM 6

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