A reassessment of the East African ranges of two subspecies of Yellow-fronted Tinkerbird *Pogoniulus chrysoconus* based on a comparison of plumage, biometrics and song

Alexander N. G. Kirschel and Matteo Sebastianelli

Summary

The distribution of the nominate subspecies of Yellow-fronted Tinkerbird *Pogoniulus chrysoconus* has long been thought to extend throughout Uganda south into northwestern Tanzania, with *extoni* replacing it from southwestern Tanzania southwards. But little or no evidence has been available from southern Uganda or western Tanzania to confirm this. We performed fieldwork in Uganda and Tanzania, recording songs, ringing and measuring tinkerbirds and photographing their plumage. Our analyses of plumage, biometrics and bioacoustics reveal that nominate *chrysoconus* was present in most of Uganda, however, in southern Uganda, near Lake Mburo National Park, it was replaced by *extoni*, which extends southwards into Tanzania. Our findings suggest that published distribution maps and descriptions will require revisions.

Keywords: Uganda, Lybiidae, plumage coloration, song, morphology

Introduction

The Yellow-fronted Tinkerbird *Pogoniulus chrysoconus* is a barbet with a widespread distribution in mostly woodland savannah habitat in sub-Saharan Africa (Short & Horne 1988). In East Africa, it is represented by all three subspecies currently recognized in the IOC world bird list (Gill *et al.* 2022). *P. c. chrysoconus*, ranges from southwestern Mauritania east to western Kenya, *P. c. xanthostictus* occurs in Ethiopia, and *P. c. extoni* from South Africa north to southern Tanzania (Short & Horne 2001). Several authors have suggested that the northern extent of the distribution of *P. c. extoni* is southern Tanzania (Short & Horne 1988, Short & Horne 2001), with *P. c. chrysoconus* extending northwards from Gombe Stream and Kibondo (Britton 1980). However, there are no specimen records from western Tanzania or southern Uganda west of Lake Victoria (Snow 1978), to confirm if and where their distributions meet, and whether possible intergrades might occur.

Nominate *chrysoconus* differs morphologically from *extoni* primarily in the former's bright lemon-yellow underparts, whereas in *extoni* the underparts are a greyer, buff-tinged colour. The forecrown is described as yellow-gold in *chrysoconus* and

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gold to orange in *extoni* (Short & Horne 2001). Short & Horne (1988) describe *extoni* as slightly larger than *chrysoconus*, but that variation is clinal with birds further south and at higher elevation being larger. This pattern of variation in body size is consistent with Bergmann's rule, which is in accordance with findings in tinkerbirds from across the continent (Sebastianelli *et al.* 2022). No differences in vocalizations have been described.

Yellow-fronted Tinkerbird forms a superspecies with Red-fronted Tinkerbird with which it occurs in parapatry across much of East Africa as well as in southern Africa. Subspecies have long been assigned to one species or another based on forecrown colour, but recent phylogenetic reconstructions using mitochondrial DNA suggest *P. c. chrysoconus* and *P. c. extoni* are not even sister taxa (Nwankwo *et al.* 2019, Kirschel *et al.* 2021). Kirschel *et al.* (2021) proposed that Red-fronted Tinkerbird *Pogoniulus pusillus* is two distinct species based on phenotypic and genetic differences between southern and northern forms, yet nominate *chrysoconus* and *P. c. extoni* are genetically more differentiated in mitochondrial DNA than the two forms of Red-fronted Tinkerbird, suggesting that these northern and southern forms of Yellow-fronted Tinkerbird may also warrant separate species status.

Our aim was to revise the distributions of *P. c. chrysoconus* and *P. c. extoni* based on recent fieldwork in Uganda and Tanzania. We compared morphology, including plumage coloration, and song among individuals sampled in different populations of *P. c. chrysoconus* and *P. c. extoni* and the subspecies of Red-fronted Tinkerbird occurring in the region (*P. p. affinis*, but see Kirschel *et al.* (2021) for a proposed taxonomic revision). Although song differences have not previously been described between populations of Yellow-fronted Tinkerbird, recent work on Red-fronted Tinkerbird found distinct differences between taxa (Kirschel *et al.* 2021), and similar differences could be found between Yellow-fronted Tinkerbird populations.

Methods

Fieldwork was performed in Uganda from 18 May to 5 June and from 16 April 2022 to 8 May 2022 in Pian Upe, Matheniko-Bokora, and Karuma Game Reserves, in community land across northwestern Uganda (around Mount Kei, Otze and Ajai Forest Reserves), in Queen Elizabeth National Park (QENP), in and around Lake Mburo National Park, and in Entebbe. We also traversed much of the area between QENP and Lake Mburo National Park (Fig. 1). Songs were also recorded and observations made in Tanzania from 8 May 2022 to 27 May 2022 in Ibanda Game Reserve, Burigi-Chato National Park, Biharamulo Game Reserve, Geita Forest Reserve and Grumeti Game Reserve as well as on community land.

We recorded songs of Yellow-fronted and Red-fronted Tinkerbirds using a Marantz PMD 661 digital recorder and a Sennheiser MKH 8050 microphone. Tinkerbirds were captured in mist nets using song playback. Birds were measured and ringed then released. Biometrics recorded included body mass, wing, tarsus and tail length, bill length (exposed culmen and from anterior of nares to tip), width, and depth. We also took photographs of the birds to compare plumage characteristics described as being different between these two subspecies (Short & Horne 2001).

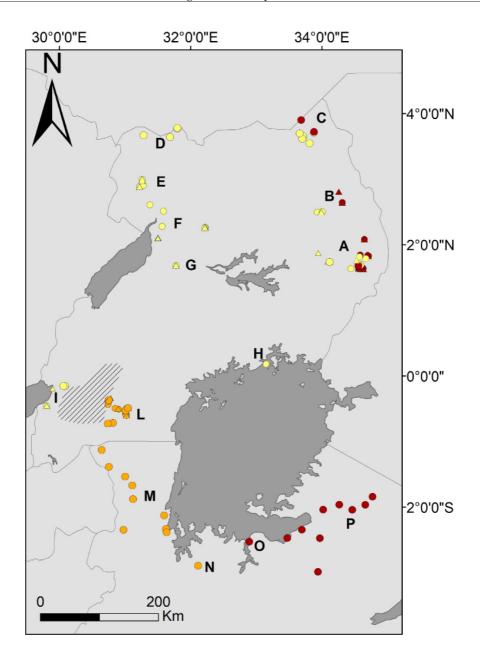


Figure 1. Map of Uganda showing the spatial distribution of recordings (circles) and birds ringed (triangles) for *extoni* (orange), *chrysoconus* (yellow) and *affinis* (burgundy) in (A) Pian Upe, (B) Matheniko-Bokora, (C) Kidepo Valley National Park, (D) Otze forest and Mount Kei, (E) Acha-Ajai, (F) Karuma-Murchison Falls, (G) Masindi, (H) Entebbe, (I) Queen Elizabeth National Park, (L) Lake Mburo National Park, (M) Kagera, (N) Geita, (O) Mwanza and (P) Simiyu / Mara. The hatched lines represent an area where neither *chrysoconus* nor *extoni* were found.

Song analyses

Acoustic measurements were made using the methods described by Sebastianelli *et al.* (2022). In brief, recordings were imported into Raven Pro (Center for Conservation Bioacoustics, 2019) and notes detected using the built-in band limited automated energy detector. The notes were visually inspected to correct any errors in detection. From each detection, the following measurements were extracted: note duration, peak frequency, mean of the peak frequency contour slope, and relative peak time. The inter-onset interval (IOI), a measure of the speed at which notes are delivered, was also calculated from start times of consecutive notes detected.

Statistical analyses

We used Principal Component Analysis to reduce dimensionality in both acoustic and morphological data for use as response variables in Generalized Linear Mixed Models (GLMM) in the *glmmTMB* R package (Brooks *et al.*, 2017). We used peak frequency, delta time, IOI, mean peak frequency slope and peak time relative in the acoustic PCA, and all eight biometrics measured in the morphology PCA. We used PCs with eigenvalues >1 as response variables in gaussian GLMM including presumed subspecies as a fixed factor. For the song models, we used a three-way nested random factor with recording nested in individual, nested in location, whereas for the morphology models we included individual nested in location. The best fit models were validated through graphical inspection using the *DHARMa* package (Harting 2019).

Results

Fieldwork

We analysed 106 recordings, comprising 84 recordings from Uganda (19 *extoni*, 30 *affinis* and 35 *chrysoconus*) and 22 (10 *extoni*, 12 *affinis*) from Northern Tanzania. Specifically, in Uganda we recorded a total of 21 Red-fronted Tinkerbirds and 10 Yellow-fronted Tinkerbirds in Pian Upe, 3 and 2 in Matheniko-Bokora, and 4 and 2 in Kidepo Valley National Park respectively. Four Yellow-fronted Tinkerbirds were recorded in northwestern Uganda and 4 in Karuma/Murchison Falls, 1 near Masindi, 4 between Ajai and Acha, 1 in QENP, 1 in Entebbe, and 19 in the Lake Mburo area, In northern Tanzania, we recorded 10 *extoni* from the Kagera region (west of Lake Victoria) and 12 *affinis* from Mwanza to Mara regions. Moreover, we ringed and obtained biometrics from a total of 31 Red-fronted Tinkerbirds and 10 Yellow-fronted Tinkerbird in the Pian Upe area, 2 and 1 in Matheniko-Bokora, and 9 and 4 in Kidepo respectively, and 5 Yellow-fronted Tinkerbirds in Karuma/Murchison Falls, 1 near Otze forest, 4 between Ajai and Acha, 2 near Masindi, 4 in QENP, and 18 in the Lake Mburo area between QENP, Lake Mburo and Katonga Game Reserve (hatched area in Fig. 1).

Statistical analyses

We extracted two principal components from each PCA with eigenvalues >1. For the PCA on song measurements, PC1 was positively associated with IOI and note duration, and PC2 with relative peak time, peak frequency average slope and peak frequency. For the PCA on biometrics, PC1 was negatively associated with the beak measurements and mass, whereas PC2 was positively associated with beak tip and tarsus (Table 1).

Our results show that *extoni* differed significantly in morphology from *affinis* and *chrysoconus* in PC1 but not in PC2 (Table 2, Fig. 2).

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a) Song	PCI	PC2
Eigenvalue	1.36	1.07
% Variance	37.5	23.17
Peak frequency	-0.28	0.48
Delta frequency	0.54	-0.25
IOI	0.63	-0.13
Average slope	0.38	0.49
Peak time relative	0.27	0.65
b) Morphology	PCI	PC2
Eigenvalue	1.68	1.22
% Variance	35.43	18.76
Mass	-0.46	0.11
Wing	-0.09	-0.27
Tarsus	-0.22	0.49
Tail	-0.36	0.01
Culmen	-0.07	0.64
Exposed	-0.41	-0.39
Depth	-0.45	0.18
Width	-0.45	-0.24

Table 1. Table showing eigenvalues, percentage of variance explained and factor loadings for the principal components with eigenvalues >1 for a) song PCA and b) body PCA.

Table 2. Table showing GLMM output on a) PC1 and b) PC2 extracted from the PCA on biometrics.

	Estimate	Std. Error	Z	р
a) Response				
PC1 (51.23%)				
Intercept	-0.240	0.319	-0.753	0.451
P. pusillus affinis	-1.107	0.380	-2.677	0.007
P. chysoconus chrysoconus	2.191	0.397	5.507	< 0.001
b) Response				
PC2 (14.36%)				
Intercept	0.179	0.294	0.608	0.543
P. pusillus affinis	-0.064	0.349	-0.185	0.853
P. chysoconus chrysoconus	-0.391	0.369	-1.062	0.288

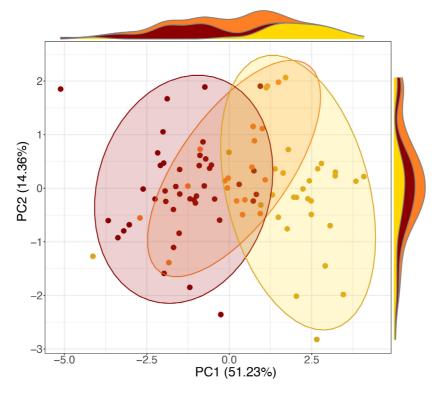


Figure 2. PCA plot on biometrics with 95% CI ellipses. The three taxa are shown in orange (*P. chrysoconus extoni*), burgundy (*P. pusillus affinis*) and yellow (*P. chrysoconus chrysoconus*). Axes show distribution of sample sizes within each taxon for each PC.

Songs of *extoni* were significantly different from those of nominate *chrysoconus*, but not from those of *affinis* according to PC1, with no significant differences in PC2 (Table 3, Fig. 3).

	Estimate	Std. Error	Z	р
a) Response				
PC1 (37.50%)				
Intercept	-0.920	0.151	-6.064	<0.001
P. pusillus affinis	0.200	0.195	1.027	0.304
P. chysoconus chrysoconus	2.488	0.203	12.245	< 0.001
b) Response				
PC2 (23.17%)				
Intercept	-0.171	0.203	-0.845	0.398
P. pusillus affinis	0.423	0.261	1.622	0.105
P. chysoconus chrysoconus	-0.057	0.272	-0.212	0.832

Table 3. Table showing GLMM output on a) PC1 and b) PC2 extracted from the song PCA.

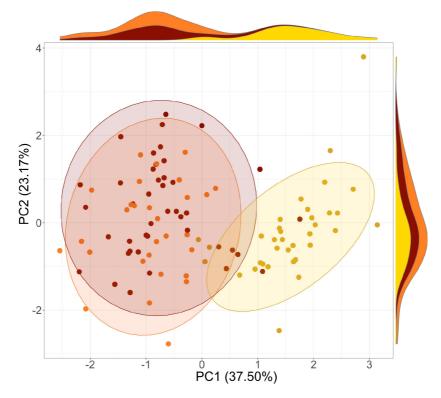


Figure 3. Song PCA plot with 95% CI ellipses showing higher degree of similarity between *P. chrysoconus extoni* (orange) and *P. pusillus affinis* (burgundy) than with *P. chrysoconus chrysoconus* (yellow). Axes show distribution of sample sizes within each taxon for each PC.

Photos of birds in the hand revealed distinct differences in underpart coloration, with individuals from Pian Upe, Kidepo, Murchison Falls, Acha and QENP all with bright lemon-yellow underparts, consistent with nominate *chrysoconus*, and birds from Lake Mburo and its vicinity, all greyer below, consistent with expectations for *extoni* (Fig. 4).

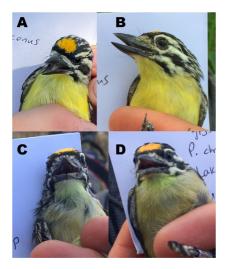


Figure 4. Photos of four Yellow-fronted Tinkerbirds ringed in Uganda in 2021. Underparts of nominate *chrysoconus* from (A) Pian Upe and (B) Acha, are bright lemon yellow in colour, but birds from around the vicinity of Lake Mburo (C, D) have greyer, buff-tinged underparts, consistent with expectations for *P.c. extoni*.

Discussion

In previous fieldwork performed in Tanzania looking for the contact zone between nominate *chrysoconus* and *extoni* in western Tanzania, all individuals of Yellow-fronted Tinkerbird found were clearly *extoni*, based on morphology, and confirmed as such in genomic analyses (Kirschel *et al.* 2020). Searching resources online, photos of Yellow-fronted Tinkerbird from Rwanda on eBird, and a recording from Akagera NP by Lester Short and Jennifer Horne (Macaulay Library), were also identifiable as *extoni* (ANGK pers. obs.) according to distinct song differences between these taxa consistent with our findings in this study. There are also records of a number of species common in Miombo woodland in Tanzania, whose ranges extend into southern Uganda, including within Lybiidae, such as Black-collared Barbet *Lybius torquatus* and Crested Barbet *Trachyphonus vaillantii* (Short & Horne 2001). Therefore, the presence of *extoni* in southern Uganda should not be unexpected.

During our fieldwork in Uganda, having recorded nominate *chrysoconus* at the sites visited prior to arriving at Lake Mburo NP, we had become very familiar with the characteristics of its song. As soon as we heard a tinkerbird song in Lake Mburo NP in May 2021, it was immediately recognized as being much faster than typical nominate *chrysoconus* song. There are records of Yellow-fronted Tinkerbird from Lake Mburo in the *Bird Atlas of Uganda* (Carswell *et al.* 2005), and reports from 2000 and 2001 collected for the atlas even suggested the presence of Red-fronted Tinkerbird in southern Uganda (H. Tushabe pers. comm.). We believe such reports of Red-fronted Tinkerbird from southern Uganda were identified by voice, and were instead the *extoni* form of Yellow-fronted Tinkerbird, whose song is much more similar to Red-fronted Tinkerbird, as shown by our findings here.

Our findings of differences in song and morphology between *extoni* and nominate *chrysoconus* are consistent with the hypothesis that these represent different species, as suggested by Kirschel *et al.* (2021). Although a taxonomic revision is not the aim of the present study, we believe our findings will support any future investigation incorporating genetic data into the species status of these different forms of Yellow-fronted Tinkerbird. If supported, then an additional species would be added to the Uganda bird list.

Despite the extent of genetic differentiation among forms in the Yellow-fronted / Red-fronted Tinkerbird complex, they still commonly interbreed at contact zones, including between Yellow-fronted and Red-fronted Tinkerbirds in southern Africa (Nwankwo *et al.* 2019, Kirschel *et al.* 2020). Although there are distinct song differences between the two forms of Yellow-fronted Tinkerbird in Uganda, and song differences have been shown to elicit differential responses among other tinkerbirds (Kirschel *et al.* 2009, Nwankwo *et al.* 2018), they are likely still similar enough here to allow interbreeding between them if a contact zone exists. Our fieldwork in Uganda did not reveal a contact zone, with intervening areas between their ranges characterized mostly by cultivated areas in shrubland, forest and swamps; but this does not preclude the possibility that a contact zone exists.

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References

BRITTON, P.L. 1980. (ed) Birds of East Africa. Nairobi: East Africa Natural History Society.

- BROOKS, M.E., KRISTENSEN, K., VAN BENTHEM, K.J., MAGNUSSON, A., BERG, C.W., NIELSEN, A., SKAUG, H.J., MAECHLER, M. & BOLKER, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. *The R Journal* 9: 378–400.
- CARSWELL, M., POMEROY, D., REYNOLDS, J. & TUSHABE, H. 2005. *The Bird Atlas of Uganda*. Peterborough: British Ornithologists' Union.
- CENTER FOR CONSERVATION BIOACOUSTICS. 2019. Raven Pro: Interactive Sound Analysis Software (Version 1.6) [Computer software].
- GILL, F., DONSKER, D. & RASMUSSEN, P. (EDS). 2022. IOC World Bird List (v12. 1).
- HARTING, F. 2019. DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. https://CRAN.R-project.org/package=DHARMa.
- KIRSCHEL, A.N.G., BLUMSTEIN, D.T. & SMITH, T.B. 2009. Character displacement of song and morphology in African tinkerbirds. *Proceedings of the National Academy of Sciences of the United States of America* 106: 8256–8261.
- KIRSCHEL, A.N.G., MOYSI, M., LUKHELE, S.M., SEBASTIANELLI, M., ASFAW, T., HADJIOANNOU, L., MORTEGA, K.G., MONADJEM, A. & MOYLE, R.G. 2021. Taxonomic revision of the Red-fronted Tinkerbird Pogoniulus pusillus (Dumont, 1816) based on molecular and phenotypic analyses. Bulletin of the British Ornithologists' Club 141: 428–442.
- KIRSCHEL, A.N.G., NWANKWO, E.C., PIERCE, D.K., LUKHELE, S.M., MOYSI, M., OGOLOWA, B.O., HAYES, S.C., MONADJEM, A. & BRELSFORD, A. 2020. CYP2J19 mediates carotenoid colour introgression across a natural avian hybrid zone. *Molecular Ecology* 29: 4970–4984.
- NWANKWO, E.C., MORTEGA, K.G., KARAGEORGOS, A., OGOLOWA, B.O., PAPAGREGORIOU, G., GRETHER, G.F., MONADJEM, A. & KIRSCHEL, A.N.G. 2019. Rampant introgressive hybridization in *Pogoniulus* tinkerbirds (Piciformes: Lybiidae) despite millions of years of divergence. *Biological Journal of the Linnean Society* 127: 125–142.
- NWANKWO, E.C., PALLARI, C.T., HADJIOANNOU, L., IOANNOU, A., MULWA, R.K. & KIRSCHEL, A.N.G. 2018. Rapid song divergence leads to discordance between genetic distance and phenotypic characters important in reproductive isolation. *Ecology and Evolution* 8: 716–731.
- SEBASTIANELLI, M., BLUMSTEIN, D.T. & KIRSCHEL, A.N.G. 2021. Higher-pitched bird song towards the coast supports a role for selection in ocean noise avoidance. *Bioacoustics* 31: 41–58.
- SEBASTIANELLI M., LUKHELE S.M., NWANKWO E.C., HADJIOANNOU, L. & KIRSCHEL, A.N.G. 2022. Continent-wide patterns of song variation predicted by classical rules of biogeography. *Authorea*. March 07, 2022.
- SHORT, L.L. & HORNE, J.F.M. 1988. Family Capitonidae in Fry, C. H., Keith, S. & Urban, E. K. (eds) The Birds of Africa Vol. 3., London: Academic Press.
- SHORT, L.L. & HORNE, J.F.M. 2001. *Toucans, Barbets and Honeyguides*. New York: Oxford University Press.
- SNOW, D.W. 1978. An atlas of speciation in African non-passerine birds. London: British Museum Press.

Alexander N. G. Kirschel

Department of Biological Sciences, University of Cyprus, PO Box 20537, Nicosia 1678, Cyprus. Email: kirschel@ucy.ac.cy

Matteo Sebastianelli

Department of Biological Sciences, University of Cyprus, PO Box 20537, Nicosia 1678, Cyprus. Email: sebastianelli.matteo@ucy.ac.cy

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