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Field characters, taxonomy and distribution of the 'buff-bellied' forms of the Grey Penduline Tit *Anthoscopus caroli* (Sharpe) in East Africa

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Summary

We review the distribution and taxonomy of the buff-bellied subspecies of the Grey Penduline Tit *Anthoscopus caroli* in East Africa using photographs of specimen material as well as of birds in the field. Our study reveals three distinct taxa in the group, including, in addition to the currently recognized *sylviella* of eastern Tanzania and *sharpei* of south-central and western Tanzania, recognition and reinstatement of the form *rothschildi* from eastern Kenya (previously synonymized with *sylviella*). We show that contrary to literature accounts, *sylviella* has richer underparts and darker upperparts than *sharpei*, and the range of *sharpei* extends southeast from Tabora to the Iringa area of Tanzania and not northwards into southwestern Kenya, as had been previously thought. Meanwhile, we extend the range of *sylviella* from eastern Tanzania to areas west of the Rift Valley in the Serengeti National Park of Tanzania as well as southwestern Kenya, both areas previously considered occupied by *sharpei*. We further demonstrate that these two taxa intergrade where they meet in the southern reaches of the Serengeti National Park, and that *sylviella* also intergrades with *rothschildi* across a small area to the east of the Rift Valley in Kenya immediately south of Nairobi. Further work may show birds in the Chyulu Hills, Kenya, to be a distinct form, while birds in the central Kenya Rift Valley remain only tentatively assigned to *sylviella*.

Keywords: *Anthoscopus caroli*, Grey Penduline Tit, taxonomy, distribution, field identification

Introduction

The Grey Penduline Tit *Anthoscopus caroli* Sharpe, 1871 is a small, short-billed and short-tailed bird occurring in wooded habitats throughout much of East Africa and the southern tropical woodland zone from Mozambique west to Angola and south to the eastern parts of South Africa (Fry *et al.* 2000). It is typified by the nominate subspecies which occurs from northern Namibia and southern Angola east through northern Botswana to southwest Zambia and is plain grey above, slightly paler below, and with pale cinnamon-buff forehead, cheeks and vent. The species is currently considered to comprise no fewer than eleven subspecies (Dickinson & Christidis 2014, Clements *et al.* 2019, Gill & Donsker 2020), separable into five groups (Harrap & Quinn 1995, Clements

et al. 2019, Fry *et al.* 2000). Six subspecies have been reported from East Africa, representing four of these groups as follows (Britton 1980, Harrap & Quinn 1995, Fry *et al.* 2000):

1) The ***caroli*** **('Buff-vented') group**, represented in East Africa by the subspecies *A. c. robertsi* Haagner, 1909 (including '*taruensis*' van Someren, 1921), occurring from interior east Tanzania north to Kilosa, Korogwe and Naberera and to southeast Kenya at Taru and Samburu north to the lower Tana River. Similar to nominate , but more olive-grey above; sides of head pale yellowish buff (rather than cinnamon-buff); throat and breast whiter, tinged yellowish; buff lower underparts paler, tinged more yellowish. Wing: 48–54 mm (compared with 51–55 mm in nominate *caroli*). Birds in northeastern Tanzania, inland coastal Kenya (*'taruensis'*) average slightly smaller; wing 49–51 mm.
2) The ***ansorgei*** **Hartert, 1905 ('White-bellied') group**, represented in East Africa by two subspecies:

i. *A. c. rhodesiae* Sclater, 1932 occurring in southwest Tanzania from border regions with Zambia north to the Ufipa Plateau. Differs from *A. c. ansorgei* in having forehead paler yellow (vs brighter and richer in *ansorgei*), olive-green upperparts duller (vs brighter apple green), sides of head and chin to breast greyish-white, and rear of underparts pale cinnamon-buff (underparts uniform whitish in *ansorgei*); secondaries, tertials, greater coverts and tail feathers edged pale olive-yellow. Wing: 48–57 mm.
ii. *A. c. pallescens* Ulfstrand, 1960 occurring from Kigoma to the Mahale Mountains in western Tanzania. Like *rhodesiae* but paler, more greyish green above; greyish-white underparts slightly washed yellow, under tail-coverts tinged buff. Wing: 53–57 mm.

3) The ***sylviella*** **Reichenow, 1904 ('Buff-bellied') group**, endemic to East Africa and represented by two subspecies:

i. *A. c. sylviella* Reichenow, occurring from south-central Kenya east of the Rift (Murang'a and Kitui, south to Kajiado, Simba and Voi) and central Tanzania (Longido south to Dodoma, Iringa and the Mbeya-Rungwe District) to the west of *robertsi*. Similar to nominate, with grey upperparts (olive tones faint or absent), but whole underparts tawny-buff to deep tawny-buff, paler on chin and throat; forehead pale buff to deep tawny-buff; sides of head pale buff. Wing: 51–58 mm.
ii. *A. c. sharpei* Hartert, 1905 from southwestern Kenya and northern Tanzania east and south of Lake Victoria (Kakamega and Nyanza to Lolgorien, Masai Mara GR, Serengeti and Usambiro), while birds in the central Kenya Rift at Lake Baringo to the Kerio Valley and Nakuru District probably belong here. Although less distinct, they are almost as richly-marked as *sylviella* and certainly more so than all other forms in the other groups. Like *sylviella*, but darker, more cinnamon below, forehead dull cinnamon. Wing: 54–59 mm.

4) The ***roccatii*** **Salvadori, 1906 ('Yellow-bellied') group**, represented by a single subspecies *A. c. roccatii* Salvadori, from Burundi and Rwanda in the Akanyaru and Kagera basins, north through northwest Tanzania at Kagera to Uganda, east to west Kenya borders (Kongelai and Kapenguria to Bungoma). Upperparts greyish-olive; forehead and superciliary stripe pale yellow; sides of head, chin and throat tinged grey, rest of underparts pale yellow, deeper and buffier on vent and under tail-coverts. Wing: 51–56 mm.

Ranging from central Kenya to southern Tanzania (Fig. 1), the Buff-bellied Penduline Tits addressed in this paper are readily distinguished from all other subspecies by their grey upperparts and warm buffy to clay-coloured underparts, these being off-white to greyish-yellow in other subspecies occurring peripherally to this group, and with any buff tones restricted to the vent and/or forehead and cheeks. In addition to the distinctive underpart colours and an absence of intergrades with non Buff-bellied types, the vocalizations are also described as very different, including a high trill variably reported to be the song or call (Boesman in del Hoyo & Collar 2016). As such, the Buff-bellied types have been considered distinct enough by del Hoyo & Collar (2016) to be elevated to species rank as Buff-bellied Penduline Tit *A. sylviella*. The Buff-bellied Penduline Tit taxa also specialize mostly in *Acacia*-dominant, bush or grassland associations, further differentiating them from other forms of *A. caroli* in East Africa, which occupy other woodland types.

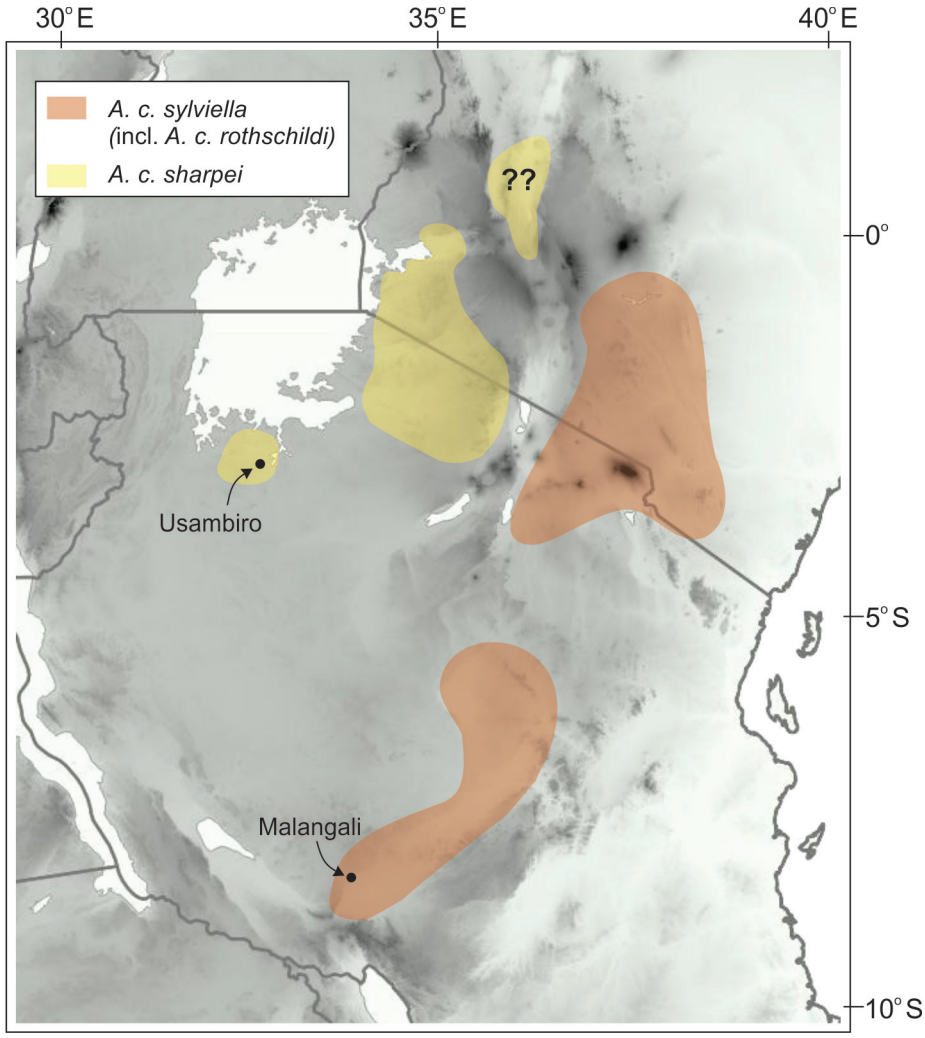

Figure 1. Map showing the currently understood distribution of the forms *A. c. sylviella* and *A. c. sharpei* of the African Penduline Tit in East Africa (distribution adapted from Harrap & Quinn 1995 and Fry *et al.* 2000).

Within the Buff-bellied Penduline Tit complex, the recognition of *sharpei* as distinct from *sylviella* is comparatively recent, with earlier authors preferring to treat it as a synonym of *sylviella*. These include Hellmayr in Wytsman (1911), who concluded that *sharpei* was "not distinct from *sylviella*", followed by Sclater (1930) and Jackson & Sclater (1938), who concluded that *sharpei* was "probably a synonym of *sylviella*". Meanwhile, Hartert (1920) himself stated that "the identity of the two was still doubtful". Since Grant & Mackworth-Praed (1948), however, successive authors have argued that variation in the depth of colour of the underparts is sufficient to distinguish *sylviella* and *sharpei* (e.g. Harrap & Quinn 1995, Fry *et al.* 2000, Madge *et al.* 2020; see descriptions above), maintaining these to be darker in *sharpei (*which also shows a paler throat, cheeks and forehead) and paler in *sylviella*.

However, birds recently photographed in eastern Tanzania at Iringa, where the subspecies has been thought to be *sylviella*, show underparts that are considerably paler than other birds photographed in eastern Tanzania at Tarangire NP (400 km north of Iringa) and also thought to be *sylviella* on the basis of the distribution east of the Rift Valley. However, these birds show rich clay-coloured underparts unlike the pale underparts of birds in Iringa. Additionally, field observations we have made of birds in eastern Kenya, which are widely referred to *sylviella*, show their underparts to be completely lacking in any rusty clay tones at all, *contra* descriptions of *sylviella* and wholly unlike the birds photographed at Tarangire NP. Originally, these east Kenyan birds were described under the name *rothschildi* Neumann, 1907 from a specimen collected at Simba in southeast Kenya. This taxon, however, has not been recognized since White (1963) treated it as a synonym of *sylviella,* without providing his reasoning, though van Someren (1932) did comment that *sharpei* was different from *rothschildi* in being "darker on the belly but lighter on the throat and frontal area". The few details of *rothschildi* are:

> in the eastern districts of Kenya from Ukambani to the Upper Tana River including Simba, Kiu, Kitui, Thika and Murang'a districts (van Someren 1932, Friedmann 1937) *rothschildi* Neumann, 1907, was described as being "much smaller than *sylviella*, with pure ashy grey crown and upper parts, considerably paler ochre-yellow under parts and a rich ochre coloured forehead". Wing: 51.5 mm.

In light of recently obtained field photographs and field observations that conflict with our current understanding of field characters and distributions of the different forms in the Buff-bellied Penduline Tit grouping, a detailed review of the group is warranted. In this paper we assess field photographs and specimen material of the Buff-bellied Penduline Tit subspecies of *A. caroli* in East Africa. We compare type specimens with topotypical field photographs as well as with specimen material and field photographs from elsewhere within the range of *sylviella*, *sharpei* and *rothschildi*. In reviewing this evidence in combination with literature accounts detailing phenotypic variation, as well as the range limits of each subspecies, we ask:

1) Do the subspecies *sylviella* and *sharpei*, with ranges attributed to the east and west of the Rift Valley respectively in Tanzania and Kenya, comprise two recognizable subspecies, and if so, and what are their distinguishing field characters?
2) Is *rothschildi*, currently subsumed into *sylviella*, a recognizable taxon, and if so, what are its distinguishing field characters?

3) Is there evidence of intergrading between any of these subspecies and can all birds occurring within their ranges be satisfactorily assigned?

Materials and methods

We obtained photographic material of Buff-bellied Penduline Tits through correspondence and from prominent internet-based bio-inventory and image databases including iNaturalist, the Macaulay Library, Flickr and the African Bird Club. Specimen photographs, including of the type specimens of *sylviella*, *sharpei* and *rothschildi* were obtained courtesy of curatorial staff at several museums (see Appendix A and Acknowledgements), as well as from the Global Biodiversity Information Facility. Images were imported into Corel Draw to produce composite figures. Geo-referenced observation data from Tanzania (Baker & Baker 2020) was also used to define range limits more clearly, while lists of media reviewed and locations with coordinates are provided in Appendices A and B respectively.

Results

In East Africa, we recognize three subspecies in the Buff-bellied Penduline Tit grouping of *A. caroli* as well as intergrades in two areas as follows. Distributions and the locations of field photographs and specimen photographs reviewed are shown in Figure 2.

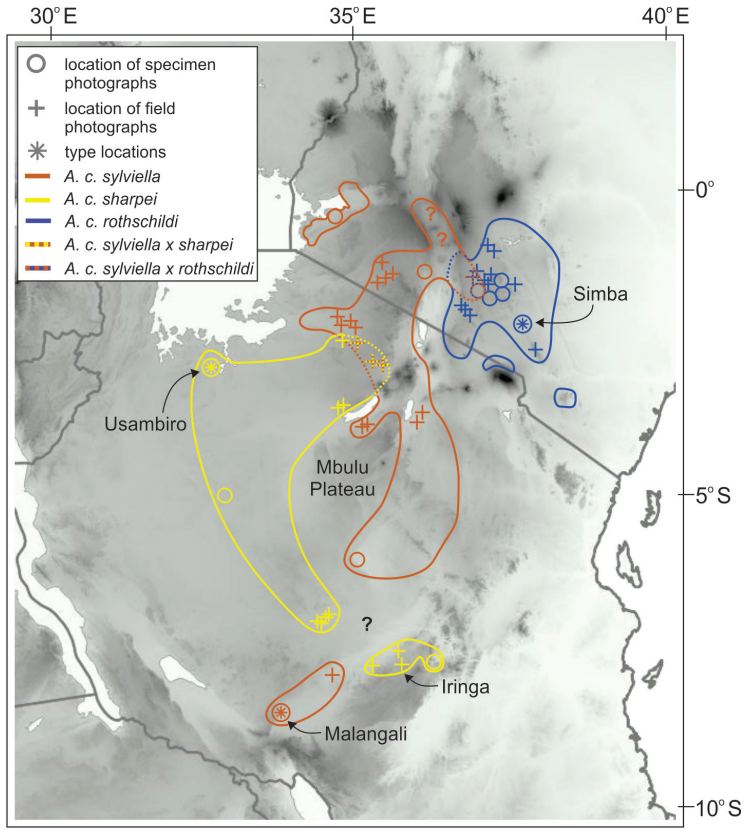

Figure 2. Map showing the approximate range limits of the buff-bellied subspecies of the Grey Penduline Tit *Anthoscopus caroli sylviella, A.c. sharpei* and *A.c. rothschildi* (and intergrades) in East Africa, as well as type localities and the locations of birds examined from field photographs or specimen photographs.

A. c. sylviella Reichenow (n = five specimens and 18 birds in field photographs). **Appearance**: a distinctive form marked by **rusty-clay underparts** which are darker than those of *A. c. sharpei,* contrary to all literature accounts which state that *sharpei* shows darker underparts (see Discussion). The throat, cheeks and forehead are largely concolorous with the lower underparts, or occasionally very marginally paler (Fig. 3A-C, Fig. 4A-D). The **upperparts are dark grey, lightly washed olive-brown**, and again darker than in *sharpei*. Wing: 55 mm. **Habitat**: in semi-arid to moist ***Acacia*-dominated savannah grasslands** (notably ***A. tortilis*** and ***A. gerardii***) from 800 to 2000 m in areas with approximately 500–1000 mm of annual rainfall. **Range**: southern and eastern Tanzania from "Malangali in Usafua" (type locality) northwards; disjunctly to Dodoma and Kikuyo, and from the Tarangire NP and the Yaida Valley, crossing the Rift Valley westwards into the Serengeti NP and north from there to the Mara GR, Kendu Bay and [rarely] Kisumu, east to the Loita Hills and the Athi River area (where it intergrades with *A. c. rothschildi* (see below)). Birds in the central Kenya Rift Valley from Gilgil to Nakuru may also belong here, as could birds reported from Lake Jipe, none of which have been collected or documented by photographs.

A. c. sharpei Hartert (n = three specimens and nine birds in field photographs). **Appearance**: a less well marked but still recognizable form that intergrades with the previous taxon where the two of them meet along the southern edges of Serengeti NP (see below). It differs from *sylviella* in its paler **tawny-orange mid- and lower underparts** (vs rusty-clay) and **with clear contrast from tawny breast to pale greyish-buff throat, cheeks and forehead,** these latter areas sometimes taking on a frosty appearance (Fig. 3D-F, Fig. 4E-H). **The upperparts, meanwhile, are paler grey and lack the olive-brown wash of *sylviella*.** A minor cline in underpart tone appears to exist from west to east, birds in the former regions (Usambiro–Tabora) being marginally richer than the latter (Ruaha NP–Iringa). Wing: 54–59 mm. **Habitat**: primarily in semi-arid ***Acacia*-dominated bushy woodlands** (notably ***A. albida*** and ***A. gerardii***) from 1100 to 1700 m in areas with approximately 600 to 1100 mm of annual rainfall. Unlike the previous taxon, however, *sharpei* also inhabits mixed semi-deciduous and *Brachystegia* woodlands, and in some regions, such as the Iringa-Dabaga area, woodland with almost no *Acacia*, may be used. **Range**: endemic to Tanzania from Usambiro (type locality), Maswa GR and the southern Serengeti NP south to the Tabora region and southeast from there to Rungwa GR, Ruaha NP and Iringa District.

A. c. rothschildi Neumann: (n = four specimens and 12 birds in field photographs). **Appearance**: a very distinctive form marked by the absence of any rusty or tawny tones to the **underparts which are a smooth cream-buff**, appearing pale yellow under soft light. Unlike the previous two forms, **the cheeks and forehead are a richer colour than the underparts**; a dull golden-beeswax tone (Fig. 3G-H, Fig. 4I-L). **The upperparts are a paler and more lavender-grey than in *sylviella*** and not dissimilar to the upperparts of *sharpei*. Wing: 51.5 mm. **Habitat**: favours semi-humid **mixed *Acacia* and broadleaf woodland in hilly terrain** (notably ***A. mellifera*** *and* ***Erythrina abyssinica***) from 1000 to 1800 m in areas with approximately 500 to 1100 mm of annual rainfall. **Range**: near-endemic to central-east Kenya from Thika, Embu and Kitui Districts south to Athi River, Machakos, Kajiado, Simba (type locality) and the Chyulu Hills, towards disjunct populations in southern Kenya near Oloitokitok, and [rarely] northern Tanzania in Loliondo District. Pale and rather nondescript birds reported from the Taita Hills, area below the known altitudinal range of *rothschildi*, may be that form, or may possibly be referable to *A. c. taruensis* (= *A. c. robertsi*).

A. c. sylviella* x *sharpei intergrade (n = no specimens and three birds in field photographs). **Appearance**: variably appearing birds show a combination of the characteristics of the two forms. Some birds show rich clay-toned underparts (including throat, cheeks and forehead) as in *sylviella*, but with paler silvery grey upperparts as in *sharpei* (Fig. 5A), while other birds show rich clay-toned underparts as in *sylviella* but with contrastingly paler, light buffy-grey cheeks and forehead as in *sharpei* (Fig. 5B) **Habitat**: primarily found in mixed *Acacia* woodland at 1400–1700 m. **Range**: birds occurring from the northern end of the Lake Eyasi and Olduvai Gorge area west through the southern parts of the Serengeti NP to the Grumeti River area appear to show the most variation.

A. c. sylviella* x *rothschildi intergrade (n = one specimen and one bird in field photographs). **Appearance**: birds show warmer buff underparts approaching those of *sylviella* (with some tawny tones) than the typical pale cream tones of *rothschildi* but with the cheeks and forehead concolorous with the lower underparts unlike the contrastingly richer tones of these parts in *rothschildi* (Fig. 6). **Habitat**: found in the drier parts of the range of *rothschildi*, where inhabits riparian *Acacia* woodlands at 1400–1500 m. **Range**: Athi River to Machakos, in east-central Kenya.

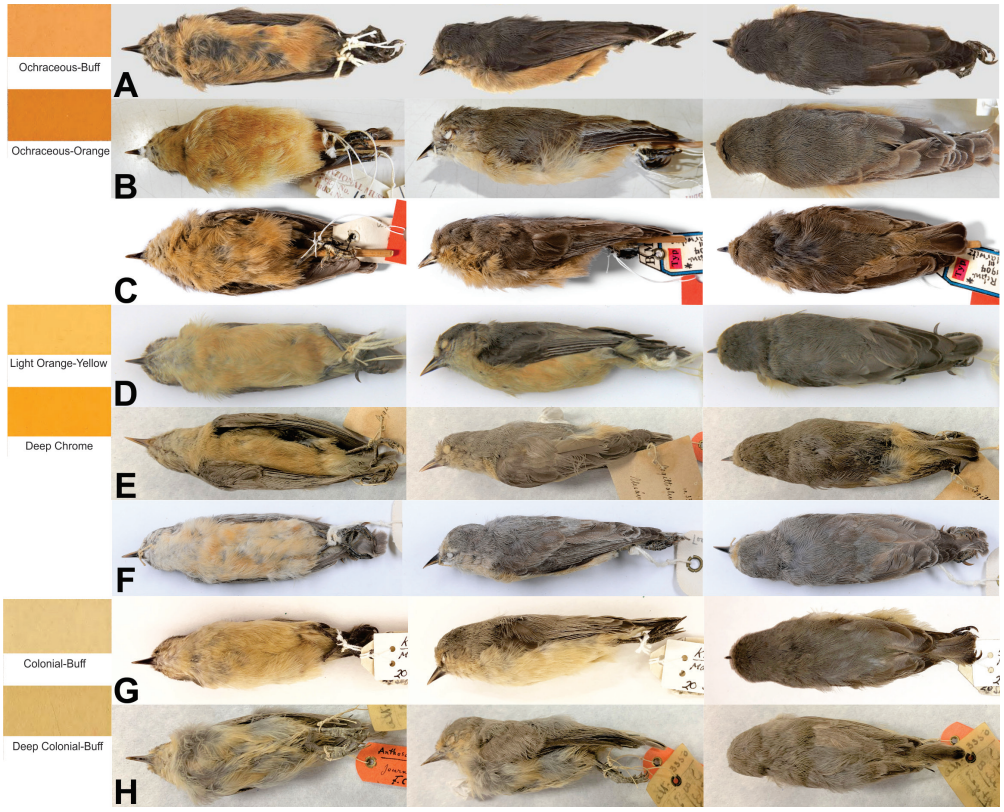

Figure 3. Comparative specimen material of *Anthoscopus caroli* representing the three taxa of the Buff-bellied Penduline Tit grouping: *A. c. sylviella* from Dodoma (A), the Loita Hills (B) and Malangali (C; holotype) in Tanzania and Kenya, *A. c. sharpei* from Tabora (D), Usambiro (E; holotype) and Iringa District (F) in Tanzania, and *A. c. rothschildi* from Machakos (G), and Simba (H; holotype) in Kenya. Comparative colour inserts (Ridway 1912) show the range of underpart tones for each taxon.

Figure 4. Comparative field photographs of *Anthoscopus caroli* representing the three taxa of the Buff-bellied Penduline Tit grouping: *A. c. sylviella* from Ruaha NP at Jongomero (A; R. Glenn), the Yaida Valley (B; D. Peterson), Serengeti NP (C; J. Mittermeier) and Masai Mara GR (D; A. Scott-Kennedy), *A. c. sharpei* from Iringa (E; T. Gwilliams), Rungwa GR (F; T. Chansac), Serengeti NP (G; G. Douglas) and Maswa GR (H; P. Oliver), and *A. c. rothschildi* from Athi River (I; B. Finch), Thika (J; E. Wolfer), Kajiado (K; P. Wairasho) and Machakos (L; J. Kashangaki). Comparative colour inserts (Ridway 1912) show the range of underpart tones for each taxon.

Figure 5. Field photographs of presumed intergrade *Anthscopus caroli sylviella x sharpei* from Olduvai Gorge (A; C. Artuso) and Serengeti NP (B; G. Johnson) in Tanzania.

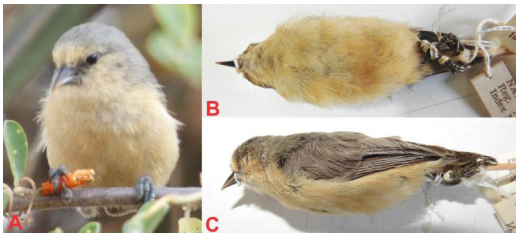

Figure 6. Specimen photographs of presumed intergrade *Anthoscopus c. sylviella x rothschildi* from Athi River (A; J. Linner) and Machakos (B-C) in Kenya.

Atypical birds

We also draw attention here to a bird photographed in the Chyulu Hills, Kenya (Fig. 7), which appears slightly different from typical *A. c. rothschildi* that might be expected to occur here. The image shows a small bird with a rich buff forehead patch, as in *rothschildi*, but the cream-buff of the underparts is more centrally restricted with the

flanks, and the undertail coverts snowy-white. These features fit no described taxon precisely and this individual could be an example of an aberrant *A. c. rothschildi*. We highlight it here, however, as several other unique taxa are known to have evolved on the Chyulu Hills, parts of which are still comparatively poorly known.

Figure 7. Photograph of *Anthoscopus caroli* taken in the Chyulu Hills, KE (S. Dolrenry), showing a bird which is most similar to the form *rothschildi,* but which differs from typical individuals in its two-toned underparts, resulting from the flanks and undertail coverts being snowy white and not buff.

Discussion

Taxa sylviella and sharpei

A review of field photographs and photographs of specimen material shows that *sylviella* and *sharpei* each comprise recognizable taxa. However, contrary to the prevailing sources (e.g., Harrap & Quinn 1995, Fry *et al.* 2000) that comment on the differences between *sylviella* and *sharpei*, it is *sylviella*, not *sharpei,* that shows darker rusty-clay underparts, which in the latter are paler and more tawny (more yellow, less red pigment). Furthermore, unlike the more silvery-grey upperparts of *sharpei* (and *rothschildi*), *sylviella* also shows an olive-brown cast to its grey upperparts resulting in a darker appearance than *sharpei*. Descriptions by Mackworth-Praed & Grant (1960) also state that the forehead of *sylviella* is pale buff vs a richer tawny in *sharpei*, when in fact, the opposite is the case.

These contradictions are difficult to explain but it seems possible that they may be related to the incorrect referral of specimens from Iringa to *sylviella* by Lynes (1934), who compared his material from Iringa with only the type specimen of *sylviella* but not with that of *sharpei*. Given the buff underparts of both forms, a referral to *sylviella* without review of the type material of *sharpei* would be quite understandable. Moreover, the debate at the time as to whether *sharpei* was actually a recognizable subspecies (see Introduction) may have prompted Lynes to refer Iringa birds to *sylviella* in the absence of any other widely accepted "buff-bellied" form. While Lynes's four specimens could not be traced for this study, our specimen images and field photographs from Iringa District show a bird with pale underpart tones and silvery-grey upperparts matching most closely with the type specimen of *sharpei* from Usambiro, the *sharpei* specimen from Tabora, as well as that from the Dabaga area immediately east of Iringa. The distribution of *sharpei* has hitherto not been known to extend southeast from Usambiro beyond Tabora, while the finding that *sharpei* and *sylviella* occur within close proximity of each other in the Ruaha NP–Iringa area of south-central Tanzania is also novel.

Meanwhile, it seems possible that on examining birds with richly coloured underparts from southwest Kenya, Mackworth-Praed & Grant (1960) incorrectly treated these as *sharpei* on the basis of closer proximity to the type locality of that taxon at Usambiro, and on the basis of Lynes's specimens with pale underparts from Iringa which had been incorrectly referred to *sylviella*. In fact, birds in Iringa resemble *sharpei* more closely despite some proximity to "Malangali in Usafua" (type locality of *sylviella*), while birds in southwest Kenya (and most of the Serengeti NP) resemble *sylviella* more closely, despite their proximity to Usambiro (type locality of *sharpei*).

Taxon rothschildi

Our study also confirms the presence of a third distinct form of the Buff-bellied Penduline Tit group of *A. caroli* in East Africa, in addition to the subspecies *sylviella* and *sharpei*, currently recognized (Dickinson & Christidis 2014, Clements *et al.* 2019, Gill & Donsker 2020). Taxon *rothschildi* is no less distinctive than *sylviella* or *sharpei* and should be recognized as the form occurring east of the Rift Valley in Kenya. The reasons for White's (1963) decision to synonymize *rothschildi* with *sylviella* are unclear. However, the misconception that birds east and west of the Rift Valley in Tanzania comprised paler *sylviella* and richer *sharpei* respectively (see above), may have clouded the situation in Kenya. Such a misunderstanding, that east of the Rift Valley in Tanzania the form *sylviella* comprised a paler version of *sharpei* to the west of the Rift Valley, may simply have been applied across the same geographic break in Kenya where *rothschildi* to the east of the Rift Valley is paler than *sylviella* to the west of the Rift Valley. Hypothetically, and in the possible absence of adequate specimen material, this could have led, incorrectly, to the synonymy of *rothschildi* with *sylviella* by White (1963).

Therefore, the progressive discrepancies in identification criteria in literature accounts appear to be possibly based on misconceptions that, firstly, birds in Iringa represented *sylviella* (rather than *sharpei*), secondly, that birds in southwest Kenya represented *sharpei (*rather than *sylviella*), and lastly, that birds in eastern Kenya represented *sylviella* (rather than *rothschildi*). Our detailed review presented here, disputes all of these previously understood literature accounts. Both specimen evidence and field photographs show that *rothschildi* differs from *sylviella* to a considerable degree, and that *sharpei* shows an underpart tone somewhat intermediate between the two.

Intergrades and atypical birds

The forms *sylviella* and *sharpei* taxa appear to intergrade in the southern parts of the Serengeti NP, where gaps in the Rift Valley in the vicinity of Lake Eyasi and Ngorongoro Crater have permitted a westerly intrusion of *sylviella* into north-central Tanzania and southeast Kenya, both areas to the west of the Rift Valley. To the south of here, however, where distance between the populations is maintained by the high and largely unsuitable woodlands of the Mbulu Highlands, the two taxa assume distinct appearances as is shown by the type material and additional specimens. It is unclear whether the two forms meet anywhere in eastern parts of Ruaha NP to the Iringa area (designated by a "?" in Figure 2) but it seems possible that subtle differences in ecological preferences (e.g., altitude and/or rainfall regimes) may keep them separated.

Much as *sylviella* intergrades with *sharpei* across a portion of the southern Serengeti, it also appears to intergrade with *rothschildi* across a small area of central-east Kenya. This is permitted by way of only limited barriers to the movement of birds representative of each form in intervening areas that would otherwise separate distributions. *A. c. rothschildi*, meanwhile, is separated at the southern end of its range from *sylviella* at its northern extremity, by an arid corridor extending westwards from the Somali–Masai steppe of eastern Kenya and Tanzania to Lake Natron, which is occupied by Mouse-coloured Penduline Tit *A. musculus*.

Lastly, birds in the Chyulu Hills may merit further study. The few photographs reviewed from this area reveal a form that we treat here as *rothschildi* but with some reservations (Fig. 7). A distinct two-toned quality to the underparts is inconsistent with *rothschildi* and this range of hills is known for supporting several divergent forms, some regarded as separate subspecies (e.g., see Gill *et al.* 2020).

Conclusions

Our study presented here has clarified the field characters and corrected a number of misconceptions and oversights regarding the taxonomy of the Buff-bellied Penduline Tit subspecies of *A. caroli* in East Africa, and we propose a revised treatment for this complex following an integrated assessment of specimen and field evidence. We clarify the field characters for *sharpei* and *sylviella* and confirm each as recognizable taxa that, while apparently remaining separated in the southern reaches of their ranges, intergrade where they meet in the north of it in the vicinity of the southern Serengeti NP. Similarly, we also clarify field characters for, and recognize *rothschildi* of eastern Kenya, where birds have been incorrectly treated as *sylviella* for more than half a century. We document a narrow zone of intergrading with *sylviella* near Nairobi, for these otherwise distinct forms. Lastly, we highlight atypical birds in the Chyulu Hills suggesting an avenue for further study. Further work on this complex should focus on the genetic relatedness between these three taxa, and the extent to which they differ in all respects from other forms within the Grey Penduline Tit.

Acknowledgements

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Appendix A. Field and Specimen Material

Taxon	Location	Media	Photographer	This paper	Reference
A. c. sylviella	Dodoma (Kikuyo), TZ	specimen	NA	Fig. 3A	NHMD #075650, Fjeldså 2015
A. c. sylviella	Loita Hills, KE	specimen	Sidney Shema	Fig. 3B	NMK #18493/18226
A. c. sylviella	Kendu Bay, KE	specimen	Sean Lyon		FMNH #199060
A. c. sylviella	Kendu Bay, KE	specimen	Sean Lyon		FMNH #199059
A. c. sylviella (holotype)	Malangali, TZ	specimen	Sylke Frahnert	Fig. 3C	ZMB #48/68
A. c. sharpei	Tabora (Kazima), TZ	specimen	Robert Faucett	Fig. 3D	UWBM #95720 (MBM 5909)
A. c. sharpei (holotype)	Usambiro, TZ	specimen	Paul Sweet	Fig. 3E	AMNH #683337
A. c. sharpei	Dabaga, Iringa Dist., TZ	specimen	Sean Lyon	Fig. 3F	FMNH #216940
A. c. rothschildi	Machakos, KE	specimen	Brett Benz	Fig. 3G	UMMZ #208864
A. c. rothschildi	Machakos, KE	specimen	Sidney Shema		NMK #18490/13758
A. c. rothschildi	Athi River, KE	specimen	Sidney Shema		NMK #18498/13755
A. c. rothschildi (holotype)	Simba, KE	specimen	Paul Sweet	Fig. 3H	AMNH #683335
A. c. sylviella x rothschildi	Machakos, KE	specimen	Sidney Shema	Fig. 6B-C	NMK #18488/13757
A. c. sylviella	Ruaha NP (Jongomero), TZ	field image	Rob Glenn	Fig. 4A	Pers. comm.
A. c. sylviella	Tarangire NP, TZ	field image	Neil Bachmann		www.flickr.com
A. c. sylviella	Tarangire NP, TZ	field image	Lara Tranter		www.tanzaniabirds.net
A. c. sylviella	Tarangire NP, TZ	field image	Markus Lilje		iNat #81332093
A. c. sylviella	Yaida Valley, TZ	field image	Daudi Peterson	Fig. 4B	Pers. comm.
A. c. sylviella	Yaida Valley, TZ	field image	Daudi Peterson		Pers. comm.
A. c. sylviella	Loita Hills, KE	field image	Nik Borrow		Pers. comm.
A. c. sylviella	Maasai Mara GR, KE	field image	Adam Scott-Kennedy	Fig. 4D	Pers. comm.
A. c. sylviella	Maasai Mara GR, KE	field image	Stratton Hatfield		ML #160466171
A. c. sylviella	Maasai Mara GR, KE	field image	Stratton Hatfield		Pers. comm.
A. c. sylviella	Maasai Mara GR, KE	field image	Jenny Bowman		ML #210904891
A. c. sylviella	Serengeti NP, TZ	field image	Dan Borman		ML #250765021
A. c. sylviella	Serengeti NP, TZ	field image	Bradley Hacker		ML #302702841
A. c. sylviella	Serengeti NP (Singita), TZ	field image	Gary Douglas		ML # 253671341

Taxon	Location	Media	Photographer	This paper	Reference
A. c. sylviella	Serengeti NP (Singita), TZ	field image	John Mittermeier	Fig. 4C	ML #246824341
A. c. sylviella	Serengeti NP (Seronera), TZ	field image	Markus Lilje		iNat #6484936
A. c. sylviella (juvenile)	Serengeti NP (Mbalagati), TZ	field image	Brian Lawrence		www.flickr.com
A. c. sylviella (juvenile)	Serengeti NP (Singita), TZ	field image	Gary Douglas		ML #168291091
A. c. sylviella x sharpei	Olduvai Gorge, TZ	field image	Christian Artuso	Fig. 5A	iNat #33286813
A. c. sylviella x sharpei	Serengeti NP, TZ	field image	Sheau Torng Lim		www.flickr.com
A. c. sylviella x sharpei	Serengeti NP, TZ	field image	Greg Johnson	Fig. 5B	www.flickr.com
A. c. sharpei	Iringa, TZ	field image	Tommy Gwilliams	Fig. 4E	Pers. comm.
A. c. sharpei	Nduli, Iringa, TZ	field image	Neil Baker		NA
A. c. sharpei	Rungwa GR, TZ	field image	Thibaut Chansac	Fig. 4F	NA
A. c. sharpei	Rungwa GR, TZ	field image	Thibaut Chansac		NA
A. c. sharpei	Rungwa GR, TZ	field image	Thibaut Chansac		NA
A. c. sharpei	Maswa GR, TZ	field image	Paul Oliver		Pers. comm.
A. c. sharpei	Maswa GR, TZ	field image	Paul Oliver	Fig. 4H	Pers. comm.
A. c. sharpei	Serengeti NP, TZ	field image	Gary Douglas	Fig. 4G	ML # 351513171
A. c. sharpei	Serengeti NP, TZ	field image	Alastair Kilpin		Pers. comm.
A. c. rothschildi	Machakos (Lukenya), KE	field image	Peter Steward		Pers. comm.
A. c. rothschildi	Machakos (Lukenya), KE	field image	Brian Finch	Fig. 4I	NA
A. c. rothschildi	Machakos (Maanzoni), KE	field image	Mark Bullough		Pers. comm.
A. c. rothschildi	Machakos (Mutetheni), KE	field image	James Kashangaki	Fig. 4L	ML #206082611
A. c. rothschildi	Nairobi NP, KE	field image	Brian Finch		NA
A. c. rothschildi	Thika, KE	field image	Elvira Wolfer	Fig. 4J	Pers. comm.
A. c. rothschildi	Thika, KE	field image	Elvira Wolfer		Pers. comm.
A. c. rothschildi	Kajiado, KE	field image	Peter Wairasho	Fig. 4K	Pers. comm.
A. c. rothschildi	Kajiado, KE	field image	Peter Wairasho		Pers. comm.
A. c. rothschildi	Kajiado, KE	field image	Martin Mwangi		Pers. comm.
A. c. rothschildi	Chyulu Hills, KE	field image	Stephanie Dolrenry	Fig. 7	ML #114838911 & #114838501
A. c. rothschildi (juvenile)	Thika, KE	field image	James Bradley		ML #48817121
A. c. sylviella x rothschildi	Athi River, KE	field image	Jan Linner	Fig. 6; A	ML #48387551 & #48387571

Appendix B. Gazetteer

Locations in Kenya	Latitude	Longitude	Locations in Tanzania	Latitude	Longitude
Athi River	1°26'6"S	36°59'48"E	Dabaga (foothills)	8°2'19"S	35°50'56"E
Chyulu Hills	2°34'4"S	37°49'12"E	Iringa	7°47'11"S	35°42'14"E
Embu	0°32'53"S	37°27'36"E	Kikuyo, Dodoma	5°52'42"S	35°4'18"E
Fort Hall (Muranga)	0°43'52"S	37°9'28"E	Longido	2°43'35"S	36°42'57"E
Kajiado	1°51'16"S	36°47'13"E	Malangali in Usafua	8°25'00"S	33°50'00"E
Kendu Bay	0°22'29"S	34°39'3"E	Maswa GR	3°31'26"S	34°40'53"E
Kitui District	1°21'14"S	38°1'26"E	Nduli, Iringa	7°38'5"S	35°45'12"E
Lake Elementaita	0°24'33"S	36°12'41"E	Olduvai Gorge	2°59'50"S	35°20'28"E
Lake Nakuru NP	0°25'36"S	36°6'13"E	Ruaha NP	7°41'48"S	34°57'10"E
Lambwe Valley	0°38'33"S	34°16'13"E	Rungwa GR	6°50'32"S	34°16'38"E
Loita Hills	1°22'8"S	35°44'14"E	Serengeti NP (Seronera)	2°26'34"S	34°48'18"E
Maasai Mara GR	1°28'45"S	35°14'14"E	Serengeti NP (Singita)	2°4'43"S	34°29'28"E
Machakos	1°31'42"S	37°16'23"E	Serengeti NP (Sopa)	2°35'46"S	34°40'41"E
Machakos (Lukenya)	1°29'3"S	37°4'45"E	Tabora (Kazima)	4°59'49"S	32°54'15"E
Machakos (Maanzoni)	1°29'25"S	37°7'49"E	Tarangire NP	3°55'47"S	36°1'25"E
Machakos (Mutetheni)	1°30'5"S	37°31'0"E	Usambiro	3°05'00"S	32°40'00"E
Simba	2°9'26"S	37°35'26"E	Yaida Valley	4°0'32"S	34°59'25"E
Taita Hills	3°25'52"S	38°24'50"E			
Thika	1°1'44"S	37°4'18"E			
Voi	3°24'15"S	38°33'12"E			