Speciation in the Karamoja Apalis Apalis karamojae

Authors: Boesman, Peter, and Collar, N. J.

Source: Bulletin of the British Ornithologists' Club, 143(4) : 576-586

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v143i4.2023.a11

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

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

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

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

Downloaded From: https://complete.bioone.org/journals/Bulletin-of-the-British-Ornithologists'-Club on 07 Jul 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Speciation in the Karamoja Apalis *Apalis karamojae*

by Peter Boesman & N. J. Collar

Received 3 July 2023; revised 23 August 2023; published 4 December 2023
http://zoobank.org/urn:lsid:zoobank.org:pub:282FFF60-EA8E-43A6-BA67-078576C7198F

Summary.—The Karamoja Apalis *Apalis karamojae*, a threatened species (IUCN Vulnerable), consists of two subspecies, the nominate in Uganda and *stronachi* in Tanzania plus south-west Kenya, the latter distinguished by being slightly darker with more extensive grey on the underparts. Recent evidence, however, indicates that the two taxa are highly divergent in voice. Analysis of recordings of their duets confirms this: the nominate sings very rapid phrases of short simple notes whereas *stronachi* uses musical slurred whistles, very different in note length and strongly different in max. frequency; moreover, in two independent tests nominate birds failed to react to *stronachi* songs, indicating reproductive barriers between them. Re-examination of specimen material and a review of online photographs confirm the greater amount of grey on the underparts of *stronachi*. Taken together these differences indicate that *stronachi* merits species rank. The two taxa are specialists of mature whistling-thorn *Vachellia drepanolobium*, which is cut for fuelwood and to open up pasture, so that their long-term survival is likely to depend on the integrity of protected areas.

The Karamoja Apalis *Apalis karamojae* is a rather rare cisticoline warbler known from relatively few semi-arid localities in north-east Uganda (nominate subspecies), north-central Tanzania and adjacent south-west Kenya (subspecies *stronachi*), with an IUCN Red List status of Vulnerable (Ryan 2006, Shaw & Mungaya 2006, BirdLife International 2023). Research has progressively shown that the species' long-known association with whistling-thorn acacia *Vachellia drepanolobium* (Collar & Stuart 1985, Urban *et al*. 1997, Stevenson & Fanshawe 2002) reflects a strong dependency (Shaw & Mungaya 2006, Shaw *et al*. 2010, Salmah & Onongo 2023), and only its presence in patches of the similar *V. seyal* prevents this dependency from being total (P. Shaw *in litt*. 2023). Indeed, the birds' white wing line and outer rectrices appear to mimic the long white spines of whistling-thorn, whilst their grey upperparts blend well with the colour of the plant's galls (P. Shaw & B. W. Finch *in litt*. 2023), suggesting a highly specific adaptation in plumage. However, whistling-thorn is widespread in eastern Africa, across seven countries, so the question arises over what causes the bird to be so much more restricted in range than the plant (Shaw & Mungaya 2006). At one stage it was speculated that 'the very extensive clearing and cultivation in recent times round the shores of Lake Victoria' might be responsible for producing the 'extraordinary distribution' of the species' Ugandan and Tanzanian populations (Hall & Moreau 1962, Turner 1977), but this suggestion became less plausible once the Tanzanian birds were recognised as taxonomically distinct (Collar & Stuart 1985, Stuart & Collar 1985).

Against this, it has to be said that the characters that distinguish southern *stronachi* from the northern nominate are few in number and weak in strength, so that it could be argued that the differences involved might simply reflect a cline in which the intervening populations have been extirpated (plausibly due to habitat conversion, as suggested above). Stuart & Collar (1985) diagnosed *stronachi* as 'darker brownish-grey on the mantle, back, rump and uppertail-coverts', the male being 'mottled grey against a very pale creamy-

ISSN-2513-9894 (Online)

white background' on the underparts, very pale grey on the throat but 'much darker on the breast and flanks and paler again on the belly', whereas the male nominate has 'creamy-white underparts' but grey flanks. Female *stronachi* has 'creamy-white underparts with a slight but variable suffusion of grey', the female nominate 'a white underside and only a slight creamy suffusion'. Males of both taxa are consistently darker than their counterpart females, such that *stronachi* females are only slightly darker than nominate males. (Somehow from this female *stronachi* emerged as 'paler than nominate' in Urban *et al*. 1997.) These distinctions were made using a tiny sample of specimens (one male, one female from Uganda, one male from Tanzania in the Natural History Museum, Tring, UK [NHMUK], one male from Uganda, three females from Tanzania in the National Museums of Kenya, Nairobi [NMK])—these being all the material available in museums except one from Uganda in the Field Museum of Natural History, Chicago (*fide* VertNet)—and must be subject to caveats about individual variation. Nevertheless, basic mensural data suggested that *stronachi* is a somewhat larger phenotype, which was supported by measurements of 17 live birds from Tanzania (Shaw *et al*. 2005).

For the entirety of the 20th century the voice of Karamoja Apalis remained undocumented (e.g. Urban *et al*. 1997). However, the pioneer of research into the species in Tanzania, Philip Shaw, established that the song there, atypically for an *Apalis*, consists of 'a series of musical, fluid phrases, each comprising 2–5 (commonly four) notes… [in] a rapid, well-synchronised, antiphonal duet… [at] 2.7–3.2 notes per second' (Shaw *et al*. 2005). He further found that 'most pairs (though not individuals) were highly responsive to taped songs, approaching closely from distances of 50 to 100 m, and singing persistently' (Shaw & Mungaya 2006). Indeed, it was by speculatively broadcasting the song in an area dominated by whistling-thorn near the Maasai Mara National Reserve that Shaw obtained the first record of the species for Kenya (Boy 2004, Shaw 2007). Consequently when in 2011 colleagues in Uganda sought to search an area of their country for the species they took a copy of Shaw's recordings to facilitate their work. But it did not: on all three occasions when the opportunity arose to play the song to birds already detected 'there was no response whatsoever' (Opige & Skeen undated, Nalwanga *et al*. 2016). More intriguingly, by chance the survey team managed to hear a snatch of song from a pair, and found it 'quite different to that of the Tanzanian birds, being sharper and faster' (Opige & Skeen undated, Nalwanga *et al*. 2016).

The circumstance in which the song of one population sounds 'quite different' ('quite' taken here to mean 'very', not 'somewhat') from that of another, and in which birds from one population do not respond to the song of birds from the other, intimates a level of taxonomic differentiation greater than is typical of subspecies. We therefore sought to assemble and review what material we could, focusing naturally on the acoustic evidence.

Methods

Acoustic evidence.—During a visit to Pian-Upe Wildlife Reserve, Uganda, in June 2022, PB made several sound recordings of at least three duetting pairs of *A. k. karamojae*, finding it easy to attract singers by playing back their songs initially recorded at a considerable distance (and noting a complete absence of response to the song of *A. k. stronachi*). These were seemingly the first recordings of the nominate to be made publicly available, on both Macaulay Library (ML; https://www.macaulaylibrary.org/) and Xeno-canto (XC; https://www.xeno-canto.org) databases, although more recently D. Muhumuza has posted a recording (ML 509203471) made in the same general area in December 2022. However, a reasonable sample of online recordings of subspecies *stronachi* is available in both ML and

ISSN-2513-9894 (Online)

XC (albeit with considerable overlap), in addition to the information in Shaw *et al*. (2005). Recordings analysed of both taxa are indicated in Appendix 1.

The very different songs of the taxa are immediately obvious to the ear, but to quantify vocal differences we defined and measured the following sound parameters: max. note length, pace of the notes sung by a single individual, highest frequency in a song phrase, and min. and max. frequency of the notes in a song phrase. We made sonograms using CoolEdit Pro (Blackman-Harris window at 1,024 band resolution for the sharpest image), and measured sound parameters manually using visual rulers for time and frequency on screen.

Recordings of call notes proved to be too scarce to attempt to quantify any differences.

Morphological evidence.—In the paper establishing *A. k. stronachi* (Stuart & Collar 1985) Simon Stuart measured and examined all the specimens used in the diagnosis, whereas NJC inspected only the material in NHMUK. For the present study NJC could only re-examine the NHMUK material (male holotype of *stronachi*, male and female *karamojae*), but requested photographs of the four specimens (male *karamojae*, three female *stronachi*) in NMK. However, a search was also conducted online for photographs of the two taxa, using only the first of any taken on the same day by the same photographer, resulting in a sample of seven reasonably sharp digital images of *karamojae* and 15 of *stronachi* (Appendix 2). These were assessed informally and independently by PB & NJC.

Taxonomic criteria.—To help decide taxonomic rank under the Biological Species Concept, we employed the system of scoring in Tobias *et al*. (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g. a distinct hue rather than different colour) 2, and minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, which cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two non-covarying biometric characters (both these and vocal characters assessed for effect size using Cohen's *d* where 0.2–1.9 is minor, 2.0–4.9 medium, 5.0–9.9 major and 10+ exceptional) and one behavioural or ecological character (allowed 1) may be counted. Effect sizes were obtained via the online calculator at https://lbecker.uccs.edu/.

Results

Acoustic evidence.—Pairs of both *A. k. karamojae* and *A. k. stronachi* typically sing a synchronised antiphonal duet. In nominate *karamojae* each bird sings a phrase that very rapidly repeats 1–3 very short, simple, unslurred notes, usually visible on a sonogram as straight, steeply ascending or descending lines (Fig. 1). Often, one bird would utter only whip-like ascending note types and the other respond with descending note types alone, either perfectly synchronised or at a different pace, resulting in, e.g, a loud urgent rhythmic fast *chip/wip-chip/wip-chip/wip-chip/wip*… or cyclical *WIbidi-WIbidi-WIbidi-WIbidi*… sometimes breaking into a rapid bubbling-piping reminiscent of an excited Eurasian Oystercatcher *Haematopus ostralegus*. By contrast, in *stronachi* each bird typically whistles a relatively relaxed phrase of two musical slurred notes repeated many times, with one individual singing A C A C and the other B D B D, thereby resulting in a typical structure ABCDABCD (Fig. 2). Occasionally, only a single whistle is repeated by each bird. During a song phrase, a bird may change note type, which may induce the mate to change notes as well, e.g., *piiuu-wíid-yuwíid-yuwíid-yuwíid… dyuuwíid-dyuuwíid piiuu… yuwíid-yuwíid*, etc., the result as melodious as in an accomplished singer like Oriole Warbler *Hypergerus atriceps*. In some cases, the simple structure ABCD is less evident on a sonogram, for example

ISSN-2513-9894 (Online)

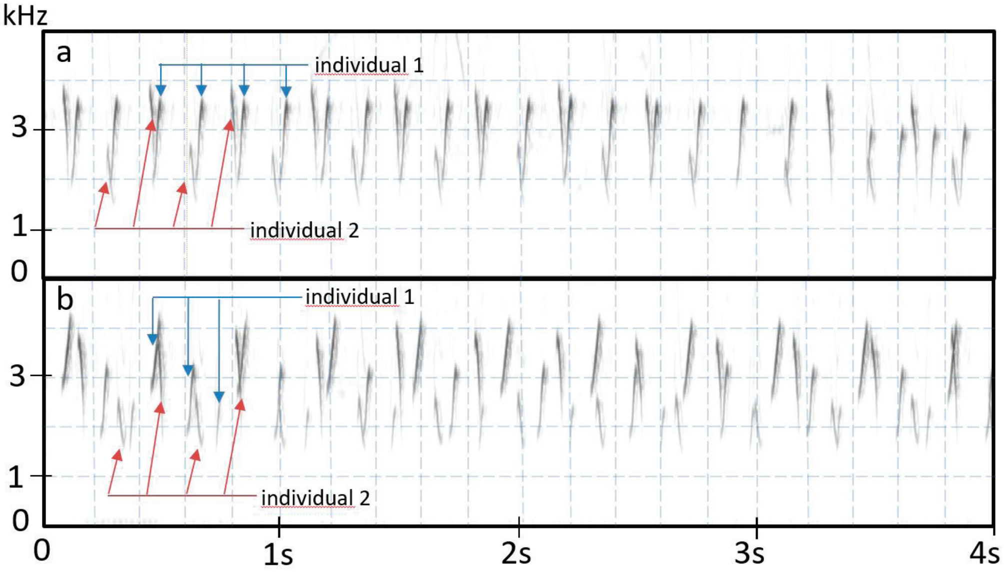

Figure 1. Sonograms of duets of Karamoja Apalis *Apalis k. karamojae*. Two different fragments of XC 739395, Uganda, P. Boesman. **a**: one bird gives a single ascending note and the other gives two different descending notes in perfect synchrony; **b**: one bird repeats three different descending notes while the other gives two ascending notes, with a slight difference in pace.

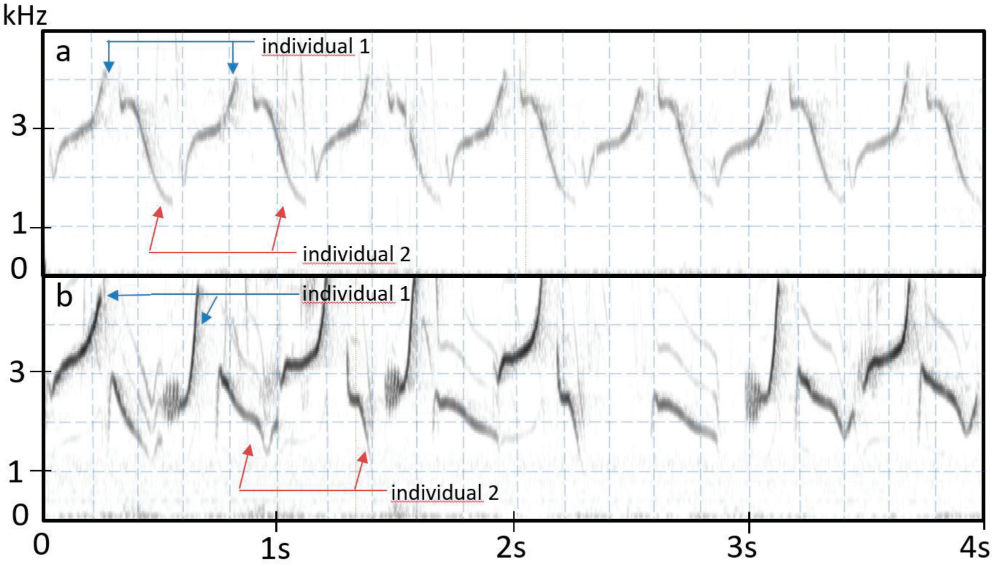

Figure 2. Sonograms of duets of Karamoja Apalis *Apalis karamojae stronachi*. **a**: ML 332837061, Tanzania, C. Leven. One bird gives a single upslurred note and the other a descending note in perfect synchrony; **b**: XC 146332, Tanzania, C. Leven. One bird gives two different ascending notes, the other utters two complex descending ones, with frequent switches in note type.

when a bird loses synchrony for a while, when a change in note type is not immediately picked up by the mate, or when a third bird (possibly an offspring) joins in. Notes can be either underslurred, overslurred, ascending or descending, or may possess a slightly more complex modulation.

ISSN-2513-9894
(Online)

Figure 3. Three Karamoja Apalis *Apalis karamojae* in the Natural History Museum, Tring, left and centre *A. k. karamojae* (female NHMUK 1976.9.33 left, male NHMUK 1933.2.6.18 centre), right *A. k. stronachi* (holotype, male NHMUK 1962.10.8) (N. J. Collar, © Trustees of the Natural History Museum, London)

Figure 4. Four Karamoja Apalis *Apalis karamojae* in National Museums of Kenya, Nairobi, left *A. k. karamojae* (male 12907), other three *A. k. stronachi* (female NMK 12904, female NMK 12906, female NMK 12905) (© Peter Njoroge)

Figure 5. First photograph in Kenya of *Apalis karamojae stronachi*, Naibor-Mara Camp between Narok and Keekorok, Maasai Mara National Reserve, 4 January 2005 (© Brian Finch)

Morphological evidence.—Photographs of the material from which *stronachi* was described show that it is softly mottled grey on the underparts, rather than plain whitish as in the nominate (Figs. 3–5). This is most obvious in the (male) holotype of *stronachi*, NHMUK 1962.10.8, which is strikingly clouded with mid-grey on the underparts, in contrast to the pure white of the male and female nominate (NHMUK 1933.2.6.18 and 1976.9.33, respectively), although its markings are somewhat patchy and smudgy, not regular (Fig. 3). The NMK material does not show the difference so clearly (these are the specimens responsible for the remark in Stuart & Collar 1985 that *stronachi* females 'are only slightly darker than nominate males'), but it is still apparent that the Ugandan (left-hand) bird is plainer and paler below than the three from Tanzania (Fig. 4). The online photographic sample and first photograph taken in Kenya (Fig. 5) confirm that *stronachi* has pale greyish breast-sides and flanks, sometimes also across the breast, suffused and / or mottled, whereas

TABLE 1
Measurements of four sound parameters in the songs of *Apalis k. karamojae* and *A. k. stronachi*: duration of longest note in a song phrase; max. pace in notes per second of a single individual; highest frequency reached in a song phrase; and total bandwidth (max. minus min. frequency) of a song phrase. Values indicate average ± standard deviation.

	Max. note duration (seconds)	**Max. pace** (notes/second)	**Max. frequency** (Hz)	**Frequency range** (Hz)
A. k. karamojae (*n* = 5)	0.041 ± 0.004	7.0 ± 1.3	4,340 ± 196	3,020 ± 312
A. k. stronachi (*n* = 8)	0.274 ± 0.016	2.0 ± 0.2	5,062 ± 283	3,662 ± 364
Effect size	21	5.5	3	1.9

nominate *karamojae* lacks this feature or shows much less of it, at the breast-side or flank, tucked along the line of the folded wing.

Taxonomic criteria.—Measurement of sound parameters in song phrases (see Table 1) indicates an exceptional difference in note duration (effect size 21 [!], Tobias score 4) and a major difference in pace (effect size 5.5, score 3), with also a medium difference in max. frequency (effect size 3, score 2). Given that note duration and pace are not wholly independent parameters (short notes can be delivered slowly, but long notes cannot be uttered quickly) we set aside pace here and allow scores of 4 for note duration and 2 for max. frequency. A score for the difference in underpart coloration would be 2 based on Fig. 3 but only 1 based on Fig. 4, and we opt cautiously for the latter; moreover, although the holotype of *stronachi* is very slightly darker above than the two birds from Uganda, this might simply reflect individual variation (and in any case judging subtle differences in shades of plumage in online photographs is not wise). In that same tiny sample re-measured at NHMUK we found that while bill and tarsus of the holotype of *stronachi* show little or no difference in length from the two Ugandan birds, the wing (54 mm vs. 48 [male] and 47 [female]) and tail (48 mm vs. 43 [male] and 42 [female]) certainly do. This conforms with the extra evidence in Stuart & Collar (1985), and the online photographs also tend to suggest a longer tail in *stronachi*, but we offer no score for this apparent distinction.

Discussion

Taxonomic conclusion.—The lack of response in nominate birds to playback of *stronachi* (independently observed twice) strongly suggests that their songs serve as species identifiers and thus also reproductive barriers (naturally a reverse test, exposing *stronachi* to nominate song, is desirable, but the one-way barrier is close to conclusive). Furthermore, species which duet for territory defence and pair bonding, assisted by their offspring (which thereby gradually learn perfect duet synchronisation), possess a fairly complex social behaviour that further promotes reproductive isolation. These insights vindicate the scoring of the distinctiveness of *stronachi* in the paragraph above, which totals 7 and thereby qualifies it for species rank. We suggest that this is a conservative characterisation of the differences between *stronachi* and the nominate, for several reasons. First, given that the threshold for an 'exceptional' difference is an effect size of 10, triggering a score of 4, an effect size of 21 would appear so remarkable—we have never encountered a degree of difference remotely as strong in more than a decade of applying the Tobias criteria to closely related taxa—as to merit a higher score still. Second, the evidence certainly points towards a difference in wing and tail length which, when more birds are sampled, will probably yield a score of 1, possibly 2. There is also the claim of a darker shade on the upperparts (see above) which might hold true, and another concerning a difference in call: Nalwanga *et al*. (2016) believed they had detected such a difference in the nominate, without

ISSN-2513-9894 (Online)

stating their evidence, but they mentioned that a pair gave a '*teeeng-teeeng*' double note, 'higher pitched at the beginning', which does not accord with any call mentioned by Shaw *et al*. (2005) for *stronachi*. Moreover, Phil Shaw (*in litt*. 2023), who spent a total of seven weeks in the Wembere Steppe and Serengeti ecosystem, reports that the call of a nominate bird recorded by PB on Xeno-canto (XC739393)—a curt gruff buzz: *hrr*—is 'not one I recognise'.

Despite the relatively low sample sizes in the comparisons between songs (five for the nominate, eight for *stronachi*), the duets produced by the two taxa were consistent within the sample and with (a) the evidence in Shaw *et al*. (2005), who were using their own extensive, independent set of recordings of *stronachi*, and (b) the testimony of Opige & Skeen (undated) and Nalwanga *et al*. (2016) concerning the nominate. Moreover, although the differences in plumage and morphometrics could be argued to represent no more than the ends of an interrupted cline, the difference in song cannot reasonably be considered clinal or dialectal. Dialects in oscine passerines have been documented for many species (Marler & Slabbekoorn 2004) and are typically reflected by subtle changes in adjacent populations which, over longer distances, may cumulatively result in song phrases that sound quite different at the geographical extremes. In the case of Karamoja Apalis, however, the known min. distance between the two taxa is only *c*.350 km, and the difference in song structure and note properties is very abrupt, entirely unlike the circumstances and conditions involved in dialects (or clines).

For several decades, vocal differences among oscine passerines have been used in a multitude of cases to settle the taxonomy of species complexes (Alström & Ranft 2003), based on the assumption that they represent a strong reproductive barrier between closely related species (Remsen 2005). This assumption has been confirmed by extensive playback experiments that prove a strong correlation between the degree of acoustic divergence and the ability of birds to discriminate taxa by their songs (Freeman & Montgomery 2017). Even in the genus *Apalis* several taxa have been accorded species status based largely on vocal evidence (Morel & Chappuis 1992). In the case of cryptic species, vocal divergence has often been the first or sole indirect indicator of genetic divergence, e.g. many species in the genera *Acrocephalus*, *Cisticola*, *Phylloscopus*, *Anthus*, *Sheppardia*, *Certhia* and, perhaps most notably, the *Vidua* indigobirds (Morel & Chappuis 1992, Payne 1982, Martens 2010, van Els & Norambuena 2018). Even in genera composed of species that are morphologically rather distinctive, many cases are known of a few members that are extremely similar except in voice, e.g. Eastern *Phylloscopus orientalis* and Western Bonelli's Warblers *P. bonelli* (Helb *et al*. 1982), Eastern *Sylvia crassirostris* and Western Orphean Warblers *S. hortensis* (Svensson 2012), Little *Bradypterus baboecala* and Highland Rush Warblers *B. centralis* (Boesman 2016a, Dowsett-Lemaire 2022), Choco *Myiothlypis chlorophrys* and Golden-bellied Warblers *M. chrysogaster* (Boesman 2016b), Ethiopian *Psophocichla simensis* and Groundscraper Thrushes *P. litsitsirupa* (Boesman 2016c). Continued treatment of Karamoja Apalis as a single species, thereby rejecting the taxonomic significance of a very different voice, would be wholly inconsistent with the above and indeed with a multitude of recent cases promoting and accepting taxonomic rearrangements on the basis of far less prominent vocal differentiation. We therefore recommend the treatment of *Apalis karamojae stronachi* as a species.

The vernacular name for *A. stronachi* might be Maasai Apalis; but we do not offer this as more than a suggestion. It is not even certain that the species is an apalis. D. Moyer in Shaw *et al*. (2005) considered *stronachi* to resemble a prinia more than an apalis in behaviour and voice, and Shaw *et al*. (2005) themselves thought that the vocal difference of *stronachi* suggested it might better be placed in a different genus. However, the song of the newly restricted monotypic *A. karamojae* (for which the name Karamoja Apalis should surely be retained) is in fact not that different from, e.g., Brown-headed Apalis *A. alticola* or Grey

ISSN-2513-9894 (Online)

Apalis *A. cinerea*. Consequently the notion that *A. karamojae* and *A. stronachi* belong in a different genus from other apalises is perhaps less plausible than the possibility that *stronachi*, under unknown evolutionary pressures, diverged vocally so much that it lost the typical features of the genus. Such vocal anomalies within a genus are not unusual; even in *Apalis* the long trilling whistle of Chestnut-throated Apalis *A. porphyrolaema* stands out as an example.

Genetic analysis will of course help to resolve these uncertainties, and we strongly encourage such a study. This is an interesting case to investigate how long the taxa have been separated, as there is scant information on the time it takes for bird taxa to reach such levels of vocal divergence, or on the drivers of such changes. While the standard taxonomic case in an integrative assessment would seek complementary differences in morphology, voice and genetics, nonetheless there are some species that have long been separated but evolved only minimal vocal differences, e.g. a multitude of species in the genus *Zosterops* (Pearson & Turner 2017), Rote Leaf Warbler *Phylloscopus rotiensis* (Ng *et al*. 2018) and the *Calliope* rubythroats (Liu *et al*. 2019), while few species are known that separated very recently but diverged significantly in voice, as in the special case of brood-parasitic *Vidua* indigobirds (Sefc *et al*. 2005). In the present case, we have to express the view that, even if *A. karamojae* and *A. stronachi* were to be found to be genetically near-identical, we would be reluctant to accept that they could be considered conspecific under the Biological Species Concept, given the strong reproductive barriers that their songs represent.

Conservation prognosis.—Splitting a species necessarily means that the new 'offspring' species have smaller ranges and populations than their 'parent', requiring reassessments of their conservation status. In cases of species already threatened with extinction the need for such assessments is all the more pressing. Here, while not presuming to trespass into the formal process of re-evaluating their Red List status, we briefly review the circumstances of the two 'offspring' species as we judge them to be.

Historical and recent records of Karamoja Apalis *sensu novo* were mapped by Salmah & Onongo (2023). Recent records indicate the species' persistence in Kipedo National Park in far north-east Uganda and 200 km to the south near 'Mount Kamalinga' (Collar & Stuart 1985), i.e. the Kamalinga Hills, extending into Napak District and Bokora Wildlife Reserve, but there is no confirmation of presence at the two other historical sites, Mount Moroto (north-east of Napak near the Kenya border) and Mount Kadam ('Napiananya' or 'Napianyenya', west and north of Pian-Upe Wildlife Reserve). Most importantly, however, recent records also involve 15 new localities south of Mount Kadam, spanning around 100 km from Soroti in the west to just north-east of Mount Elgon in the east, eight of them inside the southern limits of Pian-Upe Wildlife Reserve. These findings are supported by (but omit mention of) a record of one 25 km north of Mbale in 2015 (D. Pomeroy *per* P. Shaw in BirdLife International 2023), i.e. at *c*.01.30°N, 34.18°E, slightly further south than any of the sites in Salmah & Onongo (2023).

All Tanzanian records of the 'Maasai Apalis' up to May 2016 are mapped in the Tanzania Bird Atlas (http://tanzaniabirdatlas.net/maphtm/0820_nmap.htm), and involve 29 localities ('plots'), all positioned between 02°S and 05.25°S and all but two between 33°E and 35°E (the two outliers being further east but the more distant one, in Tarangire National Park, earmarked for deletion for lack of documentation). A record from square 3303A, first reported as Shinyanga in Shaw *et al*. (2010), is labelled as 'a significant range extension' made 'the only time this area has been visited for birding'. The degree to which this record represents an extension in knowledge rather than an expansion of range may not be easy to gauge. However, the rigorous ecological field work that established the species' strong association with whistling-thorn (Shaw & Mungaya 2006) generated a highly

ISSN-2513-9894
(Online)

plausible hypothesis that the apalis expanded its range in Tanzania from the Wembere Steppe northwards into the Serengeti ecosystem and adjacent Maasai Mara in Kenya as a knock-on effect of rinderpest elimination in the 1960s: this enabled a sixfold increase in wildebeest *Connochaetes taurinus* numbers, which caused grass volume and hence grass fires to diminish, which in turn enabled whistling-thorn acacia to expand within grassland areas (Shaw *et al*. 2010).

This body of research showed that the apalis in Tanzania requires the tallest, densest stands of *Vachellia drepanolobium* and is therefore negatively affected by cutting and clearing of such habitat (Shaw *et al*. 2005, 2010, Shaw & Mungaya 2006). A similar ecological constraint in Uganda seems also to affect the apalis, which was recorded in recent surveys only in taller than average whistling-thorn habitat (Salmah & Onongo 2023). The future of the two species therefore appears to depend on the proactive management of extensive tracts of mature whistling-thorn, which (given the increasing human demands for grazing land and fuelwood) seems unlikely to occur in the long term anywhere outside protected areas. On the other hand, the record from Shinyanga in Tanzania and the multiple records extending the southern boundary of the range in Uganda indicate that undiscovered populations of both species are highly likely to exist. A redoubling of research and survey effort in Uganda, Kenya and Tanzania is needed to help clarify the true range of the two species and the measures—including, conceivably, translocation, e.g., to the relatively well-protected but isolated Laikipia (P. Shaw *in litt*. 2023)—most appropriate to their long-term conservation.

Acknowledgements

We warmly thank the recordists and photographers (see Appendix 1 and 2) who posted their material on Macaulay Library and Xeno-canto, and Peter Njoroge (NMK) for taking the photograph in Fig. 4 and permitting its use here. Brian Finch took the photograph in Fig. 5 and he, Phil Shaw and Simon Stuart provided very helpful comments as referees, with Lincoln Fishpool kindly adding others.

References

Alström, P. & Ranft, R. 2003. The use of sounds in avian systematics and the importance of bird sound archives. *Bull. Brit. Orn. Cl*. 123A: 114–135.

BirdLife International (2023) Species factsheet: *Apalis karamojae*. http://datazone.birdlife.org/ (accessed 3 June 2023).

Boesman, P. 2016a. Notes on the vocalizations of Little Rush-warbler (*Bradypterus baboecala*). HBW Alive Ornithological Note 237. *In* del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) *Handbook of the birds of the world Alive*. Lynx Edicions, Barcelona. https://birdsoftheworld.org/bow/ornith-notes/JN100237 (accessed 3 June 2023).

Boesman, P. 2016b. Notes on the vocalizations of Golden-bellied Warbler (*Basileuterus chrysogaster*). HBW Alive Ornithological Note 377. *In* del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) *Handbook of the birds of the world Alive*. Lynx Edicions, Barcelona. https://birdsoftheworld.org/bow/ornith-notes/JN100377 (accessed 3 June 2023).

Boesman, P. 2016c. Notes on the vocalizations of Groundscraper Thrush (*Psophocichla litsitsirupa*). HBW Alive Ornithological Note 303. *In* del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) *Handbook of the birds of the world Alive*. Lynx Edicions, Barcelona. https://birdsoftheworld.org/bow/ornith-notes/JN100303 (accessed 3 June 2023).

Boy, G. 2004. A first record for Kenya. *Swara* 27: 14.

Collar, N. J. & Stuart, S. N. 1985. *Threatened birds of Africa and related islands: the ICBP/IUCN Red Data book*. International Council for Bird Preservation, Cambridge, UK.

Dowsett-Lemaire, F. 2022. A review of the vocalisations of Little and Highland Rush Warblers *Bradypterus baboecala* and *B. centralis*, and a comparison with sympatric White-winged Warbler *B. carpalis*. *Bull. Afr. Bird Cl*. 29: 31–48.

van Els, P. & Norambuena, H. V. 2018. A revision of species limits in Neotropical pipits *Anthus* based on multilocus genetic and vocal data. *Ibis* 160: 158–172.

Freeman, B. & Montgomery, G. 2017. Using song playback experiments to measure species recognition between geographically isolated populations: a comparison with acoustic trait analyses. *Auk* 134: 857–870.

Hall, B. P. & Moreau, R. E. 1962. A study of the rare birds of Africa. *Bull. Brit. Mus. (Nat. Hist.) Zool*. 8: 313–378.

ISSN-2513-9894 (Online)

Helb, H. W., Bergmann, H. H. & Martens, J. 1982. Acoustic differences between populations of western and eastern Bonelli's Warblers (*Phylloscopus bonelli*, Sylviidae). *Experientia* 38: 356–357.

Liu, Y., Chen, G., Huang, Q., Jia, C., Carey, G., Leader, P., Li, Y., Zou, F., Yang, X., Olsson, U. & Alström, P. 2016. Species delimitation of the White-tailed Rubythroat *Calliope pectoralis* complex (Aves, Turdidae) using an integrative taxonomic approach. *J. Avian Biol*. 47: 899–912.

Marler, P. R. & Slabbekoorn, H. 2004. *Nature's music: the science of birdsong*. Elsevier Academic Press, London.

Martens, J. 2010. A preliminary review of the leaf warbler genera *Phylloscopus* and *Seicercus*. *Brit. Orn. Club Occas. Publ*. 5: 41–116.

Morel, G. J. & Chappuis, C. 1992. Past and future taxonomic research in West Africa. *Bull. Brit. Orn. Cl*. 112A: 217–224.

Nalwanga, D. W., Opige, M. & Skeen, R. Q. 2016. Status of the population of Karamoja Apalis *Apalis karamojae* in north-eastern Uganda. *Ostrich* 87: 179–183.

Ng, N. S. R., Prawiradilaga, D. M., Ng, E. Y. X., Suparno, Ashari, H., Trainor, C., Verbelen, P. & Rheindt, F. E. 2018. A striking new species of leaf warbler from the Lesser Sundas as uncovered through morphology and genomics. *Sci. Rep*. 8(1): 15646.

Opige, N. & Skeen, R. Q. undated [2011]. A survey of the Karamoja Apalis *Apalis karamojae* and a first nest record in Iriiri, eastern Uganda. https://www.africanbirdclub.org/past-projects/ (accessed 3 June 2023).

Payne, R. B. 1982. Species limits in the indigobirds (Ploceidae, *Vidua*) of West Africa: mouth mimicry, song mimicry, and description of new species. *Misc. Publ. Mus. Zool. Univ. Michigan* 162: 1–96.

Pearson, D. & Turner, D. 2017. A taxonomic review of the genus *Zosterops* in East Africa, with a revised list of species occurring in Kenya, Uganda and Tanzania. *Scopus* 37: 1–13.

Remsen, J. V. 2005. Pattern, process, and rigor meet classification. *Auk* 122: 403–413.

Ryan, P. G. 2006. Karamoja Apalis *Apalis karamojae*. Pp. 478–479 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 11. Lynx Edicions, Barcelona.

Salmah, J. & Onongo, J. 2023. A report on the survey of the Karamoja Apalis in north-eastern Uganda. https://www.africanbirdclub.org/wp-content/uploads/2023/02/A-Survey-of-the-Karamoja-Apalis-in-North-eastern-Uganda-Jombela-Salmah.pdf (accessed 3 June 2023).

Sefc, K. M., Payne, R. B. & Sorenson, M. D. 2005. Genetic continuity of brood parasitic indigobird species. *Mol. Ecol*. 14: 1407–1419.

Shaw, P. 2007. The distribution and habitat of Karamoja Apalis *Apalis karamojae* in the Serengeti, 2005–06. Unpubl. rep. Wildlife Conservation Society of Tanzania, Dar es Salaam.

Shaw, P. & Mungaya, E. 2006. The status and habitat of Karamoja Apalis *Apalis karamojae* in the Wembere Steppe, Sukumaland, Tanzania. *Bird Conserv. Intern*. 16: 97–111.

Shaw, P., Mungaya, E., Mbilinyi, N. & Mbilinyi, M. 2005. The voice and bill length of Karamoja Apalis *Apalis karamojae* are atypical of the genus. *Bull. Brit. Orn. Cl*. 125: 122–129.

Shaw, P., Sinclair, A. R. E., Metzger, K., Nkwabi, A., Mduma, S. A. T. & Baker, N. 2010. Range expansion of the globally Vulnerable Karamoja apalis *Apalis karamojae* in the Serengeti ecosystem. *Afr. J. Ecol*. 48: 751–758.

Stevenson, T. & Fanshawe, J. 2002. *Field guide to the birds of East Africa*. First edn. T. & A. D. Poyser, London.

Stuart, S. N. & Collar, N. J. 1985. Subspeciation in the Karamoja Apalis *Apalis karamojae*. *Bull. Brit. Orn. Cl*. 105: 86–89.

Svensson, L. 2012. A new subspecies of Western Orphean Warbler *Sylvia hortensis* and criteria for separating Western from Eastern Orphean Warbler *S. crassirostris*. *Bull. Brit. Orn. Cl*. 132: 75–83.

Tobias, J. A., Seddon, N., Spottiswoode, C. N., Pilgrim, J. D., Fishpool, L. D. C. & Collar, N. J. 2010. Quantitative criteria for species delimitation. *Ibis* 152: 724–746.

Turner, D. A. 1977. Status and distribution of the East African endemic species. *Scopus* 1: 2–11.

Urban, E. K., Fry, C. H. & Keith, S. (eds.) 1997. *The birds of Africa*, vol. 5. Academic Press, London.

Addresses: Peter Boesman, Duinenweg 3, B-2820 Rijmenam, Belgium, e-mail: tangara@skynet.be. N. J. Collar, BirdLife International, Pembroke Street, Cambridge CB2 3QZ, UK; and Bird Group, Natural History Museum, Tring, Herts. HP23 6AP, UK, e-mail: nigel.collar@birdlife.org

Appendix 1: Sound recordings analysed in this study

Apalis k. karamojae: XC 739394/ML 466839481, XC 739395/ML 466839491, XC 739396/ML 466839861, XC 739397/ML 466840171, ML 509203471.

Apalis k. stronachi: XC 146332/ML 332837021, XC 648013, XC 718598/ML 440009331, XC 755876, ML 332837061, ML 332837121, ML 550227171, ML 547993521.

ML = Macaulay Library; XC = Xeno-canto. Recordists: Abdul Adam, Peter Boesman, James Bradley, Isaac Kilusu, Paulo Kivuyo, Catriona Leven, Deogratius Muhumuza.

ISSN-2513-9894 (Online)

Appendix 2: Online photographs inspected in this study

Apalis k. karamojae: ML 438235841, ML310449731, ML 496910021, ML 486375761, ML 473365201, ML 405679141, Salmah & Onongo (2023: fig. 5).

Apalis k. stronachi: (Kenya) ML 577089561, ML 555463391, ML 547994721, ML 477479131, ML 472399641, ML 441255561, ML 415114251; (Tanzania) ML352403481, ML 253848101, ML 170629521, ML 119518351, ML 108697311, ML 335533951, ML 302702781, ML 205491021.

ML = Macaulay Library. Photographers: Nik Borrow, James Bradley, Nancy Christensen, Gary Douglas, Bradley Hacker, Neil Hayward, Charley Hesse, Marcel Holyoak, Victor Ikawa, Alain Jacot, Alex Kanzira, Helmut Laussmann, Alexander Lees, Lisa & Li Li, Larry Moss, Jonathan Onongo, Niall D. Perrins, Fanis Theofanopoulos.

ISSN-2513-9894
(Online)