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Geographical variation in the Bar-tailed Trogon *Apaloderma vittatum*

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Summary.—Distributed in four areas of Africa ('Eastern'—east of the Gregory Rift Valley from central Kenya south to Malawi; 'Central'—west of the Gregory Rift from western Kenya and western Uganda south to Burundi and eastern Democratic Republic of Congo; 'Western'—Nigeria and Cameroon plus Bioko; and Angola), Bar-tailed Trogon *Apaloderma vittatum* is at present widely judged to be monotypic. However, photographic evidence reveals three different facial patterns in these populations, with a bare ear spot and whitish-green bill in Eastern and Angolan birds, a bare ear spot, golden-yellow bill and bare gape line in Central birds, and these same features plus a distinct bare crescent above the eye in Western birds. Central and Western birds also have broader, more distinct barring on the wing panel. Moreover, there is a stepped cline in sizes in these three distinct populations, from Eastern plus Angola (largest) through Central to Western (smallest), with Bioko birds having notably short tails; and songs also decelerate from east to west, but with too much overlap to be diagnosable. Nevertheless, under the Tobias criteria the morphological differences of Central and Western birds vs. Eastern and Angolan populations accord the former species rank, for which the name *camerunense* is available. This latter species itself breaks into three subspecies, with the nominate in Nigeria and Cameroon, *francisci* on Bioko, and a new name for the hitherto taxonomically unrecognised Central populations.

The Bar-tailed Trogon *Apaloderma vittatum* is one of three species of Trogonidae endemic to the Afrotropics. It is confined to moist montane forest at 900–3,000 m, mainly above 1,600 m, in four general areas which we circumscribe as follows: (1) east of the Gregory (or Great) Rift Valley in central Kenya, Tanzania, northern Mozambique, Malawi and north-east Zambia (hereafter 'Eastern' range / populations); (2) west of and adjacent to the Gregory Rift in western Kenya and the highlands fringing the Albertine Rift in Uganda, eastern Democratic Republic of Congo (DRC) south to Mt. Kabobo, Rwanda and Burundi (hereafter 'Central'); (3) eastern Nigeria, western Cameroon and Bioko, Equatorial Guinea (hereafter 'Western'); and (4) western Angola (Snow 1978, Cunningham-van Someren & Fry 1988, Collar 2001, Forshaw 2009).

Despite the considerable disjunction involved in this range, attempts to identify geographical variation in populations worthy of taxonomic rank have been few in number and low in uptake. Western populations were named 'var. *camerunensis*' (gender agreeing with the genus *Heterotrogon*, but name hereafter spelt to agree with *Apaloderma*) by Reichenow (1902) on the basis of being 'always smaller' than Eastern birds (at a time when the species was unknown from the Central range), but he considered his sample too small to identify consistent plumage differences which would confirm the form as a genuine taxon, '*camerunense*', rather than simply a 'variety'. The following year, clearly without knowledge of *camerunense*, Alexander (1903) named the population on Bioko *francisci*, again

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diagnosing it from Eastern birds by its much smaller size but also by the broader white bars on the wing panel; but he gave his description in Latin, and evidently no-one other than Reichenow (1903: see below) troubled to read it, because after 1903 the wing panel was never again mentioned. Finally, Bowen (1930) gave the name *keniensis* to the Eastern population on Mt. Kenya on the basis of its broader, straighter black bars on the outermost rectrices. For completeness, however, we should mention that van Someren (1922) used the combination '*Heterotrogon vittatum minus* Chapin' by misremembering that the name *minus* was introduced by Chapin (1915) for (and is a synonym of) *Apaloderma aequatoriale* (Bare-cheeked Trogon).

A notably convoluted and entirely neglected circumstance surrounds an early validation of the form *camerunense* and indeed *francisci*. Alexander (1903) may have been unaware of Reichenow (1902), but not vice versa. In our translations, Reichenow (1902) expected that 'other differences will be detected in the Cameroon form, which will then be separated as *H. v. camerunense*' (not merely as a variety). Curiously, Reichenow (1903) reacted to Alexander's *francisci* as if his expectation had been fulfilled, whereas in reality *francisci* merely confirmed the smaller size of 'Western' birds but failed to share 'other differences' that Reichenow hoped would clinch the upgrading of *camerunense*. Presumably, however, the size factor was enough to convince him of the validity of *camerunense*, whilst the 'broader white bars on the wing-coverts' on *francisci* evidently prevented him from synonymising it with *camerunense*, because he judged that in *camerunense* 'the wingbars are not wider than in *H. vittatum*'. Very probably, since he had no specimen of *francisci*, Reichenow was assuming that its wingbars were strikingly broader, whereas the distinction, which is present in both Central and Western birds, is clear but subtle (see Results). Ironically, therefore, he validated *francisci* on a non-diagnostic character; but in any case, as noted above, his comments were entirely lost thereafter and have only come to light in this paper (see Acknowledgements).

Sclater (1924) accepted *camerunense* and *francisci* as subspecies of *vittatum*; Bates (1930) accepted *camerunense* but was silent on *francisci*. Bannerman (1933) and Peters (1945) recognised *camerunense* but synonymised *francisci*; the former called *keniensis* into doubt, implying it to be a synonym of *camerunense*, while the latter—like van Someren (1932), who judged it to reflect 'individual variation'—synonymised it with the nominate. There appear to have been no attempts to revive *keniensis* since, but Eisentraut (1965, 1973) demonstrated that *francisci* is distinctly shorter tailed, a finding which has however been entirely ignored. Moreover, *camerunense* has generally been treated with scepticism, although the initial trend into the mid-20th century, by which time the Central and Angolan populations had been found, was to accept it and to assume this name applied to all populations west of the Rift Valley (Chapin 1939, Peters 1945, Mackworth-Praed & Grant 1952, 1962, 1970, Bannerman 1953). However, after White (1965) pointed out 'a size cline with wings in East Africa 122–133, Congo and Angola 115–135, Cameroons 112–121', the trend shifted heavily towards synonymising it (Benson *et al*. 1971, Wolters 1975–82, Snow 1978, Louette 1981, Pinto 1982, Cunningham-van Someren & Fry 1988, Clements 2000, Collar 2001, Dickinson 2003, Dowsett & Dowsett-Lemaire 2006, Dowsett *et al*. 2008, Forshaw 2009, Dickinson & Remsen 2013, del Hoyo & Collar 2014, Gill *et al*. 2022), with only a few authors continuing to use it (Johnsgard 2000, Clements 2007, Clements *et al*. 2021). Where an explanation of the position taken on its validity was offered, the slight size difference was cited as a reason both to synonymise *camerunense* (Cunningham-van Someren & Fry 1988, Forshaw 2009) and to recognise it (Bannerman 1953, Johnsgard 2000); Collar (2001) blandly commented 'characters apparently not consistent'. Only Mackworth-Praed & Grant (1952) provided further justification, maintaining that in *camerunense* 'the male differs in having the top of the head green, and the female in having the top of the head bronzy green, not brown',

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which no subsequent commentator appears to have considered and which the authors themselves omitted in a later diagnosis (Mackworth-Praed & Grant 1962). Overall, therefore, the strongly prevailing view is that *A. vittatum* is monotypic.

However, in the course of researching images for a photographic guide to the birds of East Africa, ASK compiled a dossier on Bar-tailed Trogon which appears to show a consistent pattern of three-way differentiation in facial markings between Eastern (single bare coloured patch on the ear-coverts), Central (like Eastern plus a bare coloured line running back from the gape) and Western populations (like Central plus a brightly coloured line around the top of the eye). In consideration of these indicative but provisional findings, we undertook a more concerted search for evidence.

Methods

We approached the issue of possible geographical variation in *A. vittatum* on four fronts. We assembled and reviewed published literature on the species, searched the internet for photographs of living birds with clearly identified localities, examined and measured adult specimens in three museums, and analysed as many recordings of its voice as we could find in publicly accessible sound archives.

Photographs were sourced mainly from the internet, most notably the Macaulay Library (https://search.macaulaylibrary.org/catalog?taxonCode=battro1), supplemented by material held by ASK and several contacts, notably A. P. Leventis. Owing to the greater preponderance of males in photographs and their greater distinctiveness than females, we restricted our searches to adult males. When multiple photographs bore the same place, date and photographer's name, we used only one of them, assuming the same bird to be involved (although where the location was the same but the photographer and date were different we assumed different birds were involved); we only used photographs with stated provenance. Our aim was to assemble a portfolio of images that documented the facial features of living birds, namely colour of bill, presence of a bare patch of coloured skin on the ear-coverts ('ear spot'), presence / absence of a bare patch of coloured skin running back and downwards from the commissure ('gape line'), and presence / absence of a coloured narrow supraocular crescent (upper 'eyeline'). Many photographs proved uninformative because of the quality and angle of the shot and / or position of the bird. However, we found a total of 94 photographs with sufficient detail that they could be used in analysis, 39 of Eastern birds, 47 of Central birds and eight of Western birds; of these, 85 provided dependably diagnostic evidence whilst nine (three Eastern, five Central and one Western) represented an arguable challenge to consistent diagnosis (Appendix 1a, b). We also had the benefit of eight photographs involving two males from Angola.

Material measured at museums consisted of: Natural History Museum, Tring, UK (NHMUK), 16 males, ten females from the Eastern range, one male from the Central range, 16 males, ten females from the Western range, and one male, one female from Angola; Royal Museum for Central Africa, Tervuren, Belgium (RMCA), four males, three females from the Eastern range, 23 males, 13 females from the Central range; and Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS), five males, four females from the Central range. In total, our sample sizes were 20 males and 13 females from the Eastern, 29 males and 17 females from the Central, 16 males and ten females from the Western ranges, plus one male and one female from Angola. Measurements were taken with callipers accurate to 0.01 mm and involved bill from tip to skull, wing curved, tail from tip to point of insertion (a particularly delicate matter in trogons owing to their densely feathered rumps), and, as a much cruder assessment, length of the pink belly patch (from centre of transition line to tip of undertail-coverts). NJC measured the material in NHMUK and LDCF did so in

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Belgium, the two being very familiar with each other's methods and conferring beforehand to maximise consistency. Using callipers, we also counted the number of bars visible in a 20 mm span of the central area of the wing panel of every measured specimen, and we checked for evidence of bare skin patches (which fade in colour post mortem and are commonly obscured by the preparation style) on the head-sides of male specimens.

Bar-tailed Trogon has two main vocalisations, termed hereafter song and call. The song consists of a typical trogon-like series of hollow whistles, delivered at steady pace but with slightly increasing insistence before terminating abruptly: *wo-wo-wo-wa-wa-wa-wa-wa-wa-wa*. Such phrases are usually repeated many times in succession with pauses of several seconds (early phrases in a series are often shorter with fewer notes). The call is a richly whistled, mournful *whíiiiuu* that rises and falls. S. N. Stuart (*in* Stuart 1986) considered both vocalisations to be indistinguishable between Cameroon and Tanzania. PB analysed them using a total of 51 recordings of different individuals from three sound archives (itemised in Appendix 2). The samples broke down as: Eastern (except western Kenya) 11 song, ten call; Central eight song, one call, plus (western Kenya only) eight song, no call; Western four song, five call; Angola two song, two call (one recording with both song and call). For most recordings information on sex was not available, and we assumed that sex ratio in the recordings from each region would be similar and therefore not affect the results. In each recording we selected 'full' song phrases, holding at least eight notes, so that we could better evaluate possible changes over the duration of the particular phrase. Following a qualitative evaluation of the recordings, we selected the following parameters as potentially informative: average pace (notes/second), initial pace (over first three notes), middle pace (over notes 5–7), end pace (over last three notes), note duration and max. frequency of, respectively, first note, middle note (note six) and last note. Each parameter was measured manually on the selected phrases, after visualising a sonogram with maximum sharpness (Blackmann-Harris with 2,048 bands) in CoolEdit Pro.

We did not consider the number of notes in a song phrase (and the resulting song duration), not only because we pre-selected the phrases but also because most recordings did not include an entire song series from the initial utterance of a first short phrase to the conclusion of the last 'full' phrase, which would be needed to evaluate these parameters. We also measured parameters of the single call note: duration, max. frequency and min. frequency (and calculated bandwidth).

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 (assessed for effect size using Cohen's *d* where 0.2–2 is minor, 2–5 medium and 5–10 major) and one behavioural or ecological character (allowed 1) may be counted.

Results

Morphological characters.—In 35 of 38 photographs (92%), Eastern males consistently showed a greenish-white to ivory bill and an ear spot (orange or pinkish) but no gape line (Fig. 1a,b); the three other photographs showed no ear spot (see Discussion and Appendix 1b). In 42 of 47 photographs (89%), Central males consistently showed a golden-yellow bill, an ear spot and a gape line, the two latter being orange-yellow (more rarely pink)

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TABLE 1
Measurements in mm (mean, range in parentheses, and [±] standard deviation) of male and female Bar-tailed Trogons *Apaloderma vittatum* from the main areas of distribution (see text for explanation of range and of the parameters 'panel' and 'breast'). [1] sample reduced by 1; [2] sample reduced by 2.

Males

Taxon	*n*	Bill	Wing	Tail	Panel	Breast
Eastern	20	16.6 (15.5–17.8) ± 0.55	120.5 (111–126) ± 4.11	175.1 (163–186) ± 7.24	9.9 (9–11) ± 0.67	108.4 (86–129) ± 10.3
Central	29	16.0[2] (14.7–17.7) ± 0.72	117.2 (108–124) ± 3.6	165.9 (149–187) ± 8.65	8.1 (7–9) ± 0.62	104.9[2] (88–122) ± 9.15
Western	16	16.4 (15.0–17.6) ± 0.69	110.4 (107–114) ± 2.25	155.7 (141–165) ± 6.61	7.8 (7–9) ± 0.66	112.1 (98–124) ± 7.85
Angola	1	16.1	116	182	9	103

Females

Taxon	*n*	Bill	Wing	Tail	Panel	Breast
Eastern	13	16.4 (15.4–17.8) ± 0.56	122.2 (119–128) ± 3.0	172.2 (159–180) ± 6.82	9.54 (8–11) ± 0.78	77.9[2] (70–85) ± 5.5
Central	17	15.5[1] (14.5–17.1) ± 0.86	115.4 (111–122) ± 3.08	166.5[1] (156–182) ± 7.03	7.65 (7–9) ± 0.61	86.3[1] (64–100) ± 9.62
Western	10	16.3 (15.5–17.2) ± 0.55	110 (107–112) ± 1.7	157 (149–164) ± 4.55	7.6 (7–9) ± 0.84	91[2] (74–99) ± 7.48
Angola	1	16.6	120	172	9	76

Figure 1. Bill colour and bare facial skin in male Bar-tailed Trogons *Apaloderma vittatum*, (a) Mount Meru, Tanzania, October 2012 (© Tasso Leventis), (b) Udzungwa, Tanzania, December 2020 (Adam Scott Kennedy)

when the light in the photograph shows the colour fully (Fig. 2a,b); four of the five other photographs showed neither ear spot nor gape line, while one showed these features *and* a yellow supraocular mark (see Discussion and Fig. 4). In seven of eight photographs (88%),

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TABLE 2
Measurements of song phrases (selected temporal and spectral parameters): mean, range and standard deviation.

	n	Pace at start (notes/second)	Pace middle (notes/second)	Pace at end (notes/second)	Duration middle note	Max. frequency middle note
Eastern (excluding W Kenya)	11	2.7 (2.0–3.5) ± 0.4	2.7 (2.3–3.3) ± 0.3	2.7 (2.3–3.1) ± 0.3	0.11 (0.08–0.14) ± 0.01	1,274 (1,160–1,350) ± 60
W Kenya	8	2.3 (1.9 - 2.6) ± 0.2	2.5 (2.2–2.7) ± 0.2	2.5 (2.1–2.9) ± 0.2	0.10 (0.09–0.12) ± 0.01	1,345 (1,120–1,500) ± 108
Central	8	2.2 (1.8–2.8) ± 0.3	2.3 (1.9–2.7) ± 0.3	2.2 (1.9–2.6) ± 0.2	0.13 (0.08–0.17) ± 0.02	1,344 (1,180–1,450) ± 92
Western	4	2.1 (1.8–2.3) ± 0.2	2.2 (1.9–2.4) ± 0.2	2.1 (1.9–2.3) ± 0.2	0.15 (0.12–0.19) ± 0.02	1,406 (1,200–1,500) ± 112
Angola	2	2.7 (2.6–2.7) ± 0.1	2.6 (2.5–2.6) ± 0.04	2.5 (2.5–2.6) ± 0.03	0.10 (0.09–0.12) ± 0.01	1,200 (1,160–1,240) ± 33

Figure 2. Bill colour and bare facial skin in male Bar-tailed Trogons *Apaloderma vittatum*, (a) Nyungwe, Rwanda, July 2019 (Adam Scott Kennedy), (b) Kakamega Forest, Kenya, August 2015 (© Nik Borrow)

Western males showed a golden-yellow bill, an orange ear spot and gape line, and a narrow orange-yellow upper eyeline (Fig. 3a,b); one photograph is too distant and grainy to be sure of the upper eyeline.

Of 20 Eastern male specimens examined, all showed the ear spot and no bare gape line. Of 29 Central and 16 Western males, all but one of each group (i.e. 28 [97%] and 15 [94%] respectively) showed the ear spot and the bare gape line (the other specimens defied assessment), while the eyeline could not be evaluated as the supraocular skin is in any case largely bare and discoloured in museum material; moreover, preparation style relating to the area around the eye varies considerably between specimens and / or with preparator.

Eastern birds have dense thin pale bars on the wing panel (Fig. 5a,d). Central and Western birds have somewhat bolder, broader and hence fewer bars on the wing panel (Fig. 5b–d, Table 1). Eastern females have slightly more extensive olive-brown from the

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Figure 3. Bill colour and bare facial skin in male Bar-tailed Trogons *Apaloderma vittatum*, (a) Obudu Plateau, Nigeria, December 2004 (© Tasso Leventis), (b) Bioko, February 2019 (© Dubi Shapiro)

chin to mid-belly and hence slightly smaller pink belly patches than Central and Western females (Table 1). Eastern birds have longer wings and tails than Central birds, which in turn have longer wings and tails than Western birds (Table 1). It is curious that Central birds have slightly shorter bills than Eastern and Western birds; the fact that both sexes show this suggests the difference is real. It is also curious that in many photographs Eastern birds *appear* to have smaller bills than either Central or Western birds; this seems to be the product of the latter having less feathering at the base of the mandible.

Figure 4. Male Bar-tailed Trogon *Apaloderma vittatum* showing yellow supraocular mark (spot or line?), Buhoma, Uganda, October 2013 (© John van Zyl)

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Figure 5. Density and intensity of wing panel barring in male Bar-tailed Trogons *Apaloderma vittatum*, (a) Mount Kenya, Kenya, June 2012, with ear-spot half-concealed (© Mike Barth), (b) Tinderet, Mau (south-west of Kakamega), June 2022 (© Victor Ikawa), (c) Obudu Plateau, Nigeria, November 2016 (© Tasso Leventis), (d) type of *vittatum* (NHMUK 90.12.6.1, right; Eastern bird) and type of *francisci* (NHMUK 1911.12.23.938, left; Western bird) (Alex Berryman © Natural History Museum, London, UK)

The suggestion in Mackworth-Praed & Grant (1952) that the top of the head in Western males is green (rather than blue) and in females 'bronzy green, not brown' is not fully

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borne out by NHMUK material, but there is a clear trend. In a one-to-one comparison of 16 Western males with 16 Eastern males, ten of the latter had bluer crowns than their counterparts, and the effect was never reversed. Moreover, 13 of 14 assessable Western females plus the only female Central specimen had a (sometimes very slight) sheen of green on the crown, whereas only four of 15 Eastern females showed such a sheen.

On the smallest sample possible, a male and female from Angola closely matched Eastern birds in both plumage and dimensions (Table 1).

Vocalisations.—Recordings were compared between the four geographical groups indicated in the Introduction. Songs were very similar, with all parameters showing overlapping ranges. However, certain patterns emerged when these measurements were averaged, albeit with a significant unconformity in the birds of western Kenya (which comprise much the most easterly and disjunct population here assigned to the Central range) (Table 2).

Pace at the start, middle and end of the song is slowest in Western, slightly faster in Central and decidedly faster in Eastern birds; similarly, but as a separate measure, the duration of the sixth note is longest in Western, somewhat shorter in Central, and shorter still in Eastern birds. In both these parameters Angolan birds group with Eastern birds.

The pattern is disrupted by the existence of an apparent cline in speed of delivery of the song in Eastern birds, fastest in the south, slowest in the north where populations in central Kenya most closely approach the easternmost Central populations in western Kenya (all recordings from Kakamega Forest). Western Kenya birds are in fact slightly closer to the Eastern group in song speed than to the Central group to which by their morphology they belong.

Our measurements of the calls of all four groups did not reveal any appreciable differences between them.

Discussion

Evidence for three groups of Bar-tailed Trogon.—Populations of Bar-tailed Trogons show a stepped cline across their range, mainly longitudinally but in the Eastern range also latitudinally in voice. There is a stepwise reduction in size from east to west, and songs become progressively slower; heads of Western birds tend to possess a greener wash (Central birds not tested for intermediacy); and the incidence of pink rather than orange-yellow bare facial patches diminishes in our photographic sample from 13:15 in Eastern through 6:31 in Central to 0:8 in Western birds (see Appendix 1).

Nevertheless, the evidence gathered in this study strongly suggests that the Bar-tailed Trogon comprises three phenotypic groups—Eastern with Angola, Central, and Western. The museum material conformed almost totally with the pattern of bare facial patches initially identified by ASK, with just two specimens (3%) being impossible to assess. The photographs conformed well, with only nine (10%) challenging our diagnoses (ML 122574221, ML153946031, ML 170148031, ML 171483801, ML 191765831, ML 206141051, ML 352544531, https://africageographic.com/stories/uganda-birding-10-best-spots/ and one by Nik Borrow); but, of these, the seven ML photographs did so by not showing expected patches of bare skin rather than by revealing unexpected ones. This could be due to the angle of the shot, the retracted position of the head, or both, but it may also (or instead) be that birds can cover or part-cover these bare patches, and possibly depress or deflate the eyeline, when relaxed or submissive. Indeed, two photographs of the same bird taken within seconds of each other show first the ear spot entirely covered and then partly disclosed (Fig. 6a,b); several other photographs seem to show a small subocular fan of cheek feathers with the apparent capacity to cover and expose the ear spot (see, e.g., ML 45886011,

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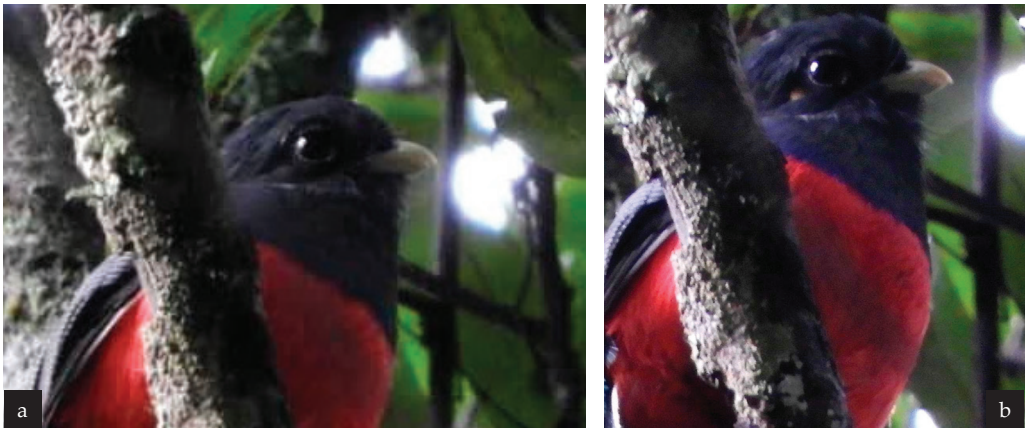

Figure 6. Covered (a) and part-exposed (b) ear-spot in a male Bar-tailed Trogon *Apaloderma vittatum* photographed seconds apart, Mafinga Mountains, Zambia, April 2018 (© Frank Willems)

ML 234482721, ML 306977531 for Eastern, ML 205987471, ML 284671041, ML 387594771 for Central, and Fig. 3 for Western birds). Trogons are not easy to find unless vocalising, and perhaps it is then, while photographers are taking aim, that their facial patches are fully exposed and eyeline swollen (see Fig. 5c), particularly if breeding and (in direct rivalry) responding to playback.

Whenever the form *camerunense* has been recognised or contemplated, the assumption has always been that birds from the highly disjunct population in Angola belong with it (e.g. Hall 1960, Traylor 1960, Clements *et al*. 2021). However, by its facial pattern, wing panel barring and dimensions, the Angolan male in Tring (NHMUK 1957.35.56) clearly groups with Eastern birds (Table 1). Very recent photographs involving two males confirm this, along with the greenish-white bill (Fig. 7a–c). Moreover, all five males from Angola in the American Museum of Natural History (AMNH 800687), Carnegie Museum of Natural History (CM 109446) and Field Museum of Natural History (FMNH 224158, 224160, 224162) lack a gapeline (R. F. Pasquier *in litt*. 2022, S. Brady *in litt*. 2022, D. E. Willard *in litt*. 2022). Still further support is found in vocal characteristics (see above). No basis for the subspecific separation of Angolan from Eastern birds has yet been identified, but on a very small sample size Hall (1960) and Traylor (1960) suggested that their wings might be somewhat shorter.

Apaloderma camerunense as a separate species.—Under the Tobias criteria Central and Western birds differ from Eastern birds by their golden-yellow vs. whitish-green bills (2), presence of a bare bright orange-yellow gapeline (3), broader-barred wing panel (effect size in Central males 2.7, in Western males 3.1, score 2), and smaller size (effect size for wing in Central females 2.3, in Western females 5.0, score 2)—total score 9. The slightly more extensive olive-brown breast and hence slightly reduced pink belly in Western females achieves an effect size of 2 against Eastern birds, but only 1.1 in Central birds; this latter triggers a score of 1, but the number of colour differences is capped at three, so this additional divergence achieves no score (and in any case is sufficiently broad in overlap to be a relatively insignificant character). It bears repeating that Central birds (except those in western Kenya) sing more slowly than Eastern birds, but the general overlap and especially the convergence in the north inhibit any score for this difference. However, it is important to stress that despite this vocal convergence, bare-part and plumage differences between these two populations remain constant.

On the basis of this considerable body of evidence, the validity of *camerunense* is unequivocally confirmed. Indeed, the total score of 9 for Central and Western birds against

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Figure 7. (a) Male Bar-tailed Trogon *Apaloderma vittatum*, Namba Mountains, Angola, June 2022 (© Michael Mills). (b) Different male, same locality and date (© Michael Mills). (c) Same bird as in (b) showing densely barred wing panel.

Eastern birds exceeds the Tobias threshold for species rank, and we are strongly inclined to judge such elevation appropriate. Given that the Tobias criteria consider 'a pronounced difference in body part colour' a major distinction and therefore worthy of a score of 3, our scoring of the bill difference is, arguably, conservative, but it pays respect to the somewhat anomalous description of the bill of Eastern birds in Mozambique as 'pale aureolin-yellow, slightly pale greenish in tinge' (Vincent 1935); indeed, there is a degree of variation in bill colour in the photographs used herein, although this may be in part an effect of light (the bird in Fig. 7b and 7c is the same yet the bill colour is a shade yellower in 7b). Certainly, however, the facial appearance that results from the combination of yellow bill and gapeline, when set beside the greenish-white bill on a plainer head, is very striking and can surely be construed as a signal that would form a strong disincentive to hybridisation if populations were ever to meet. (It bears mention that Central and Western females also possess a bare gapeline.)

There are, however, potential impediments to a new taxonomic arrangement based on these ostensibly consistent geographical characters. Three come in the form of illustrations

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in Newman *et al*. (1992), Aspinwall & Beel (1998) and Forshaw (2009). In the first two, which treat the birds of Malawi and Zambia respectively (both Eastern range states), a male Bar-tailed Trogon is portrayed with a yellow gapeline; but since our photographic evidence indicates the presence of typical Eastern birds in both countries, we consider these illustrations unlikely to have been based on local material or observations. In Forshaw (2009) a female is depicted with an orange gapeline based partly on (a) AMNH 826552, which VertNet indicates is from Tanzania and which R. F. Pasquier (*in litt*. 2022) reports as possessing no gapeline, and partly on (b) notes by another artist (W. T. Cooper), who might have made them somewhere in the Central range, most probably Uganda.

A final—and fascinating—obstacle to the split is represented by the vocal convergence of northernmost Eastern birds in central Kenya on easternmost Central birds in western Kenya. However, as noted above, this cline is in no way reflected in plumage and bare parts of the two populations, with central Kenyan birds wholly consistent with birds south to Malawi and western Kenyan birds wholly consistent with birds south to DRC and Burundi. It may be relatively rare and perhaps unorthodox to propose the elevation of a population to species rank in the absence of vocal divergence, but just as morphological features can be highly conserved whilst vocal characters are evolving, so the reverse must be allowed. Recent precedents include the newly described Rote Leaf Warbler *Phylloscopus rotiensis* (Ng *et al*. 2018) and the recently split Chinese Long-tailed Rosefinch *Carpodacus lepidus* (Liu *et al*. 2020). If these sound-alike taxa are in due course widely accepted as species, so surely should *A. camerunense*.

Apaloderma camerunense as a polytypic species.—The short tails of Bioko birds led Eisentraut (1965, 1973) to assert the validity of the subspecies *francisci*. Although there was considerable overlap in bill and wing measurements and no discernible differences in plumage, tails of male and female specimens from Bioko measured (mean and range, in mm) 143.3 (138–149, n = 8) and 142.3 (141–143, n = 4), respectively, vs. 156.4 (149–163, n = 15) and 153.9 (150–160, n = 9) from Cameroon (Eisentraut 1973). Our own measurements of ten females' tails from Cameroon and Nigeria (not part of Eisentraut's sample) produced a mean of 157 (149–164) mm (Table 1), while the female holotype of *francisci* (NHMUK 1911.12.23.938, again not part of Eisentraut's sample) has a tail of only 130 mm. With such a level of disjunction we readily concur that *francisci* merits taxonomic recognition and judge that, particularly on the female samples, its shorter tail would probably score at least 2 under the Tobias criteria.

The question of whether Central birds are sufficiently differentiated from Western birds to be accorded independent taxonomic status is more difficult to resolve. The one obvious point of distinction is their larger size, which is highly indicative (effect size for wing in males 2.3, females 2.2, Tobias score 2) but not fully diagnostic (range in males 108–124 vs. 107–114, females 111–122 vs. 107–112) (Table 1). More compelling is the absence of a yellow upper eyeline in Central birds, but again this is not 100% diagnostic: of eight Western individuals documented in photographs, seven (88%) show this eyeline clearly while one fails to show it satisfactorily (see above), whereas 44 (98%) of 45 Central individuals documented in photographs show no yellow mark above the eye while a single one (Fig. 4) clearly does.

That yellow on the upper eyeline can occasionally occur in Central birds is supported by the testimony of Chapin (1939), who wrote of the individuals he collected in what is now eastern DRC (our italic): 'The adult male has the iris red-brown, *above eye a small bare spot of yellow or gray*, two patches beneath the eye rich orange…'. In a passage that is hard to interpret, referring to the throat but not facial patches, Schouteden (1954) mentioned 'bare eye-rim/eyeline [*pourtour nu des yeux*] and bare throat patch greyish or dark blue, partly

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yellow' (our translation from French), but whether he was simply rewording Chapin's account, independently confirming it or even indicating something different is not clear; he did not mention the eye marking in his earlier (Dutch) account of the species (Schouteden 1951–52). (The colour of the bare throat when singing needs confirmation, as well as its consistency between taxa: a single photograph, ML 306977531, shows a pinkish area of bare skin in an Eastern bird.) It is worth noting that by 1939 Chapin had collected only two males (AMNH Vertebrate Zoology Collection Database), which suggests his diagnosis was biased by a small sample size; on the label of AMNH 262520 he wrote 'above eye a small spot of cadmium yellow', on that of AMNH 262521 'bare patch just above eye light gray', and on that of a further male he collected in 1957 (AMNH 764208) he noted 'naked skin above eye light greenish' (R. F. Pasquier *in litt*. 2022). These notes are evidently not interpretable as referring to the elegant thin crescent apparent in Fig. 3a,b. Moreover, even a 'small spot' is absent in the line drawing by his expedition co-leader Herbert Lang on the page opposite his description. Similarly, the eyeline mark in Fig. 4 seems to be more of a spot than a crescent line.

On this basis, under the Tobias criteria Central birds differ from Western birds by their lack of a yellow crescent line above the eye (and only occasional possession of a yellow mark there) (2) and larger size (see above, score 2)—total score 4. A score for vocal difference is withheld here: although Western birds sing more slowly than Central birds, the overlap in parameters is too great. Nevertheless, we feel that the combination of photographic and mensural evidence assembled here is sufficient to devolve taxonomic status on the Bar-tailed Trogon's Central populations.

Apaloderma camerunense delhoyoi, subsp. nov.

Holotype.—NHMUK 1906.12.23.1752, male, collected in Mpanga Forest at 5,000 feet (1,500 m), Fort Portal, Uganda, on 16 September 1906 by R. E. Dent.

Measurements of holotype.—Bill 15.8 mm, wing 115 mm, tail 163 mm, tarsus not measured.

Diagnosis.—Similar to *A. camerunense* of Nigeria and Cameroon, but with longer wings (mean of 29 Central range males 117.2 vs. mean of 16 Western range males 110.4 mm) and without a yellow crescent eyeline (albeit sometimes exhibiting a touch of yellow above the eye).

Description of holotype.—Crown dark metallic green shading to blackish on frons; carpal area (scapulars, lesser and median coverts), mantle and lower back metallic emerald-green, merging to duller metallic turquoise-blue on rump and uppertail-coverts; wing panel (formed by greater coverts, tertials and outer webs of secondaries) barred narrowly white on blackish background with faint greenish wash (number of bars in 20 mm span seven); remiges and alula dark brown, with primaries pp7–4 having a white leading edge; central and adjacent rectrices either matt blackish brown or, at a different angle, shiny indigo; outer three rectrices dark brown densely barred white (r1 almost throughout, decreasing in extent on rr2–3). Side of head blackish from frons to around eye, ear-coverts dark metallic green, bare patch of yellowish skin below eye (faded) and faded bare gapeline visible more clearly on right side; chin and upper throat blackish, central throat bare with loose displaced feathers, lower throat and upper breast dark metallic green merging into a broad deep blue reflective breast-band, brighter on upper breast-sides; belly to undertail-coverts (separated from breast by a fairly sharp line) bright reddish pink, richest on central belly; upper flanks and/or axillaries (difficult to distinguish) dark metallic green. Soft parts given on label as: 'bill pale yellow, foot black, iris d[ark] claret'.

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Remarks.—We urge observers of the taxa being distinguished here to maintain records of the incidence of males with yellow above the eye in Central and Western regions, as well as of its shape (spot vs. line), to improve the diagnosis of *delhoyoi*. Records of the colour of the bare throat when singing would also be of interest and potential taxonomic value.

Etymology.—In conceiving, creating and editing the incomparable and immense *Handbook of the birds of the world* (1992–2013) Josep del Hoyo made one of the greatest contributions to world ornithology of any single human being, and ignited new interest in the discrimination of subspecies simply by assiduously illustrating so many of them and, after vol. 2, requiring each to be given a thumbnail diagnosis. We name this new taxon for him in tribute and gratitude.

If these proposals find favour, the new taxonomic arrangement and geographical range for the populations in the Bar-tailed Trogon complex would be as follows.

Eastern Bar-tailed Trogon *Apaloderma vittatum*

—central Kenya, northern, north-east, central and south-west Tanzania, north-west Mozambique, Malawi, extreme north-east Zambia and, highly disjunctly, south-west Angola

Western Bar-tailed Trogon *Apaloderma camerunense*

—*A. c. delhoyoi*, western Kenya, Uganda, Rwanda, Burundi and eastern DRC
—*A. c. camerunense*, south-east Nigeria and south-west Cameroon
—*A. c. francisci*, Bioko (Equatorial Guinea)

For those who dislike compound qualifiers in English bird names or simply object to the fact that Angolan populations lie far to the west of some populations termed 'Western', alternative names might be 'Ivory-billed Trogon' for *A. vittatum* and 'Golden-billed Trogon' or 'Orange-billed Trogon' for *A. camerunense*. It is even arguable that *A. vittatum* could retain 'Bar-tailed Trogon' and a new name, such as Golden-billed, be assigned to *A. camerunense*.

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Appendix 1: Photographs of Bar-tailed Trogons *Apaloderma vittatum*

ABC = https://www.africanbirdclub.org/afbid/search/birddetails/species (followed by specific code). KB = https://kenya-birding.com/. ML = Macaulay Library. ON = https://www.oiseaux.net/photos. OO = https://observation.org/species/. *HBW = Handbook of the birds of the world* (see Collar 2001). Order of listing: ML first, in numerical sequence, then others in alphabetical sequence of name or surname. Code for letters in brackets concerns ear spot colour or visibility in Eastern photographs: o = orange-yellow, p = pink, p/o = pink or orange-yellow, x = patch opening visible but not colour.

(a) Diagnostic images

Eastern (*n* = 36)

Kenya (except western).—ML 39144431 (x), ML 59526501 (x), ML 103609041 (p), ML 250952301 (p), ML 291780281 (p), ML 315913481 (o), ML 396430511 (o), ML 413970141 (o), ABC/908/35345 (p/o), Mike Barth (p), Stefan Hirsch (o), ASK (p), KB2018/11/28/bar-tailed-trogon-at-the-lower-slopes-of-mt-kenya (p), ON/ paul.van.giersbergen/bar-tailed.trogon.2.html (p), *HBW* 6: 89 (o); *n* = 15.

Malawi.—ML 234482721 (p), Mike Bridgeford (p/o), *n* = 2.

Tanzania.—ML 22993721 (o), ML 45886011 (o), ML 45886041 (o), ML 119066971 (o), ML 215458051 (p), ML 215458071 (p/o), ML255034461 (p), ML 290001981 (p), ML 304382391 (o), ML 306977531 (o), ML 366499631 (p), ML 394707081 (p), ML 410862211 (o), ML 419789421 (p/o), ML 421461741 (o), Per Holmen (p/o), ASK (o), A. P. Leventis (o); *n* = 18.

Zambia.—Frank Willems (p); *n* = 1.

Central (*n* = 42)

Kenya (western; all Kakamega Forest except the last).—ML 107125531 (o), ML 207610921 (o), ML 212629601 (p), ML 307422331 (o), ML 309402971 (o), ML 390622461 (o), ABC/908/27268 (o); and (at Mau, Fig. 4b) Victor Ikawa (o); *n* = 8.

Rwanda.—ML 110483191 (p/o), ML 190582291 (p/o), ASK 1 (p), ASK 2 (p); Will Wilson (o); total 5.

Uganda.—ML 30300891 (o), ML 39602891 (p/o), ML 42797661 (o), ML 108585511 (o), ML 115757461 (o), ML 144336261 (o), ML 144860641 (o), ML 166449431 (p/o), ML 181158851 (o), ML 195617631 (o), ML 204207241 (o), ML 204259971 (o), ML 204485471 (p), ML 204897531 (o), ML 205474671 (o), ML 284671041 (o), ML 294374061 (p, or even crab-red), ML 30300891 (o), ML 357991791 (p/o), ML 360340481 (o, or even just yellow), ML 380305001 (p/o), ML 387594771 (o), ML 415698241 (p), ML 416576281 (o), ML 425162071 (o), ABC/908/20627 (o), ON/ samuel.marlin/trogon.a.queue.barree.1.html#espece, OO/71000/ (o), A. P. Leventis (o), Sherry McKelvie (o); *n* = 29.

Western (*n* = 7)

Cameroon.—ML 205104891 (o), ML 205916531 (o); *n* = 2.

Equatorial Guinea (Bioko).—ML 205104881 (two others of evidently same bird) (o); *n* = 1.

Nigeria.—A. P. Leventis (four separate birds) (all o); *n* = 4.

(b) Non-diagnostic images

Eastern (*n* = 3)

Kenya (except western).—ML 352544531 (ear spot invisible, doubtless in part a result of the angle of the head); *n* = 1.

Tanzania.—ML 170148031 and ML 153946031 (but in close-up both show a dimple in feathering where the ear spot is and could be counted as diagnostic); *n* = 2.

Central (*n* = 5)

Uganda.—ML 122574221 and ML 171483801 (vague evidence of gape line, none of ear spot), ML 191765831 (vague evidence of ear spot, none of gape line), ML 206141051, and https://africageographic.com/stories/ uganda-birding-10-best-spots/ (o; Fig. 7); *n* = 5.

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Western (*n* = 1)
Cameroon.—Nik Borrow (bare yellow eyeline *appears* to be present, but less obvious than expected by comparison with other images; however, distance too great for confidence either way) (o); *n* = 1.

Appendix 2: Sound recordings of Bar-tailed Trogons *Apaloderma vittatum*
Recordings used in the analysis of vocal differences between geographical groups of the species. The '(2)' after a catalogue number indicates that two songs were analysed from the recording. BLNS = British Library (Wildlife and Environmental Sounds); ML = Macaulay Library (Cornell Lab of Ornithology); and XC = xeno-canto.

Eastern (all except western Kenya) *Song*: BLNS 19738, 43935, 133641, 146535, cc22996; XC 48080, 364785, 397852, 397853, 429862, 621298. *Call*: BLNS 19739, 146534, 198851, 198852; ML 546437; XC 509885, 514422, 514573, 514616, 621296. (Only western Kenya, all Kakamega Forest) *Song*: BLNS 18051, 196282, 196622, 198042, 198709; ML 21295, 51531; XC 396118.

Central *Song*: BLNS 212787; XC 59077, 241061 (2), 240265 (2), 559208, 246552, 157019 (2), 182164. *Call*: XC 559209.

Western *Song*: BLNS cc1718; ML 537053 (2); XC 98989, 302952. *Call*: BLNS 110628, 137364; ML 534828, 537102; XC 407481.

Angola *Song*: BLNS 163264, 163312, 163313. *Call*: BLNS 163234, 163312.

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