

The taxonomic status of Rwenzori Nightjar *Caprimulgus ruwenzorii* Ogilvie-Grant, 1909, and Benguela Nightjar *C. koesteri* Neumann, 1931

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Received 2 September 2013

SUMMARY.—Doubts concerning the species status of Rwenzori Nightjar *Caprimulgus ruwenzorii*, and inclusion of Benguela Nightjar *C. koesteri* in its synonymy, are considered using mensural data for the Afrotropical montane nightjar complex, and by re-examining the plumage of *C. koesteri*. I conclude that both these taxa are subspecies of Montane Nightjar *C. poliocephalus*.

Chapin (1939: 413) realised that the four African montane nightjars appear to be conspecific: Abyssinian Nightjar *Caprimulgus poliocephalus* Rüppell, 1840; Rwenzori Nightjar *C. ruwenzorii* Ogilvie-Grant, 1909; Usambara Nightjar *C. guttifer* Grote, 1921; and Benguella Nightjar *C. koesteri* Neumann, 1931. They were subsequently treated as conspecific by most authorities, including White (1965), Colston (1978) and Jackson (1984). The current spelling of Rwenzori is Rwenzori, and of Benguella is Benguela. Jackson (1993: 151) recommended that traditional English names be retained for subspecies, but that the species (*C. poliocephalus, sensu lato*) be known as Montane Nightjar.

Chappuis (1981) considered the song of *ruwenzorii*, from a sound-recording made in the Impenetrable Forest (Uganda), to be very different to two songs of *poliocephalus*, recorded in Kenya at Kericho and Nairobi, in that it has a much sharper tonality and the phrases are much shorter.

Prigogine (1984) used *C. p. koesteri* as an example of an isolate representing a distinct subspecies of a polytypic species, but noted that *koesteri* might be more than a subspecies, 'as this taxon shows several differences from the other subspecies'.

In a major review of the skull morphology, song characteristics and systematics of African nightjars, Fry (1988) concluded that *C. ruwenzorii* is a species, separable specifically from *C. poliocephalus* by vocal differences. He noted that determination of the taxonomic status of two other montane isolates, *koesteri* and *gutturalis* (*sic*, a *lapsus calami* for *guttifer*), awaited voice recordings and analysis. In *The birds of Africa*, Fry & Harwin (1988) treated *C. ruwenzorii* as a species, and *guttifer* and *koesteri* as subspecies of *C. poliocephalus*, despite both being closer to *C. ruwenzorii* geographically and morphologically.

Louette (1990) commented on the inconsistency shown by Fry & Harwin (1988) of 'excluding *ruwenzorii* from the species *poliocephalus* on vocal characteristics (compared with all subspecies?), while morphologically it is in fact intermediate between two taxa admitted in the species, namely *guttifer* and nominate *poliocephalus*'. He listed this form as '*C. ruwenzorii*', clearly not accepting the proposed species status. Dowsett & Dowsett-Lemaire (1993) also challenged the specific status of *C. ruwenzorii*, partially on morphological grounds, but mainly as a result of a reconsideration of the vocal evidence. While Fry & Harwin (1988) considered a single voice recording of *ruwenzorii* to be sufficiently distinct from that of nominate *poliocephalus* to warrant specific status, examination of more tapes, not only of *ruwenzorii* but also of *guttifer*, by Dowsett & Dowsett-Lemaire (1993) led them to conclude that vocal variation is no more than dialectal. Consequently they preferred to keep all forms within the same species.

Cleere (1995) re-examined the entire montane nightjar complex and recognised two species, separated mainly by vocal differences, namely monotypic *C. poliocephalus* in the north, and polytypic *C. ruwenzorii*, with two subspecies (*ruwenzorii* and *guttifer*), in the south, and treated *koesteri* as a synonym of *ruwenzorii*. This arrangement was adopted in both major monographs of the Caprimulgiformes (Cleere 1998, Holyoak 2001). However, Cleere (1998) noted that some authorities consider the two species to be conspecific, and Holyoak (2001: 35) explained that he provisionally treated a few controversial forms as species, in order to present all relevant data separately from those of close allies, rather than from any conviction that they merited species rank.

The criticisms by Louette (1990) and Dowsett & Dowsett-Lemaire (1993), along with an examination of the sonograms presented by both the latter and by Cleere (1995), lead me to have serious doubts concerning the species status of *C. ruwenzorii*. Presented here are mensural data that may help to resolve the issue.

Methods

I treat *Caprimulgus palmquisti* Sjöstedt, 1908, as a synonym of *C. poliocephalus* Rüppell, 1840, as did Holyoak (2001); Cleere (1998) made no mention of it. Sjöstedt (1908) considered *C. palmquisti* to be nearest to *C. poliocephalus*, and his illustration of *C. palmquisti* reveals that it has the same full extent of white on the outer rectrices as does *C. poliocephalus*, one of the diagnostic characters of this form. Furthermore, the measurements provided by Sjöstedt for *C. palmquisti* all fall within the mensural ranges of *C. poliocephalus* (Table 1).

Key characters (Jackson 2000) were measured on 68 specimens of three of the subspecies involved: 42 *C. p. poliocephalus*, 21 *C. p. ruwenzorii* and five *C. p. guttifer*, listed north to south (for details of specimens see Appendix). Females, juveniles, feathers in moult and damaged characters were excluded. The data therefore refer only to sound characters on fully grown males.

The lengths of the five outer primaries (pp10–6) were measured by sliding a stopped ruler under the closed wing of the specimen until the stop met the bend of the wing, pressing the primaries flat against the ruler and then reading off the five measurements. The position of the wingbar (an isolated white or buff patch approximately halfway along the feather) was measured on p9 by taking the distance from the tip of the primary to the centre of the patch on the inner web. The extent of the emargination on the leading edge of p9 was measured from the tip of the primary to the point of flexure in the reverse curve, i.e. the neutral point between the inner and outer curves (as illustrated in Jackson 1986).

The length of the inner rectrix (r1) was measured from the skin at the base of the calamus to the tip of the feather. The calamus was exposed by parting the uppertail-coverts

TABLE 1

Measurements (from Jackson 2000, tarsus from Jackson 1984) of some key characters in male Abyssinian Nightjars *Caprimulgus poliocephalus* Rüppell, 1840, and the only known male *C. palmquisti* Sjöstedt, 1908 (measurements from Sjöstedt 1908). R1 and r5 are the inner and outer rectrices, respectively. Note that all *C. palmquisti* measurements fall within the ranges for *C. poliocephalus*.

Key character	<i>C. poliocephalus</i> Mean (range) n	<i>C. palmquisti</i> n = 1
Length of wing (mm)	152.3 (139–162) 57	155
Length of r1 (mm)	113.8 (106–124) 52	115
Length of r5 (mm)	110.1 (102–120) 52	107
Length of tarsus (mm)	14.9 (10–19) 83	17

so that the base was located visually, not by feel. The distance from the tip of r1 to the tip of r5 was measured with the tail closed and the difference was then applied to the length of r1 to derive the length of r5. All rectrix lengths are therefore relative to the base of r1. The pale apical patches on r4 and r5 were measured by taking the maximum dimension parallel to the rachis.

The length of the tomium was measured in a straight line from the tip of the bill to the inside angle of the gape and the width of the gape was measured across the bill from gape flange to gape flange. Tomium \times gape provided an approximate mouth size. The length of the tarsometatarsus was measured posteriorly from the intertarsal joint to the base of the last complete scale before the divergence of the toes. The length of the middle toe (t3) was measured from the base of the last complete scale on the tarsus to the tip of the pectinated claw. Tarsometatarsus + t3 provided the overall length of the foot.

Characters showing clinal variation were set aside. The remaining characters were each subjected to an analysis of variance (ANOVA one-way classification) to test, with a probability of 0.05, the null hypothesis that the three forms represent either a single population or three populations with equal means.

With just two known specimens of *C. p. koesteri*, this subspecies was not included in the analyses of variance. However, measurements made in accordance with the methods above were provided by M. Adams (Natural History Museum, Tring, UK) for the male and J. Trimble (Museum of Comparative Zoology, Cambridge, MA, USA) for the female. These were used to compare *koesteri* with *ruwenzorii*.

Results

Measurements of Benguela Nightjar.—Table 2 shows that, with one very minor exception, all key character measurements in *koesteri* fall within the range of *ruwenzorii*. The following results apply to the other three montane nightjars.

Clinal variation.—Three key characters display clinal variation, with mensural means decreasing from north to south (Table 3): the length of the apical patch on the outer rectrix (r5), the length of the apical patch on the adjacent rectrix (r4) and relative mouth size (tomium \times gape).

Analysis of variance.—An ANOVA was conducted on 12 characters (Table 4); seven for the wing, three for the tail and two for the foot. Tarsus length ($F_{2,64} = 8.86, P = 0.000$, Table 4k) was the only character requiring that the null hypothesis be rejected. It was not rejected by any of the results for the other 11 characters: length of p10 ($F_{2,61} = 1.40, P = 0.254$, Table 4a); length of p9 ($F_{2,60} = 1.55, P = 0.220$, Table 4b); percentage emargination on p9 ($F_{2,60} = 0.65, P = 0.526$, Table 4c); distance of centre of wingbar from tip of p9 ($F_{2,61} = 1.44, P = 0.244$, Table 4d); length of p8 ($F_{2,62} = 2.04, P = 0.139$, Table 4e); length of p7 ($F_{2,62} = 0.15, P = 0.864$, Table 4f); length of p6 ($F_{2,62} = 0.86, P = 0.430$, Table 4g); length of r1 ($F_{2,53} = 0.01, P = 0.993$, Table 4h); length of r5 ($F_{2,54} = 1.62, P = 0.207$, Table 4i); tail (r1) / wing (p9) ratio (%) ($F_{2,49} = 0.41, P = 0.669$, Table 4j); and length of t3 ($F_{2,64} = 0.10, P = 0.908$, Table 4l).

Discussion

Taxonomic status of Benguela Nightjar.—According to Cleere (1995) *C. koesteri* Neumann, 1931, is identical to *C. ruwenzorii* Ogilvie-Grant, 1909, and is best treated as a synonym of the latter. However, these two are not identical. Neumann (1931) described *koesteri* as similar to *ruwenzorii*, but smaller, with the pale bars in the tail narrower and more numerous (eight, including the terminal band) than in *ruwenzorii* (which has six). Also, *koesteri* has less white on the throat than *ruwenzorii* (Hall 1960, Colston 1978). The

TABLE 2

Measurements (mm) and ratios (%) of some key characters in (a) Rwenzori Nightjar *Caprimulgus ruwenzorii* Ogilvie-Grant, 1909, and (b) Benguela Nightjar *C. koesteri* Neumann, 1931. ** = the only *C. koesteri* measurement that does not fall within the range of *C. ruwenzorii* measurements.

Key character	Mean \pm SD (range) <i>n</i>	Key character	Mean \pm SD (range) <i>n</i>
Length of p10	(a) 145.3 \pm 4.8 (130–155) 40 (b) 146 (M) and 138 (F)	P9 patch position	(a) 60.2 \pm 3.0 (54–67) 42 (b) 60 (M) and 59 (F)
Length of p9	(a) 154.5 \pm 4.9 (141–163) 40 (b) 152 (M) and 146 (F)	P9 emargination	(a) 67.2 \pm 3.2 (58–73) 41 (b) 65 (M) and 62 (F)
Length of p8	(a) 154.8 \pm 4.7 (144–163) 40 (b) 151 (M) and 149 (F)	Ratio emargination / p9	(a) 43.6 \pm 1.4 (40.0–47.5) 39 (b) 42.8 (M) and 42.5 (F)
Length of p7	(a) 147.3 \pm 4.9 (136–156) 40 (b) 142 (M) and 141 (F)	Ratio p7 / p10	(a) 101.4 \pm 2.0 (96.5–105.7) 40 (b) 97.3 (M) and 102.2 (F)
Length of p6	(a) 126.8 \pm 5.0 (116–139) 39 (b) 122 (M) and 120 (F)	Ratio p6 / p9	(a) 82.1 \pm 2.1 (78.6–87.1) 39 (b) 80.3 (M) and 82.2 (F)
R5 patch (M)	(a) 55.0 \pm 5.6 (46–68) 20 (b) 57	Patch on r5 (F)	(a) 28.1 \pm 3.6 (23–34) 21 (b) 32
R4 patch (M)	(a) 54.8 \pm 5.5 (44–63) 20 (b) 53	Patch on r4 (F)	(a) 24.2 \pm 4.2 (16–34) 21 (b) 15**
Length of r1	(a) 115.0 \pm 5.0 (105–128) 36 (b) ? (M) and 124 (F) r1 of male is in moult	Length of r5	(a) 108.6 \pm 4.1 (100–122) 37 (b) 112 (M) and 115 (F)
Tomium length	(a) 27.0 \pm 1.3 (24–30) 41 (b) 24 (M) and 27 (F)	Length of foot	(a) 35.9 \pm 1.7 (32–40) 41 (b) 37 (M) and 35 (F)

TABLE 3

Mensural characters showing marked clinal variation in three Afrotropical montane nightjars, with means decreasing from Abyssinian Nightjar *Caprimulgus poliocephalus* Rüppell, 1840, in the north, through Rwenzori Nightjar *C. ruwenzorii* Ogilvie-Grant, 1909, to Usambara Nightjar *C. guttifer* Grote, 1921, in the south. AP = apical patch. R5 and r4 are the outer and adjoining rectrices, respectively. Mouth = tomium \times gape. Sample sizes are shown in brackets following means.

Taxon	AP on r5 (mm)	AP on r4 (mm)	Mouth (mm ²)
<i>poliocephalus</i>	90.5 (36)	87.4 (35)	703 (41)
<i>ruwenzorii</i>	55.0 (20)	54.8 (20)	653 (19)
<i>guttifer</i>	42.8 (5)	43.2 (5)	611 (5)

type specimen of *koesteri* was unsexed, but Neumann (1931) presumed that it was a male, whereas it is now known to be female (Hall 1960). As females are generally smaller than males (Table 2), this may have misled Neumann (1931) into believing that *koesteri* is smaller than *ruwenzorii*, after comparing it with specimens of the latter. Table 2, based on rather more material, shows that virtually all *koesteri* measurements fall within the range of *ruwenzorii*.

Hall (1960) noted that both sexes of *koesteri* have pale brown bars on the inner webs of the outermost rectrices, but gave their number as seven rather than eight (perhaps excluding the terminal band?). As *ruwenzorii* has only six, broader, pale bars (Neumann 1931), this character provides a simple means of separating the two forms.

The plumage differences between *koesteri* and *ruwenzorii*, together with the geographical distance (c.2,300 km) separating them, argue against the proposal by Cleere (1995) to treat *koesteri* as a synonym. While I do not agree with Prigogine (1984) that *koesteri* might be more

TABLE 4

Results of ANOVA to test, with a probability of 0.05, the null hypothesis that three of the Afrotropical montane nightjars (same as Table 3) represent either a single population or three populations with equal means. Degrees of freedom (*df*) between groups (upper) and within groups (lower) are shown. *F* is the calculated *F* statistic, *F crit* the critical value that must be exceeded by *F* in order to reject the null hypothesis. * See (k) for the only character in which the calculated value of *F* exceeds the critical value.

Taxon (<i>n</i>)	Mean	<i>df</i>	<i>F</i>	<i>P</i> -value	<i>F crit</i>
(a) Length of outer primary p10 (mm):					
<i>poliocephalus</i> (39)	143.5	2	1.401	0.254	3.148
<i>ruwenzorii</i> (20)	144.6	61			
<i>guttifer</i> (5)	147.0				
(b) Length of p9 (mm):					
<i>poliocephalus</i> (38)	152.6	2	1.553	0.220	3.150
<i>ruwenzorii</i> (20)	153.7	60			
<i>guttifer</i> (5)	156.0				
(c) Emargination on p9 (%):					
<i>poliocephalus</i> (38)	43.3	2	0.649	0.526	3.150
<i>ruwenzorii</i> (20)	43.7	60			
<i>guttifer</i> (5)	43.7				
(d) Distance of centre of wingbar from tip of p9 (mm):					
<i>poliocephalus</i> (38)	60.2	2	1.444	0.244	3.148
<i>ruwenzorii</i> (21)	60.3	61			
<i>guttifer</i> (5)	62.8				
(e) Length of p8 (mm):					
<i>poliocephalus</i> (40)	152.6	2	2.039	0.139	3.145
<i>ruwenzorii</i> (20)	153.9	62			
<i>guttifer</i> (5)	156.4				
(f) Length of p7 (mm):					
<i>poliocephalus</i> (41)	145.9	2	0.146	0.864	3.145
<i>ruwenzorii</i> (20)	146.6	62			
<i>guttifer</i> (4)	146.5				
(g) Length of p6 (mm):					
<i>poliocephalus</i> (41)	124.8	2	0.856	0.430	3.145
<i>ruwenzorii</i> (19)	126.2	62			
<i>guttifer</i> (5)	124.0				
(h) Length of inner rectrix r1 (mm):					
<i>poliocephalus</i> (35)	113.8	2	0.007	0.993	3.172
<i>ruwenzorii</i> (17)	114.0	53			
<i>guttifer</i> (4)	114.0				
(i) Length of outer rectrix r5 (mm):					
<i>poliocephalus</i> (35)	110.5	2	1.622	0.207	3.168
<i>ruwenzorii</i> (18)	108.2	54			
<i>guttifer</i> (4)	109.5				
(j) Ratio (%) of tail (r1) to wing (p9):					
<i>poliocephalus</i> (31)	74.3	2	0.405	0.669	3.187
<i>ruwenzorii</i> (17)	74.3	49			
<i>guttifer</i> (4)	72.8				
(k) Length of tarsus (mm):					
<i>poliocephalus</i> (42)	15.5	2	8.855*	0.000	3.140
<i>ruwenzorii</i> (20)	13.8	64			
<i>guttifer</i> (5)	16.4				

(l) Length of middle toe t3 (mm):

<i>poliocephalus</i> (42)	21.3	2	0.097	0.908	3.140
<i>ruwenzorii</i> (20)	21.3	64			
<i>guttifer</i> (5)	21.6				

than a subspecies, I do believe it merits taxonomic status. In October 2003, an individual of *koesteri* was heard singing at Catunda, Angola, by Michael Mills (Mills & Dean 2007). A sound-recording of this taxon's song might help to resolve its taxonomic status.

Taxonomic status of Rwenzori Nightjar.—*C. ruwenzorii* Ogilvie-Grant, 1909, was until recently treated as a subspecies of Abyssinian Nightjar, *C. poliocephalus* Rüppell, 1840. As the result mainly of distributional and vocal analysis, Fry (1988) recognised *C. ruwenzorii* as a valid species and this was followed by Fry & Harwin (1988). However, Dowsett & Dowsett-Lemaire (1993), with more sound-recordings available to them, demonstrated that the variation in song within *ruwenzorii* is at least as great as that between *ruwenzorii* and *poliocephalus*. They considered them to be conspecific. Cleere (1995) examined plumage patterns of the montane nightjars, including *ruwenzorii* and *poliocephalus*. He noted that variation in the amount of white on the outer rectrices is clinal, decreasing from north to south. He also noted variation in overall coloration and in the size of the white spotting on the four outer primaries. Cleere (1995) gave the song of *poliocephalus* as registering 2.0–3.2 kHz, compared to 2.5–3.8 kHz in *ruwenzorii*. The consistent plumage differences, coupled with the vocal differences, convinced him that two species are involved.

Coloration in nightjars is extremely variable within species, both geographically and individually, and this intraspecific variation is often greater than differences between species. Nightjar plumage patterns have evolved not as species-specific characters, but as camouflage for the bird at rest; as an adaptation to the general environment and particular substrate upon which it roosts and nests. These patterns, which may not accurately reflect historical relationships, are of minimal diagnostic value in devising identification keys; comparative measurements provide a better guide to nightjar relationships (Jackson 2000).

When identifying Afrotropical nightjars in the hand, the single most useful diagnostic character, with a low coefficient of variability, is percentage emargination on p9 (Jackson 1984, 2002). As noted in Jackson (2013), percentage emargination values for *poliocephalus* ($n = 57$) and *ruwenzorii* ($n = 39$) are 43.3 ± 1.5 (40.1–47.6) and 43.6 ± 1.4 (40.0–47.5), respectively, the very close means and ranges suggesting strongly that these two forms are conspecific. Minor differences in morphology and voice noted by Fry (1988) and Cleere (1995) appear to represent intraspecific geographic and individual variation, rather than interspecific variation, so I do not support the elevation of *ruwenzorii* to species status.

Relationships of the Afrotropical montane nightjars.—My measurements of the montane nightjars confirm that clinal variation exists in the apical patches on the rectrices, as noted by Cleere (1995), and also in mouth size (Table 3). The relative sizes of the apical patches provide a simple means of separating *poliocephalus*, *ruwenzorii* and *guttifer*, but not *koesteri* (see Table 2), which may better be separated, especially from *ruwenzorii*, by the number of bars in the tail.

Analyses of variance on 12 other key characters (Table 4) reveal that, with one only exception (length of tarsus, Table 4k), the null hypothesis, treating the montane nightjars as a single population, cannot be rejected. This means that the mensural data, mostly overlooked by previous authors, do not support splitting the montane nightjars into separate species.

DNA analysis will in due course provide a more definitive assessment of nightjar relationships. M Louette and his colleagues in Tervuren and Bonn are currently preparing a biochemical phylogeny of African nightjars, but this will not be published for some years (M. Louette *in litt.* 2013). Meanwhile, we must resort to more traditional methods.

Conclusion

Mensural data, especially analyses of variance, but also the emargination percentages and body mass data (Jackson 2003) provide no justification for separating any of the four montane nightjars of the Afrotropical region as a separate species. My conclusion is that the four forms should be re-united under Montane Nightjar *C. poliocephalus* as a polytypic species, with subspecies Abyssinian Nightjar *C. p. poliocephalus*, Rwenzori Nightjar *C. p. ruwenzorii*, Usambara Nightjar *C. p. guttifer* and Benguela Nightjar *C. p. koesteri*.

Acknowledgements

The museums listed in the Appendix permitted access to their nightjar specimens. Mark Adams (Natural History Museum, Tring) and Jeremiah Trimble (Museum of Comparative Zoology, Harvard University, Cambridge, MA) provided measurements and details of the *C. p. koesteri* male and female, respectively. Comments and corrections received from Bob Dowsett, Michel Louette and Nik Borrow during the review process greatly improved the paper. My grateful thanks to them all.

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Appendix: Museum specimens of *Caprimulgus poliocephalus* analysed.

Museum acronyms: AMNH = American Museum of Natural History, New York (USA); ANSP = Academy of Natural Sciences, Philadelphia (USA); BMNH = Natural History Museum, Tring (UK); CMNH = Carnegie Museum of Natural History, Pittsburgh (USA); FMNH = Field Museum of Natural History, Chicago (USA); LACM = Los Angeles County Museum (USA); MAK = Museum Alexander Koenig, Bonn (Germany); MCZ = Museum of Comparative Zoology, Harvard Univ., Cambridge, MA (USA); MNHN = Muséum National d'Histoire Naturelle, Paris (France); RMCA = Royal Museum for Central Africa, Tervuren (Belgium); ROM = Royal Ontario Museum, Toronto (Canada); UMMZ = University of Michigan Museum of Zoology, Ann Arbor (USA); USNM = United States National Museum of Natural History, Washington DC (USA).

C. p. poliocephalus ($n = 42$): AMNH 260591, 262388, 262390–262392, 633297, 633300, 633301, 633304–633308, 799939; ANSP 49354, 94967, 94968; BMNH 1901.2.22.361, 1912.10.15.313, 1926.5.3.211–1926.5.3.213, 1926.5.3.216, 1927.11.5.169, 1939.10.1.463, 1939.10.3.194, 1946.5.11.38, 1946.5.11.40; CMNH 139760, 149268, 149560; FMNH 82566, 194477–194479, 298272; MAK B.I.1.b.b; MNHN 1975-8; ROM 102988; UMMZ 211621; USNM 519304, 569273.

C. p. ruwenzorii ($n = 21$): AMNH 262394, 764118–764126; CMNH 145910, 146096; FMNH LD330, 346200; LACM 65122, 65124, 65126, 71353–71355; RMCA 17232.

C. p. guttifer ($n = 5$): BMNH 1932.5.10.716, 1939.2.25.475, 1939.2.25.477, 1939.2.25.478; FMNH 216752.

C. p. koesteri ($n = 2$): BMNH 1957.35.50; MCZ 165862.