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Genetic structure offers insights into the evolution of migration and the taxonomy of the Barred Long-tailed Cuckoo *Cercococcyx montanus* species complex

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Barred Long-tailed Cuckoo (*Cercococcyx montanus*) currently comprises two morphologically distinct subspecies, one resident in the Albertine Rift (*montanus*) and one in east and southeast Africa (*patulus*) in which there are migrations that are poorly understood. Based on nuclear and mitochondrial DNA sequences, we find that two specimens collected in relatively low-elevation forest in the Albertine Rift were correctly identified from plumage as the migratory subspecies whose closest known breeding area is > 800 km to the east. We discuss ways in which this unique migratory pattern could have evolved and argue that migration was gained and then lost in the C. *montanus* complex. Based on consistent morphological and genetic differences, we suggest that Barred Long-tailed Cuckoo is best treated as two species, one of which (C. *montanus*) is a non-migratory Albertine Rift endemic.

Keywords: Albertine Rift, biogeography, Eastern Arc Mountains, intra-African migration, phylogeography, systematics.

Migration within the tropics remains a mystery in many birds, especially those that are difficult to detect during the non-breeding season when they are not singing (Hockey 2000). The situation is further confused when resident and migratory populations overlap for part of the year, particularly if the populations are not easily distinguishable, a pattern found frequently in African cuckoos (Hockey 2000). Museum specimens and genetic techniques provide valuable insights into the evolutionary significance of such seasonal movements (Zink 2011) and the conservation of these taxa (Kahindo *et al.* 2007).

Most intra-African migratory routes are latitudinal, with birds breeding at temperate latitudes and moving towards the equator for the remainder of the year. This is true even for several species of cuckoos that have populations that breed at both northern and southern temperate latitudes, which may occupy the same tropical areas without temporal overlap, a pattern almost unique to Africa (Hockey 2000).

Longitudinal migrations have been documented in five species, none of them cuckoos, in southern Africa (Hockey 2000). Four Madagascan breeding species, including Madagascar Cuckoo *Cuculus rochii*, also have a strong longitudinal aspect to their migration, spending the non-breeding season in east Africa (Hawkins & Goodman 2003). Altitudinal migration is poorly documented in Africa, although Burgess and Mlingwa (2000) found some evidence of birds migrating between the Eastern Arc Mountains and the Tanzanian coast. Here we document a novel migratory pattern in a partially migratory African cuckoo and assess its taxonomic implications.

Barred Long-tailed Cuckoo *Cercococcyx montanus* is a patchily distributed species that

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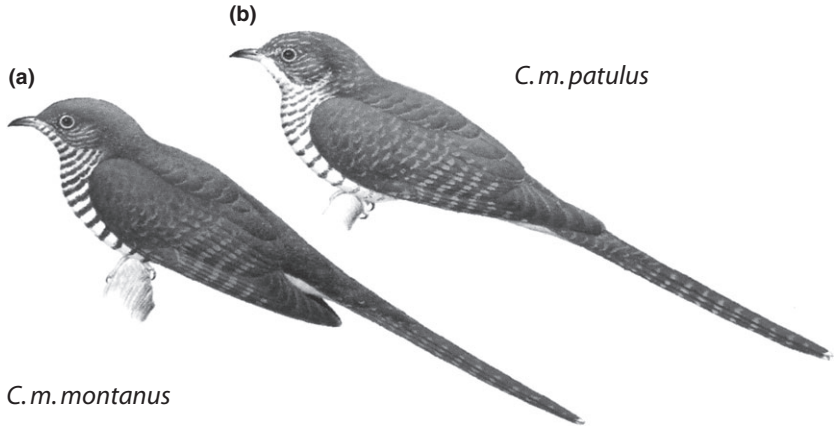

Figure 1. Illustration of plumage differences between (a) *Cercococcyx montanus montanus* and (b) *Cercococcyx montanus patulus* from Del Hoyo *et al.* (1997); used with permission. See Discussion for more information and Figure S1 for the original colour version of the illustration.

breeds in montane forests of east Africa and lowland forests of southeast Africa. There are two subspecies (Fig. 1, Fig. S1). The nominate form is considered to be a year-round resident in highland forests above 2000 m in the Albertine Rift of east-central Africa; C. *m. patulus* breeds in the highlands of Kenya and Tanzania and possibly locally in lowland areas of Tanzania, south to central Mozambique, and along the middle Zambezi on the Zambia–Zimbabwe border (Fig. 2; Irwin 1988). C*ercococcyx m. patulus* is known to depart from its highland breeding areas for part of the year, presumably migrating, but its movements are poorly known (Louette & Herroelen 1994, Burgess & Mlingwa 2000).

Although the two subspecies are distinguishable by plumage, the fact that these birds can be difficult to observe may often preclude field identification, and no vocal differences have been described. Field identification is further hindered by the fact that the subspecies are not mentioned, let alone illustrated, in the main regional field guides (e.g. Sinclair & Ryan 2011, Stevenson & Fanshawe 2001, but see Payne 1997).

Migration of C. *m. patulus* between the highlands of Kenya and Tanzania and the coastal lowlands has long been suspected (Britton 1977, Burgess & Mlingwa 2000), but some birds in Tanzania apparently remain in the lowlands year-round (Evans 1997). There also are records of post-breeding movements westward (and/or northward) of *patulus* into the Democratic Republic of the Congo (DRC) based on four

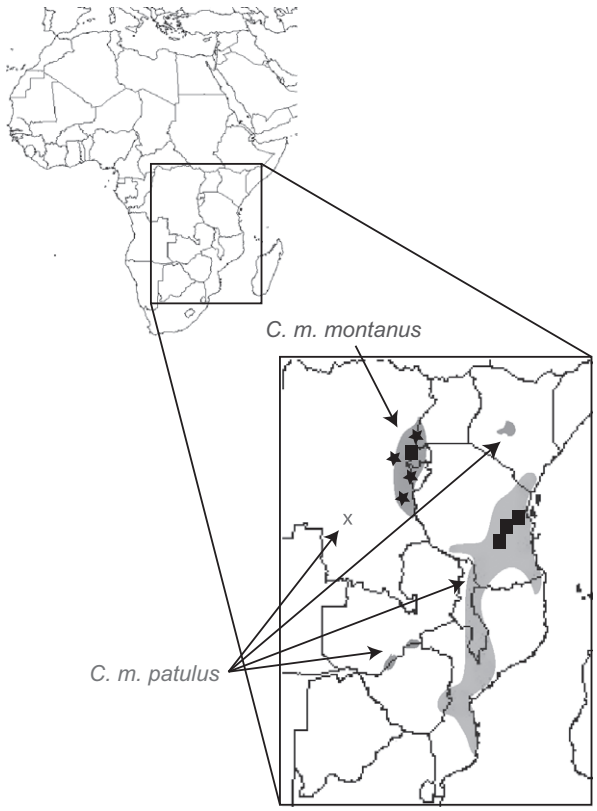

Figure 2. Map of the ranges (based on Irwin 1988 and ZMUC unpublished data) and sampling localities of *Cercococcyx montanus* samples. Solid squares (for *Cercococcyx montanus patulus*) and stars (for *C. m. montanus*) mark the localities of samples used in genetic analyses. Note the *C. m. patulus* sample in the range of *C. m. montanus*. The 'X' represents a possibly extra-limital specimen record of *C. m. patulus*.

specimens, three from Idjwi Island (1500 m asl) in Lake Kivu and one from Kasai Province (Louette & Herroelen 1994, Field Museum of Natural History (FMNH) specimens). All of these low-elevation records from the DRC are from the months of June and July, when *patulus* is not breeding. There also are records thought to be of birds on passage in October and March in eastern Zambia (Dowsett *et al.* 2008).

We present the results from sequencing three mitochondrial genes (mtDNA), NADH dehydrogenase subunits 2 and 3 (ND2 and ND3), and ATPase synthase subunit 6 (ATPase 6), and two nuclear introns (nuDNA), *β*-fibrinogen intron 5 (*β*-fib) and aldolase-b fructose-biphosphate intron 5 (ALDO), from 22 individuals of Barred Long-tailed Cuckoo, including two specimens identified as migrant C. *m. patulus* from Idjwi Island, DRC. Our objectives were to use genetic data to: (1) assess population structure within and between the two subspecies based on genetics and morphology and (2) determine whether the Idjwi Island specimens could be assigned to a particular breeding population. In doing this, we also address the taxonomic implications of our results.

METHODS

Morphological analysis and vocal data

We measured 24 specimens of C. *m. patulus* and 11 of C. *m. montanus*. A principal component analysis (PCA) was performed using the R package *Rcmdr* on the following measurements: wing chord, exposed culmen, tail-length and the ratio of the two distal bands anterior to the terminal band (one dark and one pale) along the feather shaft on the outermost rectrix. Tail-length was unavailable for five *patulus* specimens due to moult or not fully grown juvenile feathers (see Table S1 for full measurement data). Available vocalizations were obtained from the Macaulay Library (Cornell University), the British Library Sound Archive, Xeno-canto (www.xeno-canto.org) and AvoCet (avocet.zoology.msu.edu); these recordings were examined visually in RavenLite (Bioacoustics Research Program 2006).

Genetic analysis

We used 22 samples of Barred Long-tailed Cuckoo for genetic analysis: 15 from the Eastern Arc Mountains of Tanzania, one from coastal Tanzania, four from the Albertine Rift highlands of Uganda, Burundi and the DRC, and two from Idjwi Island in Lake Kivu, DRC (Table 1). Dusky Long-tailed Cuckoo *Cercococcyx mechowi* and Olive Long-tailed Cuckoo *Cercococcyx olivinus* were sampled as outgroups. All sequences are deposited in GenBank (accession numbers KF999203–KF999317).

Whole genomic DNA was extracted from blood and tissue using the Qiagen DNeasy Blood and Tissue Kit and from feathers using the Qiamp DNA Micro Kit (Qiagen Inc., Valencia, CA, USA) following the manufacturer's protocol. PCR-amplification of a total of 2064 base pairs of mtDNA was performed in 25-μL reactions using Taq Gold polymerase (ABI, Mountain View, CA, USA). NADH3 (ND3) was amplified using primers L10755 and H11151 (352 bp; Chesser 1999), ATPase 6 with CO3HMH and A8PWL (690 bp; Hunt *et al.* 2001), and NADH2 (ND2) with L5219Met (Hackett 1996) and H6313Trp (Sorenson *et al.* 1999). Sequencing of ND2 utilized internal primers H5578 (Hackett 1996) and L5575 (Ericson *et al.* 2002). The thermocycler protocol was identical for all three genes: a hotstart of 95 °C for 10 min, followed by 35 cycles of 95 °C for 30 s, 54 °C for 30 s and 72 °C for 60 s, and a final extension at 72 °C for 2 min.

Two nuclear introns also were sequenced. From the Z chromosome we sequenced ALDO intron 5, using primers ALDO5-F and ALDO5-R (Jacobsen *et al.* 2010). PCR was performed in 15-μL reactions using the following thermocycler protocol: 94 °C for 2 min, followed by 35 cycles of 94 °C for 15 s, 60 °C for 30 s and 72 °C for 20 s, and a final extension of 72 °C for 60 s. For *β*-fibrinogen intron 5 we used primers Fib5 and Fib6 (Fuchs *et al.* 2004) and followed the thermocycler protocol used for *β*-fibrinogen intron 7 in Patel *et al.* (2011).

Bands for all genes were visualized on 1% agarose gels and PCR purification was performed using ExoSAP (USB, Cleveland, OH, USA). Cycle-sequencing of PCR product using external primers was performed using BigDye v3.1 chemistry and standard ethanol/ETDA precipitation, and sequenced on an ABI 3730 Sequencer (Applied Biosystems, Foster City, CA). We assembled the sequence contigs and manually inspected chromatograms using SEQUENCHER 4.10.1 (GeneCodes, Ann Arbor, MI, USA). For nuDNA, double-peaks indicating heterozygous bases were scored using standard IUPAC ambiguity codes.

Table 1. Data for individuals from which genetic data were obtained: FMNH, Field Museum of Natural History, Chicago, IL, USA; KUMNH, Kansas University Museum of Natural History, Lawrence, KS, USA; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

Taxon	Accession no.	Country	Locality	Elevation	ND3	ND2	ATPase6	ALDO	β-fib 5
Cercococcyx m. montanus	FMNH 355263	Uganda	Rwenzori Mountains	2075 m	KF999240	KF999252	KF999288	KF999203	KF999295
Cercococcyx m. montanus	FMNH 357946	Burundi	Kibira National Park	1950 m	KF999241	KF999249	KF999289	KF999204	KF999296
C. m. montanus	FMNH 443796	D.R. Congo	Kahuzi-Biega National Park	2046 m	KF999244	KF999251	KF999292	KF999205	KF999297
Cercococcyx m. montanus	FMNH 450389	D.R. Congo	Mt Kabogo	1950 m	KF999245	KF999250	KF999293	KF999206	KF999298
Cercococcyx montanus patulus	FMNH 429714	D.R. Congo	Idwi Island, Lake Kivu	1500 m	KF999242	KF999255	KF999290	KF999209	KF999299
Cercococcyx montanus patulus	FMNH 429715	D.R. Congo	Idwi Island, Lake Kivu	1500 m	KF999243	KF999261	KF999291	KF999210	KF999300
Cercococcyx montanus patulus	ZMUC 114858	Tanzania	Dondwe Forest, Coast Region	80 m	KF999229	KF999266	KF999277	KF999214	KF999307
Cercococcyx montanus patulus	ZMUC 114235	Tanzania	Udzungwa Mountains	no data	KF999228	KF999259	KF999276	KF999207	KF999306
Cercococcyx montanus patulus	ZMUC 114229	Tanzania	Udzungwa Mountains	no data	KF999227	KF999268	KF999275	KF999213	KF999305
Cercococcyx montanus patulus	ZMUC 114227[a]	Tanzania	Udzungwa Mountains	no data	KF999226	KF999263	KF999274		KF999304
Cercococcyx montanus patulus	ZMUC 114226[a]	Tanzania	Udzungwa Mountains	no data	KF999225	KF999260	KF999273		KF999303
Cercococcyx montanus patulus	ZMUC 114225	Tanzania	Udzungwa Mountains	no data	KF999224	KF999253	KF999272	KF999212	KF999302
Cercococcyx montanus patulus	ZMUC 133138	Tanzania	Udzungwa Mountains	1440 m	KF999230	KF999265	KF999278	KF999215	KF999308
Cercococcyx montanus patulus	ZMUC 137557	Tanzania	Uluguru Mountains	no data	KF999231	KF999256	KF999279	KF999216	KF999309
Cercococcyx montanus patulus	ZMUC 138659[a]	Tanzania	Udzungwa Mountains	1550 m	KF999232	KF999258	KF999280		KF999310
Cercococcyx montanus patulus	ZMUC 138661[a,b]	Tanzania	Udzungwa Mountains	1550 m	KF999233	KF999257	KF999281		
Cercococcyx montanus patulus	ZMUC 140329	Tanzania	Udzungwa Mountains	1410 m	KF999234	KF999262	KF999282	KF999208	KF999311
Cercococcyx montanus patulus	ZMUC 140347	Tanzania	Udzungwa Mountains	1410 m	KF999235	KF999264	KF999283	KF999217	KF999312
Cercococcyx montanus patulus	ZMUC 140354	Tanzania	Udzungwa Mountains	1410 m	KF999236	KF999269	KF999284	KF999218	KF999313
Cercococcyx montanus patulus	ZMUC 140365	Tanzania	Udzungwa Mountains	1410 m	KF999237	KF999254	KF999285	KF999219	KF999314
Cercococcyx montanus patulus	ZMUC 140371	Tanzania	Udzungwa Mountains	1410 m	KF999238	KF999270	KF999286	KF999220	KF999315
Cercococcyx montanus patulus	ZMUC 140372	Tanzania	Udzungwa Mountains	1410 m	KF999239	KF999267	KF999287	KF999221	KF999316
Cercococcyx mechowi	FMNH 391659	Uganda	Budongo Forest	1000 m	KF999223	KF999248	KF999271	KF999211	KF999301
Cercococcyx olivinus	KUMNH 15716	Ghana	Ankassa Conservation Area	50 m	KF999246	KF999247	KF999294	KF999222	KF999317

[a]No sequence for ALDO. [b]No sequence for β-fib.

Akaike information criteria (AIC) calculations in PARTITIONFINDER (Lanfear *et al.* 2012) were used to identify the appropriate evolutionary models separately for each gene. The recommended partitions were used for maximum likelihood (ML) analyses of the combined mtDNA and nuDNA dataset in GARLI 2.0 (Zwickl 2006) and for Bayesian analyses in MRBAYES (Ronquist & Huelsenbeck 2003). We ran five independent search replicates to determine the best-fit tree in GARLI. Bootstrap values from GARLI were determined using 100 pseudoreplicates and mapped onto the best-fit tree using SUMTREES (Sukumaran & Holder 2010). Non-partitioned mitochondrial trees were estimated using RAXML (Stamatakis 2006) for ML and in MRBAYES. We conducted two independent runs in MRBAYES for both the combined and the mtDNA-only datasets of four chains for 10×10^6 generations, discarding the first 500 trees as burn-in. Convergence was determined by examining the potential scale reduction factor and the standard deviation of split frequencies between runs. We used PAUP* (Swofford 2003) to calculate uncorrected *p*-distances and DNASP v5 (Librado & Rozas 2009) to calculate genetic diversity indices. We used TCS v1.21 (Clement *et al.* 2000) to generate a 95% statistical parsimony network of mitochondrial haplotypes of C. *montanus*, an effective way to visualize relationships among haplotypes when overall divergence is low.

RESULTS

Morphology and vocalizations

Cercococcyx m. patulus was found to be an overall larger bird than C. *m. montanus*, on average longer-winged, longer-billed and heavier, with a slightly shorter tail (Table 2). A PCA showed no overlap in a scatterplot of the first two principal components (Fig. 3), which explained 52.5% and 25.5% of the variation, respectively. The differentiation is due to variation in PC1, which is driven by positive component loadings for wing-length (0.569) and culmen-length (0.603), and a negative loading for tail-band ratio (−0.544). Consistent differences in plumage also were found (see Discussion). A combination of plumage features and PCA was used to identify a previously unrecognized specimen of C. *m. patulus* from the Albertine Rift (AMNH 408978). This specimen, from the eastern side of the Itombwe Plateau collected in June, fits the timing of the other Albertine Rift records of *patulus*, but is from a higher elevation (2075 m), within the altitudinal range of *montanus*. Few high-quality analogous recordings of vocalizations were available

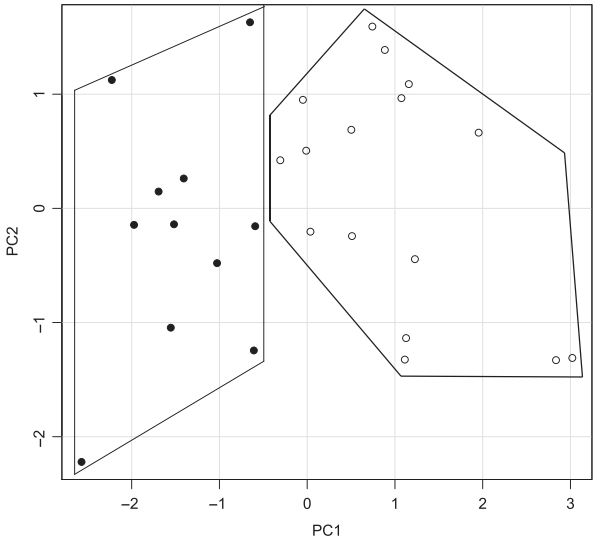

Figure 3. Scatterplot of the two principal components of the morphological measurements taken (see text for specific measurements). PC1 explains 52.5% of the variation, filled circles indicate *Cercococcyx montanus montanus*, open circles indicate *C. m. patulus*. PC2 explains 25.5% of the variation.

Table 2. Morphological values (mm) for measurements of specimens representing the Barred Long-tailed Cuckoo complex (mean ± sd).

Taxa	*n*	Wing-chord	Tail-length	Culmen-length	Tail bars[a]	Weight (g)
Cercococcyx montanus patulus (m)	15	144.8 ± 5.6	177.1 ± 6.0[b]	18.4 ± 1.0	1.56 ± 0.4	62.0 ± 6.1[c]
Cercococcyx montanus patulus (f)	8	148.9 ± 8.1	182.2 ± 9.0[c]	19.7 ± 0.8	1.68 ± 0.68	62.6 ± 1.7[d]
Cercococcyx montanus montanus (m)	4	138.0 ± 2.7	185.3 ± 3.9	17.2 ± 1.2	2.89 ± 0.4	51.0 ± 1.3[e]
Cercococcyx montanus montanus (f)	7	136.4 ± 5.1	185.1 ± 10.4	16.4 ± 1.2	2.34 ± 0.4	53.1 ± 3.0[f]

[a]Ratio of the measurement of distal dark bar divided by distal pale bar on outermost tail feather where the bars meet the shaft (excluding the pale feather tip). [b]*n* = 10. [c]*n* = 6. [d]*n* = 8. [e]*n* = 2. [f]*n* = 4.

for a substantive analysis between *montanus* and *patulus*, but a visual comparison of sonograms suggests there are no readily apparent differences between these taxa in vocalizations (Fig. S2).

Genetics

We were unsuccessful in amplifying *β*-fib for one Tanzanian sample and ALDO for four Tanzanian samples (see Table 1). The best-fit model chosen by PARTITIONFINDER for each mitochondrial gene was TVM+I+G and for each nuclear gene was TVM+I. The ML and Bayesian trees of the full concatenated dataset (Fig. 4), as well as trees of only the mtDNA data (Fig. S3), recover the monophyly of C. *m. patulus* relative to C. *m. montanus*, including the two presumed non-breeding migrants from the DRC. Reciprocal monophyly of the two subspecies was highly supported in all analyses except for the mtDNA dataset under a Bayesian optimality criterion, which had lower support for the nominate *montanus* clade. The two clades also are evident in the TCS network (Fig. 5).

The average uncorrected *p*-distance between *patulus* and *montanus* is 0.87% for mtDNA and 0.73% for the full dataset (Table S2). Despite the small geographical area from which the *patulus* samples were collected, there were 15 mitochondrial haplotypes among the 18 individuals sampled (see Table S3 for nucleotide and haplotype diversity statistics). The two *patulus* samples from the DRC were similar or identical to haplotypes from breeding birds sampled in the Eastern Arc Mountains. By contrast, the four samples of *montanus* share identical mitochondrial haplotypes despite being sampled from four widely separated highland regions of the

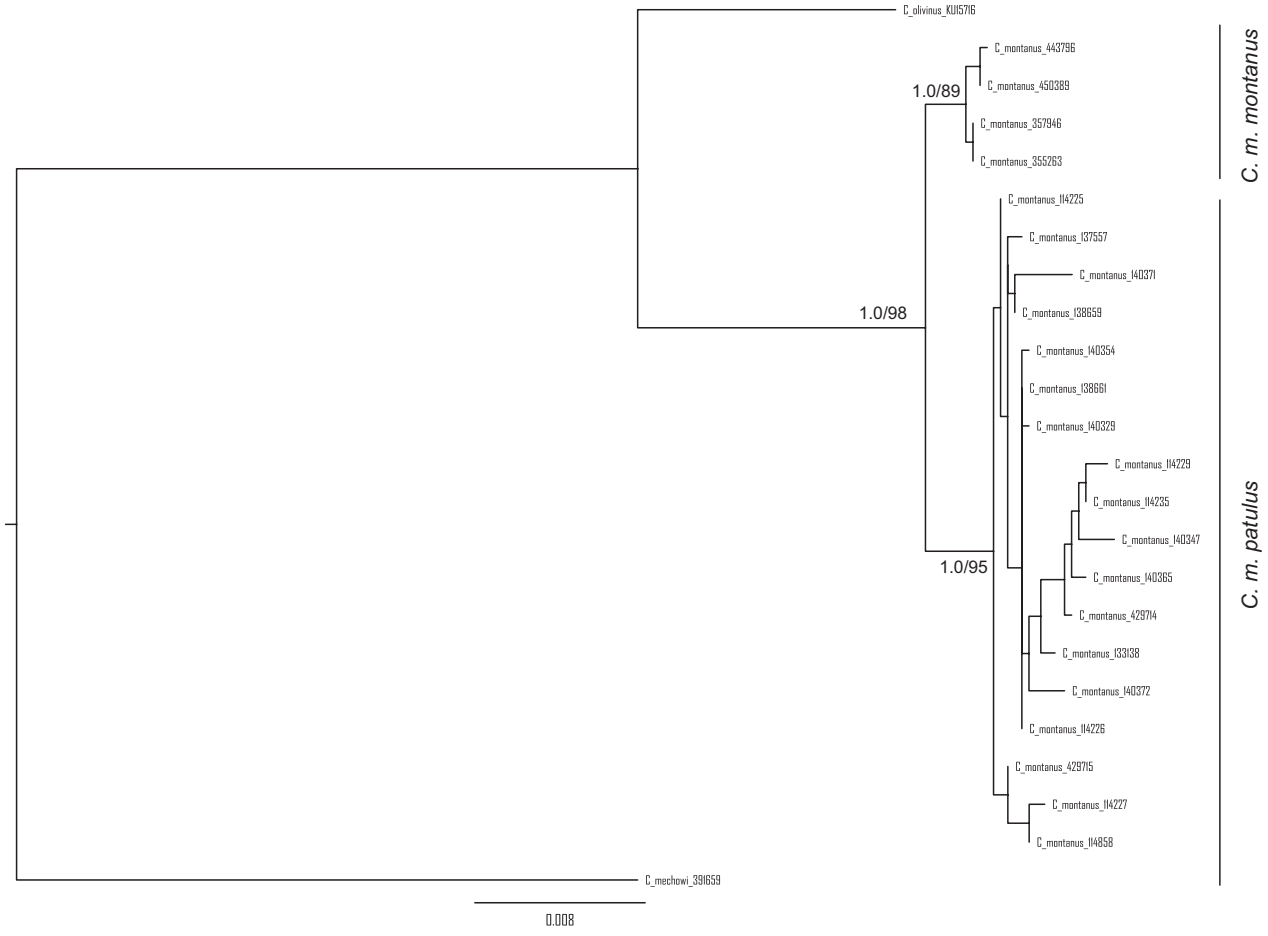

Figure 4. The consensus tree of the Bayesian analysis of the full five-gene dataset, including both mtDNA and nuDNA. Posterior probabilities ≥ 0.95 are indicated before the slash. Bootstrap values ≥ 80% from the maximum likelihood analysis are indicated after the slash.

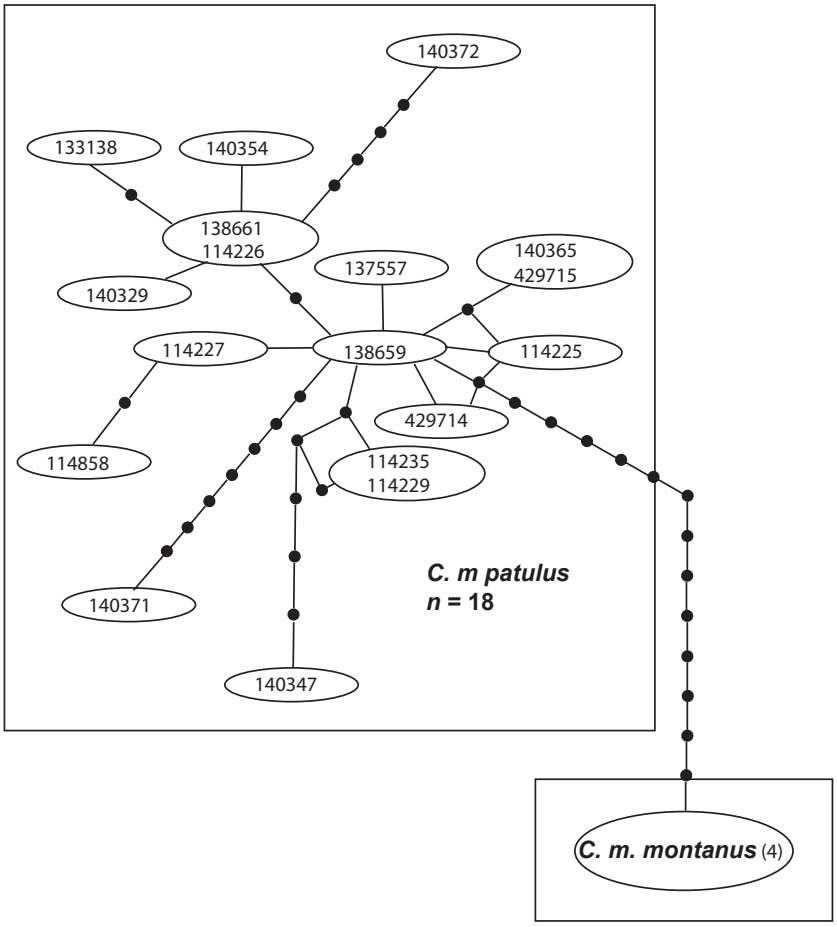

Figure 5. The 95% parsimony haplotype network of mitochondrial haplotypes for all *Cercococcyx montanus* samples. Each line represents a single mutational step with solid circles indicating unsampled haplotypes. The size of each oval is proportional to the total number of samples with the corresponding haplotype. The museum accession number of each sample is listed inside the oval except for *C. m. montanus*, where all individuals share a single haplotype.

Albertine Rift (Fig. 2). The z-linked ALDO gene showed a single fixed difference between the two subspecies. C*ercococcyx montanus* and C. *olivinus* share a 6-bp indel in β-fib.

DISCUSSION

Morphological differences

Friedmann (1928) based his description of C. *m. patulus* on Chapin's (1928) account of variation in C. *montanus*. Friedman's description is accurate but cursory, citing wing-length variation (longer in the migratory *patulus*) and differences in the barring on both the upper- and the underparts. Mackworth-Praed and Grant (1957) noted additional plumage differences, including differences in tail-bar width. Based on our examination of specimens, consistent differences in plumage and morphology are apparent (Figs 1 and S1, Table 2).

The adult C. *m. montanus* is darker overall than C. *m. patulus*. This is more strikingly apparent on the underparts, where the dark, dense and thick barring on the throat and breast of C. *m. montanus* contrasts strongly with sparser barring on the belly and flanks. This creates a dark-breasted appearance. C*ercococcyx m. patulus* lacks such a contrast, having thinner bars and less dense barring from the throat to the belly. The tips of the dark throat feathers also differ, being buffy in *montanus* and white in *patulus*. Additionally, *montanus* shows narrower white bars than *patulus* between the black bars on the tail, giving the underside of the tail an overall darker appearance.

The upperparts of *montanus* also are darker, with narrower buffy tips to feathers of the mantle and uppertail coverts, and the central tail feathers have narrow buff bands. Despite variation in some of these marks, particularly in the amount of pale edging to the upperpart feathers, a combination of these plumage differences should be distinct enough to make field identification possible.

Genetic analysis

Genetic data reveal low but consistent divergence in both mtDNA and nuDNA between *patulus* and *montanus*. Haplotypes of the two Barred Long-tailed Cuckoos collected on Idjwi Island fall with haplotypes of the *patulus* samples from the Eastern Arc Mountains (Figs 4 and 5). This agrees with the morphological identifications made based on the voucher specimens and supports a previously documented westward component to the migration of Barred Long-tailed Cuckoos (Louette & Herroelen 1994). In addition, these genetic data demonstrate differences in levels of genetic variation that support significantly different population histories between *patulus* and *montanus*. The 18 individuals of Eastern Arc *patulus* contain 15 unique haplotypes, which is consistent with a large, stable population size. Fourteen of the *patulus* samples come from the Udzungwa Mountains and even among these samples, 12 mitochondrial haplotypes exist: one of these haplotypes is shared by an Idjwi Island bird.

Although we have only four individuals of C. *m. montanus*, they come from sites in different montane highlands of the Albertine Rift that are separated by low-elevation valleys that lack suitable habitat and are separated by as much as 600 km (Table 1). Genetic structure has been found within other birds (Kahindo 2005, J. Engel & J. Bates unpubl. data) and rodents (Huhndorf *et al.* 2007) among these spatially separate montane highlands of the Albertine Rift. These four individuals were identical across 2064 bp of mitochondrial DNA, which, even with the small sample size, is consistent with a population bottleneck and/or a founder effect followed by recent population expansion.

Evolution of *patulus* and *montanus*

The other two members of *Cercococcyx*, C. *mechowi* and C. *olivinus*, are considered to be non-migratory lowland forest species with broadly overlapping ranges from West Africa across the Congo Basin to the forests bordering the Albertine Rift. Our phylogenetic results agree with those of Sorenson and Payne (2005), and it is therefore reasonable to infer that the Barred Long-tailed Cuckoo's ancestor was non-migratory. *Cercococcyx mechowi* is basal to a sister group of C. *olivinus* and C. *montanus*. The low levels of genetic divergence suggest that *patulus* and *montanus* diverged in the Pleistocene (about 450 000 years ago, at a 2% per million years mtDNA clock rate). Differing scenarios may explain the evolution of migratory behaviour of *patulus* and the lack of migration in nominate *montanus*. The resident status of C. *montanus* in the Albertine Rift is supported by specimen and survey data (A. Plumptre pers. comm.) with records in every month except October.

Migration could have been gained in *patulus* following dispersal out of the highlands of the Albertine Rift. Alternatively, a migrant *patulus* may have formed first in the Eastern Arc Mountains and subsequently led to the formation of a resident *montanus* in the Albertine Rift highlands. The high degree of genetic variation in the Eastern Arc birds is consistent with *patulus* being the older of the two populations. This, along with the lack of genetic variation in *montanus* of the Albertine Rift, may support the latter scenario (non-migratory *montanus* forming from a migratory *patulus*).

Our data do not address why *patulus* would be migratory, whereas *montanus* is not, but the question highlights several remaining gaps in our understanding of the natural history of these birds. Food supplies in the Eastern Arc Mountains are seasonally variable and many species of birds leave the highland forests in the dry season (Fjeldså *et al.* 2010); on the other hand, the palynological record suggests a remarkable long-term stability of the montane forest habitat (e.g. Marchant *et al.* 2007). Another aspect of *Cercococcyx* biology is that they are nest parasites, but there are few documented host records for C. *montanus* (Payne 2005). Differences in the species parasitized also could potentially influence the evolutionary history of the cuckoos. Better natural history data may hold important clues to understanding the behavioural differences.

Taxonomic recommendation

Although the reasons for migratory behaviour in *patulus* remain mysterious, this significant behavioural difference combined with genetic and morphological differences lead us to recommend

C. *m. montanus* and C. *m. patulus* be treated as full species regardless of the species concept one favours. For at least the non-breeding season, the two taxa co-occur in the Albertine Rift, yet there is clear evidence of genetic and morphological separation.

For C. *montanus*, we propose the English name Njobo's Long-tailed Cuckoo, after James P. Chapin's collector who procured the holotype (Chapin 1928). This species adds to the already substantial list of birds endemic to the montane forests of the Albertine Rift, a conservation hotspot (Plumptre *et al.* 2007).

For C. *patulus*, we recommend the English name of Eastern Long-tailed Cuckoo, recognizing it as the easternmost ranging member of the genus. *Cercococcyx patulus* also has its breeding distribution centred in a conservation hotspot, the Eastern Arc Mountains, where it is considered to be common (Irwin 1988). The status of *patulus* on Mount Kenya and in the regions in which it has been recorded to the south of the Eastern Arc Mountains needs to be better documented (Fig. 1). However, if a significant portion of the non-breeding habitat of this species is lower elevation evergreen forest in the Albertine Rift region, then loss of non-breeding season habitat could be a major concern, as only widely separated fragments of these forests remain below 2000 m. For example, on Idjwi Island (1500–2200 m) and along the shores of Lake Kivu, from where three of the five DRC records of *patulus* originate, only tiny fragments of forest remain.

Our ability to correlate genetic and morphologic differences in the *patulus* specimens from the DRC with series of specimens from the distributions of the two taxa highlights the value of voucher specimens and scientific collecting (Bates *et al.* 2004). There is still much to learn about these inconspicuous cuckoos. Among other questions, further documentation of what appears to be a unique migration pattern for an African bird may hold clues as to how migration evolves.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Illustration of plumage differences between (a) C. *m. montanus* and (b) C. *m. patulus* from Del Hoyo *et al.* (1997); used with permission.

Figure S2. Sonogram of homologous examples of two song-types for each subspecies of *Cercococcyx montanus* as visualized using RAVEN LITE (Bioacoustics Research Program 2006).

Figure S3. The majority-rule consensus tree of the Bayesian analysis of the three-gene mtDNA dataset, with posterior probabilities and bootstrap values mapped onto the main nodes.

Table S1. Measurements and details of all specimens examined.

Table S2. Uncorrected *p*-distance matrix for all samples included in the study.

Table S3. Genetic diversity indices calculated for the mitochondrial dataset.