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Altitudinal distributions of congeneric montane forest bird species along an elevational gradient in the Rwenzori Mountains National Park, western Uganda

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In a review of the altitudinal distribution of congeneric species, Cody (1974) found that tropical congeners tend to replace each other without overlap, while there were broad overlapping sequences in temperate zones. Elevational segregation in the altitudinal distribution of congeneric species was found by Terborgh (1971) in the Peruvian Andes, by Diamond (1972) in the Eastern Highlands of New Guinea, by Prigogine (1980) in the Itombwe Forest of Zaire (Democratic Republic of Congo) and by Willard *et al.* (1998) in the Rwenzori mountains. However, studies by Medway (1972) on Gungong Benom in Malaysia, Goodman & Gonzales (1990) on Mt Isaroq in the Philippines and Navarro (1992) on Sierra Madre Del Sur in Mexico found no such segregation.

In this paper we present the results from our study of bird species in the montane forest of the Rwenzori Mountains National Park (RMNP), which show that the altitudinal distributions of congeneric species tend to overlap.

Study areas, methods and effort

The Rwenzori Mountains are located on the border between Uganda and the Democratic Republic of Congo (Dehn & Christiansen 2001a) and form part of the rift-edge mountains of the western branch of the Great Rift Valley. Forest-covered areas are generally found above 1800 m in the national park, and this remaining forest is unique in Uganda as it is virtually undisturbed by man (Howard 1991).

Our fieldwork (111 days) took place between 30 July and 1 December 1996 in Bundibugyo and Kasese Districts, Uganda (Dehn & Christiansen 1998, 2001a, 2001b). An initial 12-day survey on the Kakuka Ridge was carried out to find out at what altitude montane forest occurred, and in preparation for the more detailed survey in the Mubuku/Mahoma/Bujuku valleys. Montane forest in the Mubuku/Mahoma/Bujuku valleys extends continuously from 1800 m to the treeline at about 3000 m. Standardised survey work was carried out in 1-ha study plots (50 m x 200 m) at 1800 m, 2100 m, 2400 m,

2700 m and 3000 m. Study plots were constructed by cutting a perimeter trail and one central trail, placed in an east-west direction. Elevations were measured with altimeters after calibration at known altitudes.

Mist-netting and observations were carried out daily between 06:00 and 11:00, but only during periods without rain. After trail-cutting, study plots were left undisturbed for at least 24 hours. Mist-nets were placed along the perimeter trails of the study plots and checked every 45 minutes. At each plot we ran an equal number of net metre-hours (mh) over a four-day period, and changed the net positions once. We used 5 x 12-m and 7 x 9-m nets of mesh size 32 mm. Ad-hoc mist-netting was also carried out on the Kakuka Ridge and between study plots in the Mubuku River system. Captured birds were colour-marked so that we could recognise recaptured individuals. In each plot we made observations according to the McKinnon & Phillips (1993) 20-species list method, slowly walking along the trails between 06:00 and 11:00 over four mornings,. Relative species abundances were estimated by counting the number of times each species appeared on all the lists from each study site (further details can be found in Dehn & Christiansen (1998)).

We classed species into abundance categories based on the number of observations, and on the number of individuals mist-netted. These are used only to give a broad idea of relative abundance; obviously, the abundance category will depend on the conspicuousness of the species, among other factors.

Nomenclature (scientific/English names) and order used in this paper follow *The birds of Africa* series (London: Academic Press) or (for species not yet covered by *The birds of Africa*) Britton (1980).

Results

We identified 139 species of which 17 were new records for the RMNP (Dehn & Christiansen 2001a). Mist-netting totalled 28,200 mh, with 991 birds captured. This included approximately 15,900 mh with 473 captures (0.029 birds/mh) during the twelve days of preparatory work on the Kakuka Ridge (western slope), and 12,300 mh, with 438 birds netted (0.035 birds/mh) in standardised mist-netting along the Mubuku River System (eastern slopes). Thirty-five of the birds ringed along the Mubuku River System were recaptured, all at the initial capture site.

We recorded 21 congeneric groups involving 55 species (Table 1). Two species in the genus *Musophaga* were clearly segregated by altitude, showing a hiatus (*sensu* Terborgh 1971, a gap between pairs of replacing species). The two *Phylloscopus* species also showed no altitudinal overlap. Congeneric species in six genera (*Accipiter, Turtur, Dendropicos, Terpsiphone, Laniarius* and *Estrilda*) showed only a narrow overlap. There was broad altitudinal overlap between congeneric species in the remaining thirteen genera (*Chrysococcyx, Pogoniulus, Andropadus, Cossypha, Bradypterus, Apalis, Muscicapa, Batis, Onychognathus, Nectarinia, Ploceus, Cryptospiza* and *Serinus*).

Sixteen of the 55 species treated here are considered to belong to superspecies (Britton 1980). Four species in the *Cryptospiza* species-group occur in the Rwenzori. On the Kakuka ridge we captured five *Cryptospiza reichenovii* (between 1920 m and 2035 m) and twelve *C. salvadorii ruwenzorii* (between 1960 m and 2050 m). In the Mubuku/Mahoma/Bujuku valleys we observed altitudinal overlap between *C. reichenovii*, *C. shelleyi* and possibly *C. salvadorii kilimensis* (see Table 1 and footnote to the table). The surveys by Willard *et al.* (1998) in the Rwenzori were carried out at slightly different altitudes than our study and their results further extend the altitudinal distributions for 23 species in our study (Table 1).

Discussion

Most congeneric species in the Rwenzori had a sympatric distribution, at least in part, with substantial areas of altitudinal overlap. There was little clear altitudinal replacement between species pairs with altitude.

According to Britton (1980), *C. salvadorii* is virtually allopatric to *C. reichenovii*, and is found mainly or entirely segregated by altitude in the few areas of apparent sympatry. But on Mt Meru and Mt Kilimanjaro, these two species are sympatric (Zimmerman *et al.* 1996). Our results from Kakuka show that *C. salvadorii* and *C. reichenovii* coexist between 1960 m and 2035 m.

As examples of possible congeneric replacements in the Rwenzori Mountains, Willard *et al.* (1998) mention *Tauraco*, *Cossypha*, *Bradypterus*, *Apalis*, *Phylloscopus*, *Laniarius* and *Cryptospiza*. Some of the species in these genera do appear to replace each other gradually along the altitudinal gradient, but no pairs are completely allopatric.

Our plots were separated altitudinally by 300 m and we could therefore not resolve questions about species ranges that met or overlapped within these intervals. An example is the two *Phylloscopus* species, Red-faced Woodland Warbler *P. laetus* and Brown Woodland Warbler *P. umbrovirens*. Members of the 1905–1906 Ruwenzori Expedition (Ogilvie-Grant 1910) found *P. laetus* between 1830 m and 2740 m and *P. umbrovirens* between 3050 m and 4270 m. Britton (1980) also reported that *P. umbrovirens* is segregated from its congeners at higher elevations in areas of apparent sympatry. We observed *P. laetus* up to 2700 m and *P. umbrovirens* at 3000 m. However, Willard *et al.* (1998) captured both species at 2700 m (*P. laetus* at 1960–2700 m and *P. umbrovirens* at 2700–4000 m). The evidence suggests that these two species only meet at about 2700 m.

We observed *Musophaga rossae* only once during 23 days at 1800 m in the Mubuku Valley (two birds seen at the forest margin). Francis & Penford (1991), who carried out most of their fieldwork in the Rwenzori at altitudes above 1670 m, did not record *M. rossae*; neither did the members of the Ruwenzori Expedition (Ogilvie-Grant 1910). Apparently *M. johnstoni* coexists with other turaco species without any signs of aggression (Fry *et al.* 1988, from Prigogine 1971). In the Mahoma Valley we observed small groups of

Table 1. Altitudinal distributions of 55 species (21 groups of congeners) in the Mubuku/Mahoma/Bujuku valleys. Abundance categories have been divided into A) >100, B) 50–99, C) 10–49, D) 1–9 observations (1 mist-net capture = 1 observation). For the study by Willard *et al.* (1996) abundance is indicated by I = 1 capture , II = 2–5 captures , III = 6–10 captures , IV = 11–20 captures , V = >20 captures and 'sro' = sight record only. Bold lettering (**sro, I, II, III, IV**) indicates a range extension or range overlap compared to our study

	Altitude (m)									
	Dehn & Christiansen					Willard *et al.* (1998)				
Scientific name	1800	2100	2400	2700	3000	1960	2075	2700	3400	4000
Accipiter tachiro	D	D	–	–	–	–	–	–	–	–
A. rufiventris	–	–	–	D	–	–	–	–	–	–
A. melanoleucus	–	D	D	D	–	–	–	sro	sro	–
Chrysococcyx cupreus	D	D	–	–	–	–	–	–	–	–
C. klaas	C	D	–	–	–	–	–	–	–	–
Musophaga johnstoni	–	–	C	B	C	–	–	I	I	–
M.rossae	D	–	–	–	–	–	–	–	–	–
Pogoniulus coryphaeus	D	D	D	D	–	III	–	–	–	–
P. bilineatus	A	A	C	–	–	II	II	–	–	–
Turtur tympanistria	C	D	D	–	–	IV	II	–	–	–
T. afer	D	–	–	–	–	–	–	–	–	–
Dendropicos fuscescens	D	D	–	–	–	–	–	–	–	–
D. griseocephalus	–	D	D	–	–	–	–	**sro**	–	–
Andropadus tephrolaemus	–	A	A	A	C	IV	V	V	–	–
A. latirostris	A	A	D	–	–	V	V	II	–	–
Cossypha archeri	D	D	C	B	B	–	II	IV	III	–
C. polioptera	C	D	–	–	–	–	–	–	–	–
C. cyanocampter	D	D	–	–	–	II	–	–	–	–
Bradypterus lopezi	C	D	–	–	–	II	II	–	–	–
B. cinnamomeus	D	C	B	A	A	–	III	IV	II	–
Apalis ruwenzori	C	C	A	A	A	IV	III	IV	–	–
A. flavida	D	–	–	–	–	–	–	–	–	–
A. personata	B	B	B	D	–	III	III	–	–	–
A. porphyrolaema	–	B	B	B	–	–	I	II	–	–
Phylloscopus laetus	–	D	C	B	–	**sro**	III	III	–	–
P. umbrovirens	–	–	–	–	C	–	–	II	II	sro
Muscicapa caerulescens	D	D	D	D	–	–	–	–	–	–
M. adusta	D	D	D	D	D	I	III	III	–	–
Terpsiphone viridis	B	–	–	–	–	II	–	–	–	–
T. rufiventer	D	D	–	–	–	–	–	–	–	–
Batis diops	–	–	C	C	–	–	II	III	–	–

Table 1. Continued.

Scientific name	Altitude (m)									
	Dehn & Christiansen					Willard *et al.* (1998)				
	1800	2100	2400	2700	3000	1960	2075	2700	3400	4000
B. molitor	–	C	C	C	–	–	–	–	–	–
Laniarius fuelleborni	–	D	C	B	C	–	III	IV	–	–
L. luehderi	C	C	–	–	–	III	–	–	–	–
Onychognathus tenuirostris	C	C	C	D	C	III	sro	sro	–	–
O. walleri	–	D	–	–	–	–	–	–	–	–
Nectarinia alinae	C	C	C	D	–	V	V	V	–	–
N. preussi	A	B	–	–	–	III	III	I	–	–
N. purpureiventris	–	C	B	D	–	II	II	–	–	–
N. regia	–	D	A	A	A	II	V	V	–	–
N. stuhlmanni	–	D	D	D	A	–	II	V	V	–
N. venusta	–	D	D	A	–	I	II	II	–	–
Ploceus alienus	D	C	D	D	D	V	III	III	–	–
P. baglafecht	D	D	D	–	–	–	II	–	–	–
P. insignis	D	D	D	–	–	I	–	–	–	–
P. nigricollis	D	–	–	–	–	–	–	–	–	–
Cryptospiza jacksonii	D	D	D	D	–	IV	III	II	–	–
C. reichenovii	D	*	D	–	–	II	–	–	–	–
C. shelleyi	–	D	D	D	D	II	I	III	I	–
Serinus burtoni	–	–	D	D	–	II	III	III	–	–
S. citrinelloides	D	D	D	D	–	II	–	V	–	–
S. striolatus	–	C	D	C	D	IV	II	IV	III	sro
Estrilda melanotis	D	D	D	–	–	sro	I	I	–	–
E. nonnula	D	–	–	–	–	I	–	–	–	–

*Species uncertain; the single bird netted was either *C. reichenovii* or *C. salvadorii kilimensis* — a darker bird than *C. s. ruwenzorii* and with conspicuous red eyelids. This record is under review by the East African Rarities Committee.

M. johnstoni in company with Black-billed Turacos *Tauraco schuetti* (observed at 1800 m, 2100 m and 2400 m) without any signs of agonistic behaviour. This sympatric distribution is locally common in forests of the Rwenzori between 2200 m and 3400 m (Fry *et al.* 1988). At around 2740 m *T. schuetti* is replaced by *M. johnstoni* (Ogilvie-Grant 1910). *Musophaga johnstoni* is reported to be most common in the Rwenzori at about 3000 m (Fry *et al.* 1988), but we found it most abundant around 2700 m, as did the Ruwenzori Expedition (Ogilvie-Grant 1910). Altitudinal movements in response to periods of heavy rain might explain this shift in abundance (K. Flavienus, pers. comm.).

Most sunbird species are active, easily observed and frequently mist-netted. Sunbirds are therefore suitable for studies of altitudinal distribution

where observation or capture is necessary. Britton (1980) report the Blue-headed Sunbird *N. alinae* to be common in the Rwenzori at 1400–2100 m, and perhaps Kingdon (1990) used the ranges provided by Britton to construct his model of the stacking of the three sunbird lineages. In Kingdon's model, *N. alinae* is confined to altitudes between 1600 m and 2100 m, but we found this species was common in the Rwenzori up to 2700 m. *Nectarinia preussi* and *N. regia* also occurred over larger altitudinal ranges than Kingdon suggests, and generally the sunbirds were found to have broad overlapping distributions.

The *Apalis* species were vocally conspicuous throughout the transect. We only once captured the Chestnut-throated Apalis *Apalis porphyrolaema* and the Montane Apalis *A. personata* (the latter species is considered a race of *A. binotata* in Britton (1980)). The Collared Apalis *A. ruwenzorii* was common in the undergrowth and therefore frequently captured (49 birds netted). There were only a few scattered trees (< 12 m tall) in the study plot at 3000 m, and both *A. porphyrolaema* and *A. personata* appeared to be absent at this altitude. *Apalis porphyrolaema* may well have been present at 1800 m, but we were unfamiliar with its cicada-like call until we reached our plot at 2100 m. Willard *et al.* (1998) also found *A. porphyrolaema* up to 2700 m, and missed this species at their lowest altitude, 1960 m. Yellow-breasted Apalis *A. flavida* was only observed once in the Mubuku Valley, at the forest edge ecotone, but was captured inside the forest at 1970 m on the Kakuka Ridge.

It appears that altitudinal range overlaps among congeneric species is the rule rather than the exception in the montane forest of the Rwenzori Mountains National Park. This pattern of overlapping ranges among congeners is even more pronounced when we combine our results with those from the surveys by Willard *et al.* (1998).

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