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The Avifauna of the Impenetrable Forest, Uganda

By Stuart Keith, Arthur Twomey, Herbert Friedmann, and John Williams⁴

INTRODUCTION

The Impenetrable Forest in southwest Uganda has for a long time deserved its name, and still does to a great extent. It lies atop a block of high ground which is divided into a series of steep, knife-edged ridges and deep, narrow valleys. It had been difficult of access, and not until 1957 was a road built through it, starting from the Ishasha River in the north and working along one of the ridges in a southeasterly direction toward Kabale. Up to that time the forest was almost unknown ornithologically. Chapin (1932, p. 156) referred to the Impenetrable when he said, "On the eastern edge of the Rutshuru Plain there is also a lowland forest which extends up into the mountains, and there takes on a montane aspect." His writings, however, indicated that he spent hardly any time in this forest and collected very little. A few forest species taken by Jackson in Kigezi probably came from the edges of the Impenetrable, but the first ornithologist to penetrate it was probably John Williams, who made a brief trip through it in 1958. He discovered

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Melaenornis ardesiaca there for the first time in East Africa, and listed other species of interest (Williams, 1959). The first major collecting expedition to the forest was made by Twomey, accompanied by Williams, for the Carnegie Museum in 1960. A number of birds not previously known from Uganda were found there, including Spizaetus africanus, Indicator pumilio, Pycnonotus masukuensis, Muscicapa lendu, Cossypha roberti, and Parmoptila jamesoni (Keith and Twomey, 1968). Keith collected in the forest for the American Museum of Natural History in May and June, 1962, and later wrote a brief outline of the avifauna, listing some important species (Keith, 1968a). In 1967 extensive collecting was done by Tony Archer, Andrew Williams, and others for the Los Angeles County Museum, resulting in further notable discoveries, e.g., Bubo poensis, Indicator willcocksi, Pseudocalyptomena graueri, Bradypterus graueri, Bradypterus barratti, Hemitesia neumanni, and Graueria vittata (Friedmann, 1968).

A new subspecies, Apalis rufogularis kigezi, has been described from the Impenetrable Forest, and is at present not known from anywhere else (Keith, Twomey, and Friedmann, 1967). Another new subspecies, Poeoptera lugubris webbi, confined to the Impenetrable and Kibale forests of Uganda, has recently been described (Keith, 1968b.)

Apart from a partial list of the birds of the Impenetrable Forest by Williams (1968, pp. 162–164) and the above-mentioned works, nothing else has been published specifically on the birds of this area. Our objectives in the present paper are to set forth all that is known about the avifauna of the Impenetrable Forest, and to show its affinities with other forest avifaunas.

ACKNOWLEDGMENTS

Our thanks are due to many people for their help. We are particularly grateful to the Uganda Forest Department for permitting us to collect in the forest, for allowing us the use of huts as campsites, and for putting at our disposal information about the forest. We wish to thank the Uganda Game Department for permitting us to collect birds.

Keith would like to acknowledge the able assistance of Joseph Mwaki in the preparation of bird skins. Twomey wishes to thank Dr. Matthew T. Mellon and the Matthew T. Mellon Foundation for making the 1960 Carnegie-Mellon East African Expedition possible. He also willhes to thank co-author Williams, Tony Archer, and his wife, Jane Twomey, for their help in collecting and preparing the specimens. Friedmann wishes to thank his team of collectors and preparators, headed by Tony Archer, who made a fine collection containing many new discoveries.

The authors wish to thank Ronalda Keith, Jane Twomey, and Tony Archer for the photographs accompanying the present paper. Thanks are due to the National Science Foundation for Grant GB-5107 under which the collection was made for the Los Angeles County Museum.

METHODS

Owing to the nature of the terrain and the almost complete absence of paths or tracks leading into the forest, most of the collecting was done along the main road, which rises from 3500 feet in the north to 8200 feet at its highest point in the south. By driving and stopping to collect at various spots, a good sample of birds was obtained. In addition, nets were set up in the vicinity of the base camps at different altitudes. Keith concentrated his collecting around three camps, in each of which he spent a week: Ruhiza, at 7500 feet; Kitahulira, at 5500 feet; and the Ishasha River, at 3500 feet. Other collectors followed a similar procedure. Friedmann's collectors were the first to discover Bwindi Swamp, at 6750 feet, which yielded Bradypterus barratti and B. graueri, among other rarities. All collectors used mist nets extensively, and thus secured many shy undergrowth species in such genera as Sheppardia, Cossypha, and Malacocincla.

The Impenetrable Forest is well named. For example, when Keith put up his nets at Ruhiza, he had to cut footholds into the steep earth to keep himself from slipping. In many places along the road the shooting had to be confined to birds almost directly overhead, because birds off to the side of the road would either drop several hundred feet down the mountain on one side, or on a steep slope on the other side, which was made inaccessible because of the sheer wall created when the road was cut into the mountainside. It is hardly surprising that earlier collectors in Uganda confined their activities to forests such as Bwamba, Budongo, and Kibale where the terrain is flat.

In addition to collecting, Keith recorded the voices of many of the forest birds, including local endemics such as Caprimulgus (poliocephalus) ruwenzorii, Apalis ruwenzorii, and Phylloscopus laetus.

THE IMPENETRABLE FOREST—A DESCRIPTION

We have drawn extensively from Legatt and Osmaston (1961), and the Department of Lands and Surveys, Uganda (1962) for the present description of the forest. The area of the forest is 150 square miles in the Kigezi Highlands in southwest Uganda. It is contained within the following coordinates: latitude 0° 49′ S. to 1° 8′ S.; longitude 29° 35′ E.



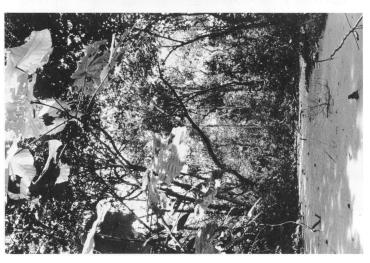


Fig. 1. Ishasha River, 3500 feet.

Fig. 2. Track in riverine forest, Ishasha River, 3500 feet.



Fig. 3 Ihihizhu River, 5000 feet.

to 29° 50' E. On the eastern edge it reaches the Uganda-Congo border between latitude 0° 54' S. and latitude 1° 4' S. There is a small amount of forest on the Congo side, reaching to the Rutshuru Plain, but this is still largely unexplored, and the few species mentioned by Chapin are all found on the Uganda side. The forest occupies the highest block of the Kigezi Highlands, which rise to 8200 feet at the southern end. The Kigezi Highlands are separated from the nearest mountain range, the Virunga Volcanoes, by the lower ground around Lake Mutanda. The Volcanoes occupy the extreme northeastern corner of Ruanda and the adjacent Kivu District of the Congo, and just reach the Uganda border at Mt. Muhavura, which straddles the border between Uganda and Ruanda. In spite of their close proximity to the Volcanoes, the Kigezi Highlands are not volcanic. They are made of Precambrian rocks of the Karagwe-Ankolean System, comprising quartzites, slates, phyllites, schists, and granitic outcrops. The Kigezi Highlands are geologically related to the Ruwenzori Mountains, which are also Precambrian in origin, rather than to the more recent Volcanoes.



Fig. 4. View near Itama Mine, 5300 feet. Note cultivation extending up to forest edge.

Of great importance to the Impenetrable Forest is the Ishasha River, which rises at the southern end of the highlands near Kabale and flows northwest into Lake Edward. It flows through the northwestern part of the forest for 15 miles, and a belt of forest follows the river down to the plain, becoming narrower as it descends, until it becomes gallery forest surrounded by savanna. In this way the Ishasha River is responsible for extending the forest below altitudes in which it could be expected to occur, and many lowland forest species are to be found in the lower reaches.

The soils in the Kigezi Highlands are mainly tropical red earths, with an overlying layer of brown to black spongy humus. The vegetation is complex, affected by altitude, topography, and soil depth. It can, however, be divided into two types. The nomenclature is that of the Yangambi classification, which is followed in the Atlas of Uganda.

1. Moist Montane Forest. Type 3a. The dominant genus is *Pygeum*, and other abundant plants are *Chrysophyllum* spp., *Newtonia*, and *Entandrophragma*. Some *Podocarpus* spp. are present, and in the highest areas, around 8000 feet, there are small patches of bamboo (*Arundinaria alpina*). The montane forest occupies roughly the southern and highest half of the forest.

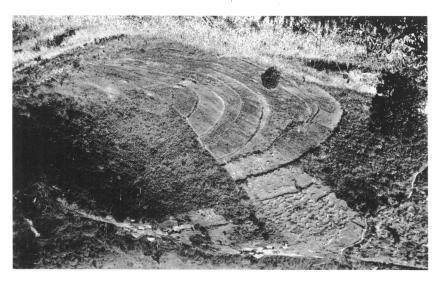


Fig. 5. Contour farming, typical in the Kigezi District, near the forest edge, 6000 feet.



Fig. 6. Bwindi Swamp, 6750 feet.

2. Medium Altitude Moist Evergreen Forest. Type 5c. Dominant plant, *Parinari*. The medium altitude forest occupies the northern half of the forest.



Fig. 7. Forested ridge, 7000 feet.

It is difficult to draw vegetational boundaries in this case because there is continuous forest from 3500 feet to 8200 feet, but the above-mentioned two forest types more or less correspond to the widely used concepts of "montane forest" and "lowland forest" (e.g., Chapin, 1932; Moreau, 1966). The Impenetrable Forest is the only one in East Africa that contains both montane and lowland forest in a continuum. Other forests do not have such an altitudinal span and can be assigned to one or another vegetation type.

Annual rainfall ranges from 45 inches in the drier montane areas to 75 inches in the north. Leggat and Osmaston (1961) noted that the forest was normally too moist to burn, but that in exceptionally dry years, for example, 1960–1961, considerable areas were burned. Twomey, who visited the forest in August, 1960, saw extensive burning on the higher ground, and on various occasions counted between 10 and 55



Fig. 8. Mixed bamboo and montane forest, 8000 feet.

individual fires burning concurrently. He frequently met an African runner carrying a charcoal burner up the mountainside to the drier ridges to start fresh fires. It is not clear whether the burned areas were part of the forest reserve or not. The present reserve consists of 115 square miles, gazetted in 1948 as the Impenetrable Central Forest Reserve. Areas outside the reserve are presumably open to agricultural use, and burned areas are put under the contour farming typical in Kigezi. Destruction of virgin forests for agriculture is a worldwide phenomenon, but East Africa has been relatively free of it up to this point. Most of the forests are under government control, and burning is not permitted.

We want to point out that confusion has been caused by the fact that the forest has been known by several different names, each one designating a different part of the forest. The lowest level was called the Kalinzu Forest; the intermediate level, the Kayonza Forest; and the higher levels only were included under the term, "Impenetrable." All these areas are contiguous, however, and we here dispose of the names Kalinzu and Kayonza and refer to the whole area as the Impenetrable Forest.

DISCUSSION OF THE CHECK LIST OF BIRDS

Table 1 is a list of all the species recorded from the Impenetrable Forest, including birds found at or near the forest edge and those flying over the forest. The altitude at which each species has been collected or observed is given, and an attempt has been made to assign an ecological classification to each species.

In the altitude columns, occurrences have been assigned to the nearest 1000 feet, except in the case of the lowest collecting area at 3500 feet. Birds that were collected at 5300 feet appear in the 5000-feet column, whereas birds taken at 6750 feet appear in the 7000-feet column. We show that there are practically no occurrences listed for 6000 feet; this is so because the road at that point leaves the forest briefly and rises over a ridge, re-entering at about 6500 feet. A dash (—) in an altitude column merely means that the bird has not as yet been taken or observed at that altitude; the forest has not yet been sufficiently explored for us to be able to say that a certain bird does not occur at a given altitude. Treron australis, for instance, is listed as occurring at 3500, 5000, and 7000 feet, but it is safe to assume that it occurs at 4000 and 6000 feet, as well.

Sight records are listed, as are collected specimens, and for 42 species there is only a sight record. These sightings were all by Keith and Williams who have had wide experience in identifying African birds in the field. In all cases the species involved are readily identifiable in the field, e.g., Bostrychia hagedash, Agapornis pullaria, and Motacilla aguimp. Sight records that were less certain have been relegated to the hypothetical list (see page 37). Those species for which there is only a sight record have not been given a trinomial, even where there is little doubt as to which subspecies should occur in the forest.

ECOLOGICAL CLASSIFICATION

Anyone drawing up a list of birds of a forest is faced with the problem of deciding which birds qualify as "forest" birds and which should be excluded as belonging more typically to another habitat. The majority of cases are easy to decide, but there are enough borderline cases

TABLE 1 CHECK LIST OF SPECIES RECORDED FROM THE IMPENETRABLE FOREST, WITH ALTITUDES AT WHICH THEY OCCUR AND ECOLOGICAL CLASSIFICATION.	ROM THE]	[MPENETR	ABLE FOI	TABLE test, with A	LE 1 н Агтт	IDES AT W.	нісн Тнеу (Occur and Eco	DLOGICAL CLASS	IFICATION.
Species	3500	4000	Altitudes in Feet 5000 6000	in Feet 6000	7000	8000	Forest	Ecological Forest and Non-forest	Ecological Classification orest and on-forest Non-forest	Migrant
Bostrychia hagedash	S					. 1		1	××	l
Anas sparsa leucostigma	1	1	Ö	I	1	I	1	l	< >	ļ
Terathopius ecaudatus	S C	I				1	1	>	∢	
Accipiter melanoleucos	'n		1		0	0	Ιİ	< ×		I
A. r. rujventris	l				י כ	5	1	×	ļ	1
A. tachtro sparsmjasciatus Rutso zufofuccus onaus	v				ט ט	\ \&		:	×	I
Duren infolusions augus B. o. oreophilus)	I	I	I	Ü	Ö	×	1	1	1
Stephanoaetus coronatus	I	1	S	I		I	×	1	1;	1
Lophoaetus occipitalis	١	1	1	I	ပ	I	1 :	ı	×	
Spizaetus africanus	I	1	1	l	Ö	ļ	×	1	l	>
Pernis apivorus		ပ	1	1		I		1 :	١	<
Aviceda cuculoides	I	I	I	1	S	1	l	×	1	I
Macheirhamphus alcinus	1	I	S	1	1	I	1	×	;	
Falco ardosiacus		Ö	1	ı	1		1 :	I	×	1
Francolinus nobilis	1	1		I	S	I	×	1	1	1
Guttera edouardi sethsmithi	ပ	1		I		I	×		>	
Limnocorax flavirostra	1	1	1	I	ပ	I	1		×	l
Columba unicincta	I	ı	I	I	S		×	I	1	
C. a. arquatrix	1	I	S	1	ပ	1	×	1	1	
Streptopelia l. lugens	١		I	1	ပ	S	×	;	1	
S. semitorquata	S	Ö	S	I		I	1:	×	l	
Turtur tympanistria	S	Ö	Ü	1	i	I	×	I	>	
T. afer	1	Ö		1	I	1	I	I	<	1

TABLE 1—(Continued)

Species			Altitude	Altitudes in Feet				Ecological (Ecological Classification	
•	3500	4000	2000	0009	7000	8000	Forest	Non-forest	Non-forest	Migrant
Treron australis gibberifrons	S	1	C		ن			×		
Agapornis pullaria	S	1	I	1	I	1	I	ı	×	١
Tauraco schutti emini	1	Ö	Ö	ı	Ö	Ö	×	1		1
T. johnstoni kivuensis	1	1	I	I	Ö	ပ	×	1	1	1
Musophaga rossae	S	1	1		1	1	1	I	×	I
Corythaeola cristata	S	I	S	1	Ö	Ö	×	1	I	1
Clamator levaillantii	1	1	ပ	ı	Ü	ı	ı	1	×	ı
Cuculus s. solitarius	I	ı	S	1	Ü	1	1	×	ı	
C. clamosus gabonensis	ပ	1	1	1	1	1	×	1	1	I
Cercococcyx mechowi	S	1	S	1	I	1	×	I	I	1
C. m. montanus	ı	1	ပ	1	ပ		×	l	1	I
Chrysococcyx klaas	S	ပ	S	I	I	1	l	I	×	-
C. caprius	S	ပ	S	1	١	1	ı		×	
C. c. cupreus	S	ပ	S	ı	I		×	1	ı	1
Ceuthmochares a. aereus	S	1	Ö	I	ı	ļ	×	١	I	1
Centropus superciliosus	S	1	1	1			1	1	×	1
Bubo p. poensis	1	1	ပ	1	Ö	ı	×	ı	ŀ	
Glaucidium tephronotum medje	1	ı	ပ	1	ပ	1	×	ı	!	1
Ciccaba woodfordi	S	ı	S	1	S	ı	×	1	ı	1
Caprimulgus e. europaeus	!	I	I	ı	ပ	1	1	I	1	×
C. pectoralis	S	١	I	1	I	1	1	1	×	
C. poliocephalus ruwenzorii	1	I	ပ	ı	ပ	Ö	1	ı	×	1
Apus myioptilus	I	1	S	1	I	ı	1	1	×	1
A. horus	1	I	1	1	ပ	1	1	1	×	
A. caffer	S	1	1	I	1	1	I	1	×	ı

			T/	TABLE 1—(Continued)	-(Continu	ed)			'	
Species	3500	4000	Altitude 5000	Altitudes in Feet 5000 6000	7000	8000	Forest	Ecological Forest and Non-forest	Ecological Classification orest and on-forest Non-forest	Migrant
Chaetura ussheri	1	1	S	I	I	1	×	l	l	l
Colius striatus kiwuensis	S	I	ပ	I	Ö	I	1	1	×	ļ
Apaloderma narina brachyurum	I	١	I	I	Ö	ı	×	1	I	
A. vittatum	I	l	Ö		Ö	Ö	×	1	-	1
Ceryle maxima	1	I	ပ	I	-	I	1	1	×	1
Alcedo quadribrachys	S	1	١	l	I	1	×	l	-	1
Halcyon leucocephala	S					I	1	ļ	×	1
H. m. malimbica	S	Ü	1	1		1	×	l	1	1
Merops lafresnayii oreobates	1	Ö	Ö	1	Ü	1	×		1	1
M. gularis australis	I	Ö	١	I		I	×	1	l	I
Eurystomus glaucurus afer	١	١	Ö	1	1	1		×	1	1
Phoeniculus bollei jacksoni	1		Ö	1	ပ	1	×	1	I	I
P. cyanomelas	S	ļ	{	ļ	1	١	1	1	×	I
Tockus alboterminatus geloensis		1	S	ļ	Ü	ı	1	-	×	1
Bycanistes albotibialis	S	١	1	1	I	1	×		ſ	1
B. subcylindricus	S	I	1	1	I	I	×		1	
Lybius bidentatus aequatorialis L. hirsutus ansoroii	I	C		1	1	I		I	×	
$(=Tricholaema\ flavipunctatum)$	S	ပ	ပ	I	1	ļ	×	-	1	ļ
Gymnobucco bonapartei cinereiceps	I	Ü	Ö	1	ပ	1	×	1	1	
Pogoniulus scolopaceus aloysii	S	Ö	Ö	I		I	×	1	1	
P. coryphaeus	1	I	I	I	Ö	S	×	I	I	1
P. bilineatus mfumbiri	İ	Ö	Ö	ပ	Ü	I	×	1	I	1
ıeı	1	1	ပ	1		-	×	I	1	
Trachyphonus purpuratus elgonensis	S	Ö	l	l	Ŋ	l	×	13	1	1
Indicator variegatus	0	ပ	1	1	Ü	1	1	×	>	I
I. indicator	S		1	l		l		1	<	l

TABLE 1—(Continued)

								Frological	Ecological Classification	
Species			Altitudes in Feet	in Feet				Forest and		
	3500	4000	2000	0009	2000	8000	Forest	Non-forest	Non-forest	Migrant
I controstris	ω	1			1		×	ŀ	I	l
I exilis	ı	Ü	ļ	I	1	I	×	1	ſ	1
I. w. willeacksi	1	Ö	1	I	I	-	×	1	1	1
I. pumilio	١	ı	ပ	١		1	×	1	1	1
Prodotiscus i. insignis	S	ı	Ö	1	S	l	×	1	l	
Campethera caroli	١	ပ	I	I	I	1	×		I	1
C. nivosa herberti	1	Ö	ပ	I	١	ı	×	1	I	ļ
C. tullbergi taeniolaema	I	1	ပ	ပ	ပ	I	×	1	1	1
Dendropicus fuscescens lepidus	S	1	Ö	I	ပ	ı	I	1	×	1
Mesopicus e. elliotii	ļ	1	ပ		ပ	1	×		1	I
M. xantholophus	S	I	I	1	ı	I	×	1	ļ	
M. griseocephalus ruwenzorii	1	I	-		ပ	S	×	I		I
Smithornis capensis meinertzhageni		ļ	ပ	I	1	1	×	1	1	1
Pseudocalyptomena graueri		I	1	I	ပ	I	×	1	1	I
Pitta reichenowi	ပ	1	١	1	I	I	×	I	1	1
Motacilla clara chapini	1	I	Ö	I	Ö	ļ	I	1	×	1
M. capensis wellsi	1	1	ပ	1	ပ	1	1	I	×	
M. aguimp vidua	S	ı	S	ŀ	I	I	1	1	×	1
Malacocincla albipectus	ပ	١	ပ	1		1	×	1	1	l
M. p. pyrrhoptera	1	1	ပ	1	ပ	1	×	I	I	1
M. fulvescens ugandae	ပ	I	Ö	l	1	1	×	1		
M. poliothorax	ı	I	Ö	I	ပ	ı	×	1	1	ı
Alcippe abyssinica atriceps	1 4	1	1	1	U i	Ü	×	1	1;	1
Pycnonotus barbatus tricolor	S	l	ပ	1	Ü	I	I		×	
Andropadus c. curvirostris	1	Ö	Ö	I	ŀ		×	1		I

TABLE 1—(Continued)

			Altitudes in Peet	: - - - -				Ecological (Ecological Classification	
species	3500	4000	5000	0009	7000	8000	Forest	Non-forest	Non-forest	Migrant
A. gracilirostris congensis	v2	υ	ت			ı	×	I		I
A. virens holochlorus	Ö	I	Ö	1	1	1	×	I	1	ı
A. latirostris eugenius	S	1	ပ		ပ	ပ	×	l	1	1
A. montanus kakamegae										
$(=Anzelocichla\ masukuensis)$	ı	I	Ö	1	I	l	×	1	1	1
A. tephrolaemus kikuyuensis	I	1	S	I	ပ	Ö	×	1	1	ı
Baeopogon i. indicator		ပ	I	1		1	×	ı	1	1
Phyllastrephus fischeri cabanisi	I	ı	ပ	1		1	×	I	1	1
P. baumanni hypochloris	١	Ö	I	I	1	1	×	1	1	1
P. flavostriatus olivaceogriseus	1	1	ပ		Ö	Ü	×		1	1
Bleda syndactyla woosnami	ပ	ı	Ö	ı	1	1	×	1	ı	1
Cringer calurus emini	ರ	1	Ü	1	1	1	×	I	1	1
Nicator chloris	S	1	ļ	1	1	1	×	ı	1	1
Muscicapa adusta pumila	1	I	Ö	1	Ü	1	×	1	1	1
M. lendu	1	I	ပ	I	l	1	×	1	1	1
M. caerulescens brevicauda										
(=M. cinerea)	S	ပ	ŀ	1	I	1	I	×	I	1
M. griseigularis	ပ		Ö	1	1	1	×	1	1	1
M. comitata		Ö	Ö	ı	1	1	×	1	1	1
Myioparus p. plumbeus	1	ပ	ı	I	1	1	I	1	×	1
Melaenomis chocolatina toruensis										
$(=Dioptrornis\ fischeri)$	ı	l	ပ		ပ	1	×		I	l
M. ardesiaca			ပ	l	ပ	1	×	1		1
Megabyas flammulata aequatorialis	1	Ö	Ö	1	1	1	×	1	1	
Bias m. musicus	S	J	Ö	1	1	1	×	ſ	f	I

TABLE 1—(Continued)

Species			Altitudes in Feet	in Feet				Ecological Forest and	Ecological Classification orest and	
	3500	4000	2000	0009	7000	8000	Forest	Non-forest	Non-forest	Migrant
Batis diops	1		Ö	ı	ت	Ü	×			1
B. molitor	1	1	Ö	1	Ö	1	ļ	l	×	1
Platysteira cyanea nyansae	1	Ö	Ö	I	Ö	I	×	I		1
P. castanea	S			1		1	×	I	1	
P. jamesoni	S	S			1	١	×	1		I
Trochocercus albicauda	1	1	١	١	Ö	I		ı	×	1
T. longicauda teresitus	1	Ö	Ö	1	1	ı		-	×	1
T. nigromitratus	1	1	Ö	1	Ö	I	×	1	l	
T. a. albonotatus	1	1	1		Ö	ပ	×	ļ	I	I
T. albiventris toroensis	1	1	Ö	1	Ö	I	×	I	1	1
Terpsiphone viridis kivuensis	1	Ö	Ö	1	ပ	I	1	×	1	1
Turdus piaggiae williamsi	1		Ö	١	1	l	×	I	l	1
T. abyssinicus bambusicola	1	1	Ö	I	Ö	l	×	l	1	
T. pelios centralis	I	1	Ö	1	İ	l	ı	×	1	I
Neocossyphus poensis praepectoralis	Ö	Ö	Ö	1		l	×	1	ı	1
Stizorhina fraseri vulpina	S	Ö	1	1		1	×	I	1	I
Saxicola torquata	i.	1	1	1	S	1	1	1	×	1
Cossypha natalensis intensa	ပ	1	1	1	Ö	1	1	×	ļ	1
C. polioptera	S	I	1	1	1	1	×	l	ı	ı
C. niveicapilla melanota	I	Ö	Ö	ļ		1	1	l	×	I
C. roberti rufescentior	1	I	Ö	1	I	1	×	1	l	1
C. archen—?subspecies	1	1	1	1	Ö	Ö	×	1	ł	1
Sheppardia a. aequatorialis	1	I	ပ	1	Ö	1	×	1	1	1
Alethe diademata	S	1	1	ļ	1	1	×	1	ı	ļ
A. p. poliophrys	I	1	ပ	1	ပ	ပ	×	1	1	
A. poliocephala	Ω	1	ł	1	1	1	×	1	1	1

TABLE 1—(Continued)

			Altitudes in Peat					Ecological	Ecological Classification	
Species	3500	4000	5000	0009	2000	8000	Forest	Non-forest	Non-forest	Migrant
Cercotrichas hartlaubi	1	1	Ö	I	S	1	I	ļ	×	-
Pogonocichla stellata ruwenzorii	1	I	I	1	Ö	Ö	×	1	1	1
Bradypterus g. graueri	!	1	1	1	ပ	1			×	I
B. c. cinnamomeus	1	١			Ö	١	×	1	1	1
B. barrattı barakae	1	١	١	1	Ö	1	×	l	1	1
Chloropeta similis		1	-	1	Ö	ပ	×	I	١	I
Phylloscopus trochilus acredula	1	1	1	!	ပ	1		I	1	×
P. sibilatrix	1	Ö		١	1	ı		I	1	×
P. l. laetus	1	1	Ö	I	Ö	I	×	ı	-	l
Sylvia a. atricapilla	1	١	Ö	-		ပ	-	I	ı	×
Apalis rufogularis kigezi	S	Ö	Ö	١	١	1	×	1	1	١
A. ruwenzoru	1	I	Ö	1	ပ	Ö	×	l	I	1
A. binontata personata	I	1	ပ	1	ပ	ပ	×	1	1	1
A. j. jacksoni	1	ပ	ပ	1	ပ	I	×	I	1	I
A. p. porphyrolaema	1	1	1	1	ပ	İ	×	I	1	1
A. c. cinerea			ပ	١	1	1	×	l	1	1
Bathmocercus cerviniventris vulpinus	1	}	ပ	1	1	1	×	1	l	1
Sylvietta virens	S	1	1	1	l	1	×	1	1	1
S. leucophrys chloronota	I	1	Ö	1	ပ	ပ	×	I	1	1
Hemitesia neumanni	I	ļ	Ü	1	ပ	1	×	I	1	1
Camaroptera superciliaris	ļ	I	Ö	1	1		×	ļ	l	1
Graueria vittata	1	1	Ö	1	Ö	I	×	ı	1	1
Cisticola chubbi	1	1	ပ	1	ပ	ပ	1	I	×	1
C. erythrops	S	1	I	1	I	1	1	!	×	1
Prinia subflava	Ø	1	I	1	1	-	1	1	×	I

TABLE 1—(Continued)

S			A 14:4:42	i. Door				Ecological	Ecological Classification	
species	3500	4000	5000	5000 6000	2000	8000	Forest	rorest and Non-forest	Non-forest	Migrant
P. leucopogon reichenowi	I	Ö	S	-	1		×	-	ı	1
P. bairdii obscura	1	١	Ö	I	Ö	ပ	×	I	1	J
Hylia p. prasina	Ö		Ö	İ	1	1	×	1	1	ı
Riparia y. riparia	1	ပ	ı	I	1	ı	1	1	I	×
Hirundo senegalensis	S	1	S	1	1	I	1	!	×	l
H. angolensis	İ	١	Ö	1	Ö	ı	1	1	×	ı
H. abyssinica unitatis	1	Ö			1	I	1	1	×	1
H. fuligula fusciventris	1	I		1	Ö	I	1	1	×	I
H. daurica	1	١	ပ	I	1	1	1	I	×	1
Psalidoprocne pristoptera										
(=holomelaena) ruwenzorii	S		Ö		ပ	ರ	×	ļ	I	1
P. albiceps	ß	ļ			ł	İ	1	1	×	1
Campephaga phoenicea	S	1	1	ı	1	I	١	1	×	ı
C. petiti	İ	1	Ö	1		1	×	1	1	1
Coracina caesia pura		1	1	١	Ö	I	×	1	ļ	1
Dicrurus modestus										
$(=adsimilis\ coracinus)$	1	1	Ö	I	1	1	×	-	1	l
Lanius mackinnoni	1	ပ	Ö	I	ပ	I	×	-	1	ı
Laniarius poensis holomelas	1	١	Ö	1	ပ	İ	×	1	-	١
L. l. luhderi	Ö	Ö	Ö	1	S	ı	×	1	1	I
Dryoscopus gambensis erwini	1	1	I	١	Ö	ı	1	1	×	1
D. angolensis nandensis		Ö	ပ	١	Ö	1	×	1	ı	1
Tchagra australis emini	1	Ö	ပ	1	I	ł	1	I	×	1
Malaconotus multicolor graueri	I	1	Ö	1	1	١	×	1	1	1
M. bocagei jacksoni	S	Ö	ပ	1	1	l	×	I	1	I

Species 3500 400 M. lagdeni Telopiorus dohertyi Parus f. fasciiventer P. f. funereus Oriolus tarvatus percivali O. brachyrhynchus laetior O. auratus notatus Corous albus C. albicollis Cinnyricinclus leucogaster C. sharpei Lamprotomis purpureiceps C. sharpei Lamprotomis purpureiceps Onychognathus walleri elgonensis O. tenuirostris theresae Poeoptera lugubris webbi P. stuhlmami O. tenuirostris stressae Poeoptera lugubris webbi S. stuhlmami									
3500		Altitudes in Feet	: بر بو				Ecological (Ecological Classification	
	4000	5000	0009	2000	8000	Forest	Non-forest	Non-forest	Migrant
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, pris %	١	1	ı	Ö	I	×	1		1
	Ö	S	١	1	ı	×	1	1	
w	١	ပ	1	Ö	1	×	1	-	
∞ ∞	1	Ö		1	1	1	×	-	
	Ö	Ö		1	1	×	I	1	1
	Ö	Ö	1	ပ	ı	×	1	I	
1	ı	Ö	l	Ö	Ö		×	1	
		1	I	Ö	I	1	1	×	1
1	1	1	1	ပ	1	×	I	1	
I	1	1	I	ပ	١		1	×	1
S	Ö	1	1	١	ı	×	I	-	
1	١	Ö	ပ	ပ	1	1	1	×	
N. chloropygia orphogaster	Ö	1		I	I	×			
						;			
I	Ö	Ö	1	ပ	ပ	×	1	1	1
1	I	ပ		Ö	I	×	1	1	1

TABLE 1—(Continued)

			A 14:14.	<u>.</u>				Ecological	Ecological Classification	
Species	3500	4000	Altitudes in Feet 5000 6000	in Feet 6000	7000	8000	Forest	Forest and Non-forest	Non-forest	Migrant
N. r. rubescens	S	C	C	1	-	1	X	ı	-	I
N. senegalensis	S	ပ	Ü	I	Ö		1	I	×	ı
N. cyanolaema octaviae	I	ပ	Ö	I	I	ı	×	I	I	l
N. verticalis viridisplendens	I	ပ	Ö	1	Ö	l	×	1	ı	1
N. alinae ?subspecies			Ö	, 1	Ö	1	×	ı		1
N. seimundi	1	ပ	1	1	I	1	×	1	1	1
N. olivacea ragazzi	ပ	Ö	Ö	1	I	I	×	ı	I	I
Anthreptes collaris garguensis	S	ပ	Ö	1	ပ	ပ	×	ļ	1	1
A. rectirostris tephrolaema	ı	ပ	Ö	1	1	1	×	١	1	I
A. fraseri axillaris	1	1	Ö	1	ļ	1	×	1	l	j
Passer g. griseus	S	I	S	1	Ö	I		ļ	×	1
Ploceus n. nigricollis	S	Ö	Ö	1	1	1	ı	×	:	l
P. alienus	1	I	Ö	ı	Ö	S	×	: I	I	1
P. melanogaster stephanophorus	1	Ö	Ö	I	S	1	×			1
P. baglafecht stuhlmanni	l	1	Ö	1	Ö	I		×		1
P. n. nigerrimus	I	Ö	1	ı	١	I	1	I	×	
P. superciliosus										
$(=Pachyphantes\ pachyrhynchus)$	Ö	1	S	1	ļ	1		I	×	1
P. tricolor	1	I	S	I	1	I	×	ļ	ļ	1
P. insignis	1	Ö	ပ	ļ	ပ	1	×	1	l	1
Malimbus r. rubricollis	S	ပ	Ö	I	I	I	×	I	I	I
Vidua macroura	ı	١	Ö	ı	1	ı	1	1	×	I
V. chalybeata centralis	1	ပ	1	I	1	1	I	ı	×	1
Lonchura c. cucullata	S	Ö	Ö	I		ı	1	I	×	I
L. bicolor poensis	S		Ö	1	1	J	l	I	×	١

TABLE 1—(Continued)

								Ecological (Ecological Classification	
Species	3500	4000	Altitudes in Feet 5000 6000	in Feet 6000	2000	8000	Forest	Forest and Non-forest	Non-forest	Migrant
Nigrita canicapilla schistacea	I	Ö	Ö	I	Ö	ŀ	×	l	-	1
N. f. fusconota	1	Ö	I	I	١	1	×	I	1	I
Parmoptila jamesoni	I	1	Ö	ı	١	ı	×	1	I	ı
Spermophaga ruficapilla	ပ		I	I	Ö	I	×	ı	ı	1
Cryptospiza salvadorii	ı	١	1	J	S	ı	×	l	I	I
C. jacksoni	I	1	ပ	ı	ပ	ပ	×	1	1	1
C. reichenovii australis	1	1	ပ	I	Ö	Ö	×	1	l	1
C. shelleyi	I		ပ	1	ပ	I	×	I	I	
Hypargos nitidulus schlegeli	1	1	ပ	1	ပ	1	×	I	I	1
Clytospiza cinereovinacea	1	١	I	Ö		ı	1	-	×	
Estrilda melanotis kilimensis	l	1	I	1	ပ	1	×	ı	1	
E. atricapilla graueri	ľ	1		I	ပ	ပ	×	1	-	1
E. n. nonnula	S	Ü	ပ	١	١	ļ	×	ı	1	I
E. astrild peasei	1	1	ပ	I	1	١	1	1	×	1
Nesocharis ansorgei	ပ	1	١	١	1	I	1	İ	×	1
Serinus canicollis sassii	1	I	1	-	ပ	S	1		×	1
S. atrogularis	ı	I	S		١	I	1	1	×	1
S. burtoni tanganjicae	I	1	1	ı	ပ	1	×	1	I	
S. s. striolatus	1	1	ı	1	Ü	I	-	l	×	1
Linurgus olivaceus prigoginei	1	I	ı	1	Ö	I	×	l	I	I
			America							

Symbols: C, Collected Specimen; S, Sight Record Only; X, Occurrence.

to give the classifier some difficult decisions. If the decision is made to include only strictly forest-dependent species, the reader may believe that certain borderline birds not included on the list may in fact be in the forest but have been excluded under some stringent rule made by the writer. On the other hand, if the forest list is padded with grassland species, waterbirds, overflying hawks, and the like, any comparison between this forest list and lists from other forests becomes meaningless. An additional problem is created if the writer is not personally familiar with the forest in question and is writing up a collection from information contained on the labels. Friedmann recently received a collection of birds from western Uganda, and the locality on each label was given as a particular forest, even though in some cases the species is most unlikely to have been collected inside the forest. In writing up these collections he decided (Friedmann, 1966) to include all species and did not attempt to distinguish between forest and non-forest birds.

In the present paper we decided to list all birds recorded from the Impenetrable Forest, including non-forest species, but in addition we have allocated them to a habitat instead of leaving this up to the reader. A bird is listed under a habitat heading according to its general habitat preference in Africa as a whole rather than its preference in the Impenetrable Forest area. Some birds behaving as forest species in the Impenetrable Forest area inhabit more open country in other parts of Africa, and these have been classed as "forest and non-forest."

We have followed the guidelines given by Moreau (1966, pp. 80-81) in deciding which birds to count as forest species. Birds whose typical habitat is primary or secondary evergreen forest are included, and also those birds which are more or less confined to the forest edge and clearings. Some may query the inclusion of the latter category as forest birds, but as Moreau put it (personal communication to Keith), "if the forest were not there these clearing species would not be either." This remark does not apply to savanna species that also inhabit the forest edge, and they are classed as non-forest. Examples of edge-dependent species from the Impenetrable Forest classed by us as forest birds are: Melaenornis chocolatina (= Dioptrornis fischeri), Prinia leucopogon, and Lanius mackinnoni. In considering species of the clearing, care must be taken to distinguish between those dependent on forest vegetation, and species of grassland or savanna which have moved into a non-forest habitat inside the forest. In Bwamba Forest, for example, in July, 1963, Keith found a thriving colony of Ploceus nigerrimus at Ntotoro village. Birds from this colony regularly joined bird parties of forest species in the forest canopy to forage for food. Nevertheless, although partial to forest clearings, they are not dependent on them, as they are also found in grassland and woodland, and should not be classed as forest birds.

Moreau (loc. cit.) excluded from his forest list birds that typically inhabit gallery forest but do not enter the rain forest proper, although they may reach its edges. Examples of such birds from the Impenetrable Forest are Musophaga rossae and Cossypha niveicapilla, and we have accordingly classed these as non-forest birds. Moreau made the point that gallery forest is normally dependent on ground water rather than on rainfall, and in his experience typical rain forest birds are absent from ground water forest. In this case too, a broad view is necessary. The lower Tana River in Kenya is bordered by gallery forest which is dependent on ground water rather than on rainfall, yet it is inhabited by such typical rain forest species as Neocossyphus rufus and Phyllastrephus fischeri. It seems certain that this is a relict patch of rain forest that is now kept alive by ground water (see discussion in Keith, 1968a, pp. 11-12).

Some species that behave as forest birds in tropical Africa become more tolerant in what they will accept as "forest" farther south in more temperate climates. Guttera edouardi and Ceuthmochares aereus are typical forest birds in East Africa, but in Rhodesia G. edouardi lives in thick bush, and in South Africa Ceuthmochares is found in coastal bush. Such species are nevertheless treated as forest birds because their preference is clearly for evergreen forest in those areas where it occurs.

In trying to determine the basic habitat preference of the birds of the Impenetrable Forest list we encountered so many difficult cases that we decided to create a separate category, "forest and non-forest." In spite of the clear division of African birds into forest and non-forest species there are yet a few birds which will live in both forest and in other habitats. Moreau (loc. cit., Table V) listed 42 species whose ecological niche he was unable to decide, and 19 species appear in the "forest and non-forest" column in table 1. Broken down into families, we list the following: Accipitridae, 5; Columbidae, 2; Cuculidae, 1; Coraciidae, 1; Indicatoridae, 1; Muscicapidae, 2; Turdidae, 2; Oriolidae, 1; Sturnidae, 1; Zosteropidae, 1; Ploceidae, 2. In many cases the individual birds will move readily from one habitat type to another, as for example the starling Onychognathus tenuirostris which nests near waterfalls but gets much of its food from forest trees. It is easy to see that wide-ranging birds such as hawks can tolerate several different habitats. A slightly different category also has to be included in the "forest and non-forest" column, namely those birds that have different races in forest and in non-forest habitats. In this case the individual birds do not move from

one habitat type to another, the forest race remains inside the forest and the savanna birds remain in the savanna. Examples from our list are Oriolus larvatus, with the forest race percivali, and the wide-ranging Zosterops senegalensis, about whose taxonomy there has been much discussion. The East African forest birds were formerly treated as a polytypic species, Z. virens, whereas senegalensis included only non-forest birds. More recent treatments (e.g., White, 1963) made senegalensis a polytypic species with both forest and non-forest forms.

The column headed "migrant" under ecological classification refers to Palaearctic migrants only, to which it seemed pointless to assign an African habitat.

Comparison with Other Forest Lists

To summarize table 1, our check list from the Impenetrable Forest contains 265 species made up as follows: Forest species, 168; forest and non-forest species, 19; non-forest species, 72; migrant species, 6.

When we compare the Impenetrable Forest list of 168 forest birds with other forest avifaunas, it becomes apparent that we have a rich avifauna. Moreau (1966, p. 87) listed a total of 409 forest species for the whole of the Ethiopian region, and the Impenetrable Forest thus contains 41.8 per cent of the total Ethiopian list. One reason for this richness is that the forest contains within its borders both lowland, intermediate, and montane forest (see discussion below for these distinctions). This fact must be borne in mind when comparisons are made with other forest lists. The largest individual forest list cited by Moreau (1966, pp. 286-287) in a table comparing various individual forest avifaunas, is that of Bwamba, which has 128 species. Bwamba, however, is only lowland forest, and all the other forests in Moreau's table are of one type only, lowland or intermediate or montane. We must therefore, for purposes of comparison, break up the Impenetrable Forest list into lowland and montane forest birds (we have not classed any of our birds as intermediate, for the sake of simplicity). Table 2 lists the 69 Impenetrable Forest birds considered to be montane, leaving a total of 99 lowland species. The forest is a good deal poorer in lowland species than is Bwamba (128) and a little weaker than Budongo (105). (Source for forest lists quoted is Moreau, loc. cit. Table XXV.) The richer avifauna of Bwamba may be explained by the fact that it is continuous with the great Congolese lowland forest belt, whereas the Impenetrable is separated from this belt by the rift valley and the highlands of the eastern Congo. Budongo is similarly separated and consequently lacks a couple of dozen lowland species.

The Impenetrable has far more montane forest birds than has any forest quoted by Moreau. The total of 69 species compares with 51 for Ruwenzori, the highest number in Moreau's table, 43 each for Cameroon Mountain and Mt. Kenya, and 37 for Kilimanjaro. This suggests that some of the montane birds possibly should be transferred to a separate category, e.g., intermediate forest, but all birds classed as montane in table 2 are so classed by Chapin (1932, p. 252), therefore the comparison is probably a fair one. Indeed, five species on Chapin's montane list (loc. cit.) which occur in the Impenetrable Forest are not listed in table 2 because they are not confined to montane forest, and are found in low-land forest as well. It is probably safe to say that the Impenetrable Forest has one of the richest montane avifaunas in Africa, if not the richest. Only the forests on the chain of mountains called by Chapin (1932, p. 186) the Western Kivu Range, which stretch from west of Lake Edward to northwest of Lake Tanganyika, contain such a variety of species.

Carcasson (1964, p. 138), in his work on African butterflies, noted that what he called the "Kivu-Ruwenzori Zone," meaning the mountains of eastern Congo and western Uganda, with its large blocks of forest, moist climate, and proximity to lowland forest, was an interpluvial forest refuge, and thus had "probably the richest montane fauna in Africa." There are many endemic species of butterflies, just as there are of birds.

ALTITUDINAL RANGE: LOWLAND AND MONTANE FOREST

It has long been known that a marked change in the composition of bird species occurs between lowland and montane forest. Many writers (e.g., Chapin, 1932; Moreau, 1966) accepted 5000 feet as the dividing line for tropical Africa, although this line becomes lower as one proceeds south toward more temperate climates. In practice, birds have little opportunity today to put this line to the test, because most African forests are found either above or below 5000 feet, or else just at 5000 feet as in the case of a number of East African "intermediate" forests. In very few places does lowland forest actually adjoin montane forest. The Impenetrable Forest therefore offers an excellent proving ground to test whether the barrier between lowland and montane forest is real or whether the present isolation of many forests and their lack of altitudinal span makes it somewhat artificial. Carcasson (1964, p. 134), on butterflies, admitted that, "there is naturally a wide zone of vertical overlap between the two divisions (lowland and montane), particularly at the equator, where highland species do not normally descend below 3,000 feet and lowland species do not rise above 6,000 feet." Similarly Chapin (1932, p. 250) remarked that, "Not a few of the lowland forms straggle higher up the slopes than they ought in due respect to our theories, and the lower level of the mountain forms is but slightly more regular."

In the Impenetrable Forest, out of 168 forest species only 23, or 13.7 per cent, are known to "cross the line," and occur at both 4000 feet or below and 7000 feet or above. These species are:

Tauraco schutti
Corythaeola cristata
Ciccaba woodfordi
Merops lafresnayii
Gymnobucco bonapartei
Pogoniulus bilineatus
Trachyphonus purpuratus
Prodotiscus insignis
Andropadus latirostris
Platysteira cyanea
Apalis jacksoni
Psalidoprocne pristoptera

Lanius mackinnoni
Laniarius luhderi
Dryoscopus angolensis
Poeoptera stuhlmanni
Nectarinia preussi
Nectarinia verticalis
Anthreptes collaris
Ploceus melanogaster
Ploceus insignis
Nigrita canicapilla
Spermophaga ruficapilla

Only Merops lafresnayii is listed in table 2 as a montane species. The others have been counted among the 99 lowland species, even though they occur in both lowland and montane forest. This is so because in our comparisons between montane forest avifaunas (see below) we limited the list in table 2 to only strictly montane species.

The fact that in the Impenetrable Forest, which has continuous forest from 3500 feet to 8200 feet, 86.3 per cent of the forest species occur at either 5000 feet and above or at 5000 feet and below (or in some cases only at 5000 feet according to present knowledge), is impressive support for the postulated 5000-feet boundary line between lowland and montane forest bird species. Most of the 23 birds that "cross the line" are typical of the intermediate-level forests of Uganda and Kenya such as Kibale and Kakamega, which are between 5000 and 6000 feet. Other species, such as Pogoniulus bilineatus and Andropadus latirostris, are widespread in both lowland and montane forest. It is most surprising to find on the list two turacos, both of which are considered purely lowland species. White (1965) said of Corythaeola cristata, "Lowland and gallery forest, occasionally to 6,000 feet," whereas we have specimens from 7000 and 8000 feet in the Impenetrable. Corythaeola cristata and Tauraco schutti are common in Bwamba forest at 2500 feet. Furthermore, there is already a resident turaco, Tauraco johnstoni, in the montane forest, which makes the intrusion of the congeneric schutti from the lowlands more surprising, as the two might be expected to be in competition.

Carcasson (1964, p. 137), in discussing the problem of altitudinal range

of butterflies, said, "Highland forest species may descend well below their normal limits where they are not competing with lowland vicariants and vice versa." With birds, this does not really seem to be the case. Indeed, the case of the two Tauraco spp. mentioned above might seem to prove the opposite, namely that the presence of a congener was no deterrent to invasion of habitat. It should be noted, though, that schutti and johnstoni are not very close, the latter having originally been placed in a separate genus, Ruwenzorornis. However, in the list of 23 species from the Impenetrable Forest that "crossed the line," none has an obvious generic counterpart whose absence might explain the invasion of an unusual habitat, with the possible exception of Nectarinia preussi. This is an intermediate-montane species whose presence at 4000 feet can possibly be explained by the absence of the closely related lowland species, N. orphogaster, above 4000 feet. Both species have been taken at the 4000 feet level. An interesting case is that of the two trogons, Apaloderma narina and A. vittatum. Normally narina is a lowland and intermediate forest bird, being replaced in montane forests by vittatum. In this case, however, narina has been taken only at 7000 feet, whereas vittatum has been collected as low as 5000 feet as well as at higher levels.

It is interesting that in Africa as a whole there is little subspecific replacement between lowland and montane forest. In the Impenetrable Forest there is not one species with two races at different levels, although in some cases the forest has highland races of birds with lowland races elsewhere. Apalis b. binotata is a lowland forest form, being replaced in the east Congo highlands and in the Impenetrable by A. b. personata; the newly described Poeoptera lugubris webbi is a montane representative of the nominate race of the lowlands.

THE EAST CONGO MONTANE FOREST AVIFAUNA

Chapin (1932, pp. 252–253) listed 101 birds "typical of the mountain forest zone in the eastern Congo." Twelve of the birds are merely races of other birds on the list, therefore the total should be 89 species. By contrast Moreau (1966, p. 201) stated that, "the total number of typically montane forest species in the east Congo mountains is 63." Some discussion of this disparity is required.

First, the wording makes it clear that the authors have slightly different objectives. Moreau's category is more restrictive; he listed only birds that are considered montane, as opposed to lowland forest species. Chapin listed all birds typical of the mountain forest zone, even if they are found elsewhere. Thus we find the following seven species on Chapin's list which also occur in lowland forest: *Pogoniulus bilineatus, Prinia bairdii*,

Psalidoprocne pristoptera, Dicrurus ludwigii, Oriolus larvatus, Zosterops senegalensis, and Ploceus bicolor.

Second, Chapin is more liberal in his interpretation of what constitutes forest, and admitted (*loc. cit.*, p. 253) that, "Not all these birds live in the heavy shade of the forest, but at least they prefer the proximity of woods, though some may be found, as a rule, in patches of scrub or bracken." The following 10 birds, all but three of which occur in the Impenetrable Forest, are not considered by us to qualify as forest species: Accipiter rufiventris, Poicephalus robustus, Caprimulgus poliocephalus, Apus aequatorialis, Cossypha caffra, Cisticola chubbi, Batis molitor, Onychognathus tenuirostris, Nectarinia venusta, and Serinus striolatus.

Chapin's list is thus reduced to 72 species. Five species, however, must be added to Chapin's list which either have been recently described (e.g., Indicator pumilio) or were not known from the area in 1932. These are: Indicator pumilio, Melaenornis ardesiaca, Prionops alberti, Poeoptera stuhlmanni, and Linurgus olivaceus. Our total for montane forest species in the eastern Congo is thus 77 species, as opposed to Moreau's total of 63. The difference in the total may be due in part to different taxonomic viewpoints; for instance, we do not consider Apalis ruwenzorii and A. pulchra to be conspecific. The bulk of the disparity is probably due to our admission of certain "intermediate forest" species as montane, such as Smithornis capensis, Phyllastrephus fischeri, and Malaconotus multicolor. Possibly, we have admitted some birds which Moreau would not have considered forest species, although we have followed his guidelines rather closely. In any case, the over-all conclusions we make below based on table 2 would be little affected by the removal of a dozen species from the list, because most species are common to the majority of the montane forests under consideration. The proportionate size of the list of each forest in table 2 would probably remain about the same.

The Impenetrable Forest has 69 of the 77 montane forest species of the east Congo area, according to our figures. The eight species lacking there are: Aplopelia simplex, Asio otus abyssinicus, Lioptilus rufocinctus, Apalis pulchra, Coracina graueri, Prionops alberti, Nectarinia rockefelleri, and Nectarinia afra.

Apalis pulchra replaces ruwenzorii on the Lendu Plateau. Prionops alberti is on the hypothetical list of the Impenetrable Forest on the basis of a sight record. The two sunbirds are unlikely to turn up in the forest as their habitat is at higher elevations, 9000–12000 feet in bamboo, Hagenia, and tree heaths. The other four species might reasonably be expected and should be sought by future collectors.

MONTANE FOREST SPECIES OF THE IMPENEIRABLE FOREST AND THEIR OCCURRENCE IN CITIES PROFITABLE CONTRACT	T SPECIES OF THE	MPENETRABLE	FORESI AND 11	IEIR OCCURRENC	T IN CINER IN	Toron Turk		
	1		W. of Lake	W. of Lake	W. of Lake	Volcanoes	Kabobo	Kenva
Species	rendu	Nuwellzori	Edwald	naixi	r angany ma			
Buteo oreophilus	1	×	×	×	×	×	ļ	×
Francolinus nobilis	×	×	×	×	×	×	×	1
Columba arauatrix	I	×	×	×	×	×	×	×
Streptobelia lugens	I	I	×	×	×	×	1	×
Tauraco 10hnstoni	1	×	×	×	×	×	×	1
Cercococox montanus	ŀ	×	×	×	×	×	1	×
A valoderma vittatum	×	I	×	×	×	!	×	×
Merops laftesnavii	l	×	×	×	×	×	×	×
Poponiulus corrohaeus	I	×	×	×	I	×	I	
Indicator pumilio	1	I	×	×	×	1	1	×
Cambethera tullberei	×	I	×	×	×	×	×	×
Mesopicus griseocephalus		×	×	×	×	×	×	1
Smithomis capensis	×	ı	×	×	×	I	1	×
Pseudocalyptomena graueri	I	1	1	1	×	1		1
Malacocincla pyrrhoptera	×	×	×	×	×	×	×	×
M. poliothorax	×	×	×	×	×	×	×	×
Alcippe abyssinica	×	×	×	×	×	×	×	×
Andropadus tephrolaemus	1	×	×	×	×	×	×	×
Phyllastrephus flavostriatus	×	l	×	×	×	1	×	×
P. fischeri	×	×	×	×	×	1	×	×
Muscicapa adusta	×	×	×	×	×	×	×	×
M. lendu	×	1	ļ	I	1		1	×
Melaenornis ardesiaca	1	1	×	×	×	1 :	!	;
M. chocolatina	×	×	×	×	×	×	;	×
Batis diops	I	×	×	×	×	×	×	l

TABLE 2—(Continued)

Species	Lendu	Ruwenzori	W. of Lake Edward	W. of Lake Kivu	W. of Lake Tanganyika	Volcanoes	Kabobo	Kenya
Trochocercus albonotatus	!	×	×	×	×	×	×	×
T. albiventris	×	1	×	ı		1	1	1
Turdus piaggiae		×	1	1	×	×	×	×
T. abyssinicus	×	×	×	×	×	×	×	×
Cossypha roberti	1	ı	×	1	×	I	1	İ
C. archeri		×	×	×	×	×	×	ı
Sheppardia aequatorialis	×	I	I	×	×	1	1	×
Alethe poliophrys		×	×	×	×	×	×	I
Pogonocichla stellata	1	×	×	×	×	×	×	×
Chloropeta similis		×	×	1	×	×	×	×
Bradypterus barratti		×	×		×	×	×	×
B. cinnamomeus		×	×	1	×	×	×	×
Phylloscopus laetus	×	×	×	×	×	×	×	-
Apalis ruwenzorii		×	×	×	×	×	×	
A. binotata	×	×	×	×	×	×	×	1
A. porphyrolaema		×	×	×	×	×	×	×
A. cinerea	×	ı	×	×	×		×	×
Sylvietta leucophrys	×	×	×	×	×	×	×	×
Hemitesia neumanni		ı	×	I	×	I	×	I
Graueria vittata	×	1	×	×	×	1	1	1
Coracina caesia	×	×	×	×	×	×	×	×
Laniarius poensis	×	×	×	×	×	×	×	1
Malaconotus lagdeni		×	×	×	×	×	1	1
M. multicolor	×		×	×	×	-	1	1
Telophorus dohertyi	1	I	×	×	×	×	×	×
Parus fasciiventer	1	×	×	×	×	×	×	l

TABLE 2—(Continued)

Species	Lendu	Ruwenzori	W. of Lake Edward	W. of Lake Kivu	W. of Lake Tanganyika	Volcanoes	Kabobo	Kenya
Cinnyricinclus sharpii	×	×	×	×	×	×		×
Onychognathus walleri	×	×	×	×	×	×	×	×
Poeoptera stuhlmanni	×	1	×	×	×	×	I	×
Nectarinia purpureiventris	1	×	×	×	×	I	I	I
N. preussi	×	×	×	×	×	×	×	×
N. regia	×	×	×	×	×	×	×	1
N. alinae	×	×	×	×	×	×	×	1
Ploceus alienus	1	×	×	×	×	×	×	I
P. melanogaster	×	1	×	1	×	ı	I	×
P. insignis	×	I	×	×	×	×	1	×
Cryptospiza salvadorii	ı	×	1	1	×	ı	×	×
C. reichenovii	1	×	×	×	1	×	1	1
C. jacksoni	×	×	×	×	×	×	×	
C. shelleyi	1	×	-	×	ı	×	1	1
Estrilda melanotis	×	×	×	×	×	×	×	×
E. atricapilla	1	1	×	×	×	×	×	×
Serinus burtoni	×	×	×	×	×	×	×	×
Linurgus olivaceus	I	ı	×	×	×	I		×
Totals	34	47	63	58	49	20	45	42



Fig. 9. Map showing location of Impenetrable Forest and major forested areas to which it is related.

RELATIONSHIPS OF THE MONTANE FOREST AVIFAUNA

Table 2 lists the 69 montane forest birds found in the Impenetrable Forest and shows their occurrence in other montane forests. A word of explanation is necessary for some of the column headings. "Lendu" refers to the mountain forest on the highland west of Lake Albert, generally known as the Lendu Plateau. The terms "W. of Lake Edward," "W. of Lake Kivu," and "W. of Lake Tanganyika" refer jointly to the Western Kiva Range. This area might well have been considered as one unit, but because the forest is not continuous and because these are three

separate and well-known collecting areas, they are listed separately. "Kenya" does not refer to Mt. Kenya but to the forests of the Kenya Highlands as a whole, both east and west of the rift. Sources drawn on in the compilation of this table, in addition to the localities mentioned by Chapin (1932, 1939, 1953, 1954), are Curry-Lindahl (1960, 1961) and Prigogine (1953, 1960). Also, a number of records for the "W. of Lake Kivu" column were obtained from a collection made in that area by Chapin and his wife from 1953 to 1958. This collection has not yet been published on, and Mrs. Chapin has kindly given her permission for the inclusion of these records in the present paper.

Chapin (1932, map p. 90) included the highlands of eastern Congo and western Uganda in the Eastern Montane District, along with the mountains of Kenya, Tanzania, and Malawi. Moreau (1966, chap. 11) subdivided this region, treating the montane bird faunas of the east Congo as one unit. The upper levels of the Impenetrable Forest, although politically in Uganda, are clearly part of this east Congo montane district, as are two other areas in Uganda, the Ruwenzori Range, part of which is in Uganda and part in the Congo, and Mt. Muhavura, which is the most northerly of the Kivu Volcanoes.

It is clear from table 2 that the montane forest avifauna of the Impenetrable Forest is most closely related to that of the Western Kivu Range. Of the 69 montane species, 64 are found in the mountains northwest of Lake Tanganyika, 63 in mountains west of Lake Edward, and 58 in mountains west of Lake Kivu. The high score of the "Itombwe" area northwest of Lake Tanganyika is especially interesting, because geographically this is farther from the Impenetrable than any other Congo area except Lendu and Kabobo. The Volcanoes, although right next to the Impenetrable, share only 50 species with it, and Ruwenzori is even poorer with 47. It is noteworthy that the montane bird faunas of Kenya, with 42 shared species, score only five fewer than the Ruwenzori. This fact gives support for the assumption that these montane forests were all joined during a recent glacial period, even though today the Kenya forests are separated from those of the eastern Congo by 300 miles of savanna.

Chapin (1932, p. 255) commented that a number of species common in the Kivu are rare or wanting on Ruwenzori, and suggested this was partly due to isolation by the rift valley, partly to differences in vegetation. The Volcanoes, although less isolated than Ruwenzori, also have a poorer avifauna than the mountains on the west side of the rift. The following species, present in the Impenetrable Forest and the Western Kivu Range, are absent from both Ruwenzori and the Volcanoes:

Abaloderma vittatum Indicator pumilio Smithornis capensis Pseudocalyptomena graueri Phyllastrephus flavostriatus Muscicapa lendu Melaenornis ardesiaca Trochocercus albiventris Cossypha roberti Sheppardia aequatorialis Apalis cinerea Hemitesia neumanni Graueria vittata Malaconotus multicolor Ploceus melanogaster Linurgus olivaceus

The following additional species are missing from either Ruwenzori or the Volcanoes but not from both. Missing from Ruwenzori only: Streptopelia lugens, Campethera tullbergi, Telophorus dohertyi, Poeoptera stuhlmanni, Ploceus insignis, and Estrilda atricapilla.

Missing from the Volcanoes only: Phyllastrephus fischeri, Nectarinia purpureiventris, and Cryptospiza salvadorii.

Subspeciation in East Congo Montane Birds

Subspeciation among the 77 montane forest birds of eastern Congo and western Uganda may be summarized as follows: Monotypic species, 25; polytypic species with the same subspecies throughout the area, 36; polytypic species with two or more subspecies within the area, 16.

The 16 species with more than one race within the area are shown in table 3, as is the race present in each forest. Endemism, as might be expected, increases on the more outlying mountains, the highest amount being on Mt. Kabobo, with six endemic races; Ruwenzori has three, Lendu and Itombwe (northwest of Lake Tanganyika) two each, and the Volcanoes, one. The central part of the east Congo montane area, comprising the Impenetrable Forest and the Western Kivu Range, has the lowest number of endemic races, but at the same time the largest number of species by a fairly wide margin. It is tempting to speculate that this central area may have been connected by forest more frequently and for longer periods during the glaciations of the Pleistocene than the more outlying mountains.

As far as subspecies are concerned, the Impenetrable Forest is much more closely related to the Volcanoes and the Western Kivu Range than it is to Ruwenzori. Out of 11 cases shown in table 3 of species shared by

TABLE 3 SUBSPECIATION IN EAST CONGO MONTANE BIRDS

Species	Impenetrable Lendu	Lendu	Ruwenzori	Subspecies W. of Lake Edward	W. of Lake Kivu	W. of Lake Tanganyika	Volcanoes	Kabobo
Tauraco johnstoni Lioptilus rufocinctus	kivuensis 		johnstoni —	johnstoni chapini	kivuensis	kivuensis rufocinctus	kivuensis	bredoi rufocinctus
Phyllastrephus flavostriatus Turdus piaggiae T. obnesmicus	olivaceogriseus williamsi hambusicola	graveri —	— williamsi haraka	graueri — hombusicolo	graueri — hambusicola	olivaceogriseus piaggiae hambusicola	— williamsi hamhisicola	olwaceogriseus piaggiae bambusicola
Cossypha archeri Alethe poliophrys Phylloscopus laetus	poliophrys laetus	ourman — — — — — — — — — — — — — — — — — — —	archeri poliophrys laetus	archeri poliophrys laetus	archeri poliophrys laetus	albimentalis poliophrys laetus	archeri poliophrys laetus	kimbutui kaboboensis schoutedeni
Apalis porphyrolaema Sylvietta leucophrys Parus fasciiventer	porphyrolaema chloronota fasciiventer	chapini —	porphyrolaema leucophrys fasciiventer	porphyrolaema chloronota fasciiventer	porphyrolaema chloronota fasciiventer	porphyrolaema chloronota tanganjicae	porphyrolaema chloronota fasciiventer	kaboboensis chloronota kaboboensis
Nectarinia regia N. alinae N. afra Melaenomis	kivuensis ?	kivuensis alinae —	regia alinae stuhlmanni	kivuensis tanganjicae chapini	kivuensis tanganjicae chapini	kivuensis tanganjicae chapini	kivuensis tanganjicae graueri	kivuensis tanganjicae chapini
chocolatina Bradypterus cinnamomeus	toruensis cinnamomeus	semicincta	toruensis mildbreadi	toruensis cinnamomeus	toruensis	toruensis cinnamomeus	toruensis cinnamomeus	cinnamomeus

Impenetrable and Ruwenzori, the subspecies in five cases is different, whereas in every case of species shared with the Volcanoes and the Western Kivu Range (excepting the two endemic races of Itombwe), the subspecies is the same.

RELATIONSHIPS OF THE LOWLAND FOREST AVIFAUNA

The 99 species in the Impenetrable Forest classed as lowland forest birds are nearly all of wide distribution, and do not indicate that the forest is related to any particular lowland forest area. With the few exceptions noted below, all the species occur both in the lowland forest of the Congo Basin, in Bwamba forest, Uganda, which is an extension of the Congo forest, and in the "intermediate" forests of Uganda, which lie mostly between 4000 and 6000 feet. Many also occur in Kakamega Forest in West Kenya, which is related to the Congolese forests.

The exceptions to this wide distribution are as follows: Impenetrable Forest species missing from the Congo Basin, Phyllastrephus baumanni; missing from Bwamba: Spizaetus africanus, Bubo poensis, Indicator willcocksi, Andropadus montanus, Dryoscopus angolensis, Parus funereus, and Apalis jacksoni; missing from Uganda Intermediate Forests: Spizaetus africanus and Bubo poensis.

DISCUSSION OF INDIVIDUAL SPECIES

We do not consider it valuable to discuss individually each species occurring in the Impenetrable Forest because in most cases there is little to add to the information contained in the three tables. The forest is not sufficiently explored for us to be able to assess the population of each species in such terms as "common" or "rare." The especially interesting birds of the forest, including new subspecies, new records for Uganda, and major range extensions are covered in the papers by authors mentioned earlier. The publication of the present paper in fact establishes a new locality for many species, and in some cases this could be construed as a minor range extension, but these are not worth mentioning individually. Most specimens are readily identifiable to subspecies. Notes made by Keith on songs and calls are included in a separate paper by him covering other parts of East Africa as well.

The discussion in this section is confined to the six species on the hypothetical list and five cases in which identification to subspecies posed a problem.

HYPOTHETICAL LIST

Turacus species Pitta angolensis Prionops alberti Malimbus malimbicus Pirenestes ostrinus Serinus citrinelloides

Turacus species. A small turaco, with wings largely green, with little or no red visible. It has been seen several times by Williams. It was reported also by Jonathan Kingdom, a lepidopterist from Makerere College, Kampala, in 1967 (personal communication to Williams). The bird is definitely not T. schutti or T. johnstoni and does not resemble any known turaco.

Pitta angolensis. This species nests in southern Africa and migrates north, and has been taken in Ugandan forests in the non-breeding season. There are no specimen records from the Impenetrable Forest, but it may well occur as a migrant. Williams has examined live birds captured on the grounds of the White Horse Inn, Kabale, in October or November, 1946. Kabale is about 15 miles southeast of the forest. The birds were captured after flying against lighted windows on a foggy night.

Turdus abyssinicus. The race bambusicola differs from baraka in the more whitish ground color on the throat and lighter rufous on the underparts. Baraka occurs on Lendu and Ruwenzori, bambusicola in the southern montane areas south to Kabobo. The whitish ground color on the throat varies considerably, however. A bird in the American Museum of Natural History collection from Djugu, Lendu Plateau, shows some white ground color, although not so much as in typical bambusicola, whereas two baraka in the American Museum of Natural History collection from Ruwenzori have throats almost plain brown, the dark streaks merging with the ground color. Three birds collected by Keith on Mt. Muhavura in the Volcanoes are all different. One has much white ground color, some feathers at the base of the throat being entirely white, with no dark shaft streaks; the second is a "normal" bambusicola; the third has no white ground color and it resembles a typical baraka. In the Impenetrable Forest, six of our seven specimens have white ground color, we therefore have stated that the resident race is hambusicola.

The tone of the rufous on the underparts is a much less distinctive character, yet it happens more or less consistently that darker throated birds have darker rufous underparts. This is true of the dark-throated baraka type from the Impenetrable Forest; the rufous of its underparts

is darker than in the other specimens.

Cossypha archeri. Friedmann (1968) assigned the series obtained in the Impenetrable Forest for the Los Angeles County Museum to the race albimentalis, which is otherwise only known from the mountains northwest of Lake Tanganyika. The nominate race occurs in between these two areas on the northern part of the Western Kivu Range and on the Volcanoes. The main character distinguishing albimentalis, which is a poorly marked race, is the white area on the upper chin; a subsidiary character is the paler coloration of the belly.

Comparison of this series with long series of both races in the American Museum of Natural History reveals that the Impenetrable Forest population is in fact somewhat intermediate. The birds have some white on the chin but not so much as do birds from the type locality of albimentalis, whereas the color of the underparts is closer to that of the nominate race. Two birds collected by Keith on Mt. Muhavura, where supposedly nominate archeri occurs, are indistinguishable from two others collected by him in the Impenetrable Forest. As noted, the two races are hard to separate, and albimentalis is perhaps not really worthy of recognition.

Prionops alberti. The late T. E. E. Jackson of Kenya, a lepidopterist, told Williams some years ago that he had seen a flock of black birds with yellow crests in the Impenetrable Forest. This description could only apply to Prionops alberti, whose occurrence is entirely likely. We prefer, however, to wait for a specimen or a sight record by an experienced ornithologist before admitting the species to the forest list.

Zosterops senegalensis. According to White's (1963) classification, the race stuhlmanni occupies most of Uganda, reichenowi occurs on the southern part of the Western Kivu Range, and birds from elsewhere in the Kivu and from Ruwenzori are intermediate.

Our series from the Impenetrable Forest, although differing from these two races, does not appear to be intermediate in character. They are closest to stuhlmanni, being a similar shade of yellow below, although a trifle less bright, and lacking the green suffusion characteristic of reichenowi. The color of the underparts thus cannot be described as intermediate. Above, stuhlmanni is green washed with a brownish tinge, reichenowi is a rather darker green, and our birds are bright green. Again, allowing that it is difficult to describe the difference between shades of green, the color of the upper parts of the birds of the Impenetrable Forest is not intermediate between that of the other two races; it is brighter than either. We therefore do not consider our birds to be intergrades between stuhlmanni and reichenowi, even though this may look nice on a map, and we propose to revive the race scotti Neumann, which was

accepted by Chapin (1954). The range of scotti is coincident with that of the populations supposedly intermediate between stuhlmanni and reichenowi, and it is worth noting that the birds collected by Keith on Mt. Muhavura are identical with those from the Impenetrable Forest.

Nectarinia alinae. There are two races of this species, nominate alinae on Lendu and Ruwenzori and tanganjicae in the other east Congo montane forests. Tanganjicae differs in having a greener sheen on the head of the males. According to White (1963) the nominate race occurs in "southwest Uganda," but our extensive series from the Impenetrable Forest seems to be intermediate between the two races. Geographically this might have been expected, and it is noteworthy that Chapin (1954) remarked that males from the nearby Kivu Volcanoes, "are like those of tanganjicae but perhaps a trifle less green on the crowns."

Malimbus malimbicus. The birds seen by Williams at 3500 feet with very dark red on the chest were probably of this species. It is a common low-land forest bird.

Nigrita canicapilla. Ten of the 15 specimens from the Impenetrable Forest have a sharp demarcation between the pale gray of the top of the head and nape and the darker gray of the mantle. In the race schistacea, within whose range the Impenetrable Forest lies, the pale gray is confined to the forehead and does not cover the top of the head. The only other race having a pale gray top to the head is N.c. candida Moreau from Mt. Kungwe, Tanzania. Keith compared Twomey's two specimens from the Impenetrable Forest with the unique type of candida in the British Museum and found that the head color in candida was an even paler, more washed-out gray. Large series of schistacea were examined in London and New York and it was found that certain individuals had a tendency toward a grayer crown, that is, the pale gray of the forehead extended part way to the crown but did not cover it. The Los Angeles Museum series of 61 specimens from various forests in Uganda has a few gray-crowned individuals, in the following proportions: Budongo (one out of five); Bugoma (two out of 10); Kibale (one out of 14); Bwamba, none. Five of the Impenetrable Forest birds do not have the pale gray crown, but the forest still has a larger proportion of gray-crowned birds than obtains anywhere else. At this point, however, in view of the amount of known variation in the head color in this species, we would prefer not to recognize the Impenetrable Forest birds by a separate name, and have included them under schistacea.

Pirenestes ostrinus. Robert Smart (personal communication to Keith) saw a bird at 7000 feet which he took to be this species, noting the red in the tail that would distinguish it from the very similar Spermophaga ruficapilla.

but he did not have a close enough look at it to be sure.

Serinus citrinelloides. Keith believed a bird he saw at 5000 feet was of this species, but owing to the difficulty of separating this species from Serinus capistratus and S. koliensis in the field, he preferred to place it on the hypothetical list.

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