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Avian diversity in forest gaps of Kibale Forest National Park, Uganda

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Abstract

We studied gap avifaunal diversity in eight forest gaps within Kibale National Park using point counts. A total of 348 individuals comprising 55 species were recorded. A species-accumulation curve showed that, although not all possible species were recorded, this was a reliable representation of the entire gap avian diversity of Kibale forest. Next, we categorized the observed avifauna in terms of forest dependence and feeding guilds. Whereas the proportions based on forest-dependency were significantly different from the expected proportions when considering the avian community for the entire forest, those based on feeding guilds were not. Gap size and vegetation cover density both had positive correlations with species richness and abundance, though not always statistically significant. This study shows that gaps significantly contribute to the overall avian species richness of Kibale forest. This could be either through supporting entirely different species, or providing a burst of new resources that enables forest species to extend their home ranges or live at higher densities.

Introduction

Tropical rain forests have often been described as mosaics of different sizes and ages of re-growth. Tree falls and consequent forest gap formations are a very important source of environmental heterogeneity, which has ramifications for ecological diversification, and evolution of rain forests. As a result, gaps, both natural and artificially generated, serve as dynamic patches of forest regeneration and recovery (Kasenene 1989, Richards 1996).

Besides naturally open areas occurring along ridges and river valleys, the commonest natural cause of forest gaps is the falling of large trees caused by wind or lightning, often with a cascading effect. Other natural causes of gap formation include landslides and elephant browsing (Richards 1996). Gaps created by humans stem largely from selective logging and encroachment. While the ecological effects of logging (e.g., Dranzoa 1998) and forest edges

1 This manuscript is based on a study carried out and originally written-up by both authors, but was revised solely by the first author after it became known that the second author was deceased. The first author therefore bears full responsibility for any errors or omissions that remain in this paper.

2 This paper is dedicated to the memory of my co-author Sileshi Dejene who suddenly passed away in 2003 at the tender age of 30. A promising life and career abruptly nipped in the bud; a great and warm persona that is truly missed.

(e.g., Murcia 1995) have been relatively widely studied, far little work has been conducted in forest gaps, particularly in Africa. It is likely that gap effects on birds will depend on several features including gap size, shape, age, vegetation and distance between gaps.

Use of forest gaps by animals varies depending on species-specific requirements and gap-related characteristics. Few studies have specifically addressed the issue of vertebrate responses to gaps in tropical rain forests (e.g., Ngabo & Dranzoa 2001). The effects of gap size and vegetation on fauna in Kibale forest, Uganda, are little known, apart from the studies on rodents and elephants (Kasenene 1984, Struhsaker 1997). The number and uniqueness of rodents in Kibale is much greater in gaps than under forest (non-gap) microhabitats. Additionally, the frequency of elephant visits and the number of gaps used by elephants was significantly greater in the logged forest than in the unlogged forest. Differential use of gaps by understorey birds has been demonstrated from studies conducted in Costa Rica where 40 % of the species found in the gaps were considered to be gap specialists (Levey 1988). There is also some anecdotal evidence suggesting that forest gaps may aid male birds in establishment and maintenance of territorial boundaries. Utilization of forest gaps, especially younger ones, as territorial boundaries may benefit males through increased visibility and song projection (Smith & Dallman 1996). Consequently, gaps are considered as keystone habitats for such species (Struhsaker 1997).

Gaps in Kibale Forest National Park originated primarily from natural tree falls, selective logging and elephant browsing (J.M. Kasenene pers. comm.). No prior studies have investigated the avifaunal composition in gaps of Kibale, and factors likely to influence this. The principal objective of this study was to investigate the effects of gap size and vegetation composition on the avian community in Kibale Forest, by comparing the patterns of occurrence of species in several gaps. We predicted that: (i) forest-dependent species occur less frequently in gaps compared to the forest (and vice versa for the non-forest dependent species), and (ii) size, and vegetation cover and composition of the gaps will affect both local abundance and species composition of birds. As a preliminary study, we hoped to provide some basis for future studies looking into more detailed aspects of the avian diversity in Kibale forest gaps.

Methods

Study area

This study was carried out in July 1997 in Kibale Forest National Park (00°13′ to 00°41′N, 30°19′ to 30°32′E; altitudinal range 1100 to 1590 m). Eight gaps were randomly selected, two in the unlogged and six in the lightly-logged forest compartments within Kibale forest. Their sizes were measured by estimation of gap diameters using an optical rangefinder, from which the area was calculated assuming a circular or elliptical shape. The basic gaps characteristics were as follows (see *Vegetation sampling* methods further for explanation):

Gap 1: was located Along R btw R15 and R16; 0.11 ha; 25% Canopy Cover CC, 20 % Mid-Strata Vegetation Cover MSVC, 50% Undergrowth Vegetation Cover UGVC, and 100% Ground Vegetation Cover GVC; main tree species was *Markhamia lutea*; and classified as a recent gap

Gap 2: was located Along R 17; 0.16 ha; 40% CC, 50 % MSVC, 50% UGVC, and 70% GVC; main tree species was *Polyschias fulva;* and classified as a recent gap

Gap 3: was located Along 17 btw A17 and B17; 0.14 ha; 50% CC, 30 % MSVC, 70% UGVC, and 100% GVC; main tree species was *Markhamia lutea*; and classified as an old gap from logging

Gap 4: was located Along GLT on trail B; 0.15 ha; 40% CC, 60 % MSVC, 80% UGVC, and 100% GVC; main tree species was *Neobutonia macrocalyx*; and classified as an old non-tree-fall gap along valley

Gap 5: was located Along GLT on trail B after gap 4; 0.22 ha; 10% CC, 10 % MSVC, 75% UGVC, and 100% GVC; main tree species was *Neobutonia macrocalyx*; and classified as an old non-tree-fall gap along valley

Gap 6: was located Along Y after Y21; 0.15 ha; 30% CC, 50 % MSVC, 70% UGVC, and 90% GVC; main tree species was *Macaranga sp.;* and classified as a recent gap

Gap 7: was located Along M on M4; 0.25 ha; 50% CC, 40 % MSVC, 75% UGVC, and 100% GVC; main tree species was *Polyschias fulva*; and classified as an old gap on valley

Gap 8: was located Along L btw L12 and L13; 0.26 ha; 50% CC, 30 % MSVC, 75% UGVC, and 100% GVC; main tree species was *Polyschias fulva*; and classified as an old gap on valley

Bird sampling

We conducted four total counts in each gap using principles of the point count technique (Bibby *et al.* 1992): two in the early morning and two in the late afternoon. The sampling sequence was randomly determined. Each count lasted for 15 minutes where we recorded all birds seen or heard within the gap. Since the gaps were reasonably clear and small, and this being an exploratory study, we observed entire gaps without sub-sampling.

To sort all birds seen, we used two methods. First, we grouped species according to their levels of forest dependence following the classification given in Bennun *et al.* (1996): (i) FF-species (*forest specialists*: true forest birds characteristic of the interior of undisturbed forest; occasionally albeit rarely occurring in non-forest habitats and secondary forest if their particular ecological requirements are met, but breeding almost invariably within undisturbed forest); (ii) F-species (*forest generalists*: occur fairly commonly in both undisturbed and secondary forest, forest strips, edges and gaps, but often breed within the forest interior); and (iii) f-species (*forest visitors*: birds repeatedly recorded in the forest interior but are not dependent on it, being more common in non-forest habitats, where they are most likely to breed). Any species not included in the Bennun *et al.* list was categorised as non-forest (nf). Second, birds were grouped into five categories based on four main feeding habits viz. fly-catching (*fly catcher*), gleaning for insects (*arboreal gleaner*), fruit eating (*frugivore*) and ground feeders (*ground feeder*), the fifth being a combination of two or more of these (*catholic feeder*). We used information in the Birds of Africa series for this classification (Urban *et al.* 1986, 1997, Keith *et al.* 1992).

From the entire species list of the birds of Kibale Forest (Skorupa 1983), we used the two classifications above to determine overall frequencies based on forest dependency and feeding behaviour. These were the 'expected' proportions that would then be compared to the 'observed' frequencies based on the species that were recorded in the gaps during the course of this study. In calculating the expected values, we excluded species not categorized by Bennun *et al.* (1996) (i.e., non-forest [nf]-species), as well as those that we would not have expected to see through our sampling protocols (e.g., nocturnal birds like owls and nightjars, and water birds), and those not obviously discernable as being within or out of the gap, usually flying over (e.g., most raptors, swallows, swifts and martins).

Vegetation sampling

We visually estimated the (percent) vegetation cover of the canopy (CVC: > 20 m), mid storey (MSVC: 2-20 m), undergrowth (UGVC: 0-2 m) and ground (GVC) at five points within each gap: the centre and four points on each compass direction near the far edge of the gap. The sum of the four cover types gave a rough index of overall vegetation cover (foliage) density at each point, and the five points were used to calculate a mean percentage cover value for the entire gap. We also noted any tree, shrub or herb species within the gaps that was in flower or fruit at the time.

Statistical analyses

Besides descriptive analyses summarising the data, chi-square tests in STATISTICA (StatSoft 2001) were used to check the goodness of fit of our data with the previously defined characteristics on forest birds (as described above). Spearman's rank correlation coefficients were calculated to check for significant correlations between gap and habitat variables with bird-related variables, namely total number of encounters, individuals, species, and FF species. To compute bird densities for each gap, total number of individuals seen over the four counts was divided by 4 to obtain mean number per count which was then divided by the gap size.

Results

Overall

We observed 358 individuals during our study, comprising of 55 species, excluding all species that were not obviously discernable as being within or out of the gap, usually flying overhead e.g., raptors, swallows, and swifts (Appendix). The species-accumulation curve plotted for successive counts in all gaps (morning and afternoon counts were regarded as independent) showed a steady increase but with a slow approach to an asymptote (Figure 1). This was mainly because only a minority of the 55 species occurred in more than five separate gaps, with more than 80% being recorded in just one or two gaps (Figure 2).

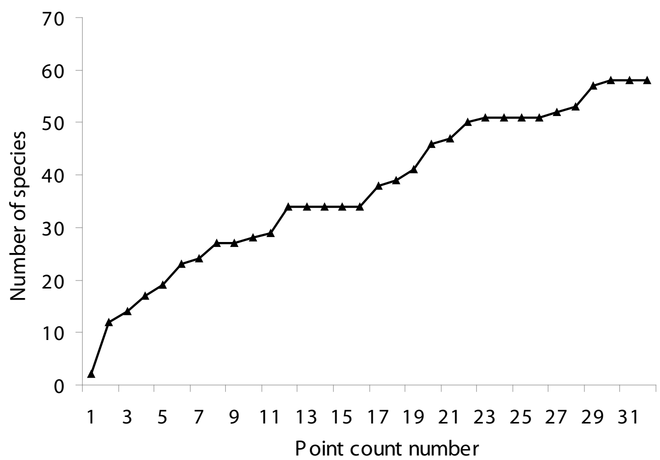


Figure 1. Species-accumulation curve for successive counts in eight gaps at Kibale Forest.

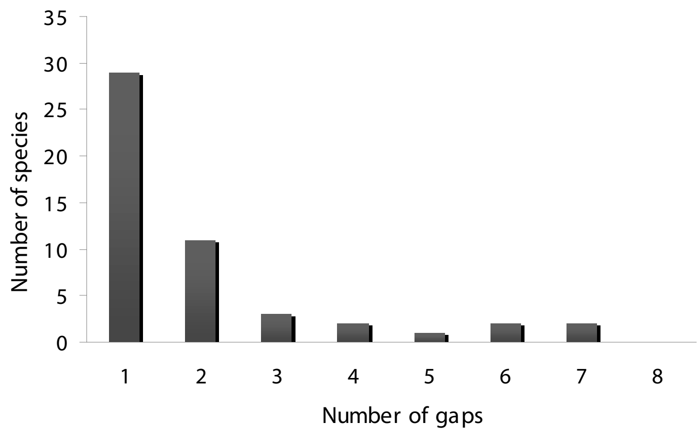


Figure 2. Bird species incidence in eight gaps of Kibale Forest National Park.

The commonest species in terms of both the number of times they were encountered and the total number seen during the study are provided in Table 1. Obligate frugivores such as Ross's Turaco *Musophaga rossa* and Great Blue Turaco *Corythaeola cristata*, as well as classic FF species like Petit's Cuckoo Shrike *Campephaga petiti*, Jameson's Wattle-eye *Dyaphorophyia jamesoni*, and White-headed Wood Hoopoe *Phoeniculus bollei*, were least common.

Table 1. The ten commonest bird species in gaps of Kibale Forest National Park (the entire list of species seen during this study is given in the Appendix).

English name	Scientific name	Total Encounters	Total Number seen
Black-faced Rufous Warbler	*Bathmocercus rufus*	17	24
Olive Green Camaroptera	*Camaroptera chloronata*	15	19
Olive Sunbird	*Nectarinia olivacea*	14	23
Little Greenbul	*Andropadus virens*	8	18
Yellow-whiskered Greenbul	*Andropadus latirostris*	7	13
Scaly-breasted Illadopsis	*Trichastoma albipectus*	7	9
Blue-shouldered Robin Chat	*Cossypha cyanocampter*	5	6
Collared Sunbird	*Anthreptes collaris*	4	10
Joyful Greenbul	*Chlorocichla laetissma*	4	8
Gray-backed Camaroptera	*Camaroptera brachyura*	4	4

Forest dependency

Of the 50 species, there were 19 FF-species, 30 F-species, 5 f-species, and one non-forest species (nf). Overall, about 90 % of all species and all individuals seen were either in the FF or F categories (by species: FF: 32%, F: 56%, f: 10% and nf: 2%; by number of individuals: FF: 45%, F: 48%, f: 6% and nf: 1%). This was also the case for each of the eight gaps, but with varying proportions of FF and F species (Figure 3). There was a significant difference between the overall expected and observed proportions of number of species in the three forest dependency categories (excluding the single nf species): FF 16 Vs 27; F 28 Vs 21; and f 5 Vs 2, for observed and expected, respectively (Chi-square test: $\chi^2 = 11.0$, df = 2, $P = 0.004$). Thus, there were fewer FF but more F and f than would be expected based on the entire bird species community at Kibale Forest.

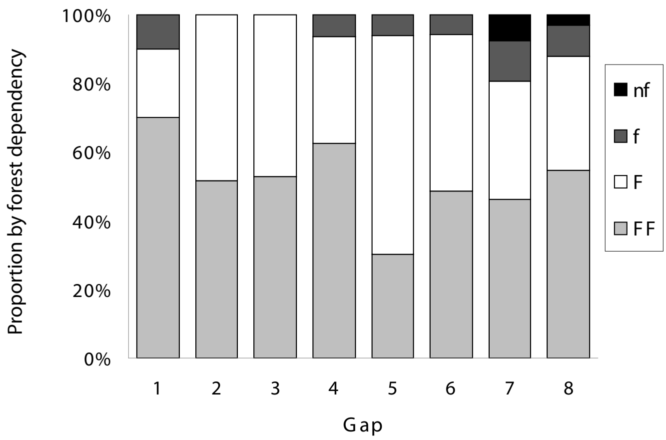
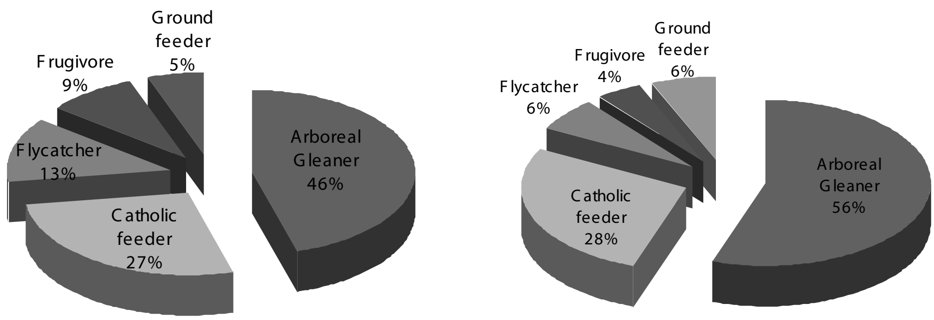


Figure 3. Percentage of bird species in the different forest-dependency categories for each gap separately.
FF: forest specialists
F: forest generalists
f: forest visitors
nf: non-forest

Feeding guilds

Based on feeding guilds, the 55 species included three ground feeders, five frugivores, seven flycatchers, 15 catholic feeders (a combination of two or more guilds) and 25 arboreal gleaners (see Figures 4a, b for relative proportions by species and number of individuals, respectively). There was no significant difference between the observed and expected (based on entire forest species list) representation of the guilds: Arboreal gleaners 23 Vs 25.5; Catholic feeders 14 Vs 15.5; Flycatchers 6 Vs 3.7; Frugivores 4 Vs 2.4; and Ground feeders 3 Vs 2.9, for observed and expected frequencies, respectively (Chi-square test: χ^2=2.9, df = 4, P = 0.58).



a) By species **b)** By numbers

Figure 4. Proportion of birds in the different feeding guilds in gaps of Kibale Forest.

Birds and gap-vegetation variables

There was a significant positive correlation between the total number of individuals and number of bird species seen within each gap (Spearman R = 0.75, P = 0.030, n = 8) (data in Table 2). Bird densities within the eight gaps ranged between 22.7 and 50 individuals ha^{-1}. Gap size was positively correlated (though always marginally non-significant) to number of encounters (Spearman R = 0.67, *P* = 0.069, n = 8), number of individuals (R = 0.57, *P* = 0.14), and number of species (R = 0.61, *P* = 0.11) (Figure 5). Vegetation index did not significantly affect either total number of individuals counted (R = 0.17, *P* = 0.69) or species seen (R = 0.41, *P* = 0.32). Neither gap size (R = 0.45, *P* = 0.26) nor vegetation index (R = 0.22, *P* = 0.60) significantly affected the numbers of FF-species seen. Lastly, gap size was negatively correlated to the proportion of birds seen that were FF species (R = -0.50, *P* = 0.20), albeit this correlation was not significant.

Table 2. Summary data for bird and gap-related variables.

Gap	Gap size (m^2)	No of Encounters	Total No Individuals	Density (No/ha)	Total No. Species	Vegetation Index	FF No.	FF %
1	1100	10	10	22.7	6	145	7	70
2	1600	16	31	48.4	11	190	16	51.6
3	1400	10	17	30.4	7	240	9	52.9
4	1500	22	32	53.3	15	240	20	62.5
5	2200	33	66	75	19	225	20	30.3
6	1500	20	35	58.3	13	240	17	48.6
7	2500	17	26	26	14	265	12	46.2
8	2600	23	33	31.7	14	255	18	54.5

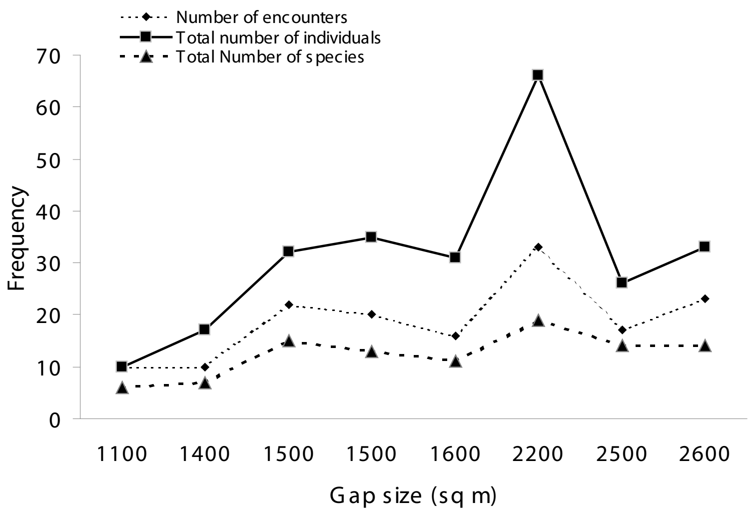


Figure 5. Relationship between gap size and bird-related variables: number of encounters, individuals and species seen.

Discussion

Overall, our results indicate that we observed many of the species that utilize gaps in Kibale forest during this study, though increasing number of gaps would probably result in a slight but steady increase in species because many species occurred in only one or two gaps. The gaps surveyed also had relatively high bird densities compared to other studies elsewhere (e.g., Nilsson 1979, Thiollay 1994). It was possible that bird species recorded in the gaps were simply extending their ranges mainly for foraging purposes, especially since the sampling times were early in the morning and late in the afternoon, which are both peak bird-activity time periods (Davies 2002). Still, with so little research done on territory sizes and behaviour of gap-specialist species, it is difficult to exclude that stable territories indeed existed in these gaps.

Gap size was positively correlated with the number of individuals and species seen (see also Greenberg & Lanham 2001). There was also a negative trend showing a decline of the proportion of FF species with increasing gap size, suggesting that FF species were replaced by F and f species in large gaps. It is hence likely that small openings created by tree-fall gaps do not significantly affect true forest species, and may increase avian diversity at a landscape scale by increasing habitat heterogeneity. The importance of vegetation structure within the gaps was not very clear from our quantitative analyses, although some trends may have failed to attain statistical significance owing to our small sample sizes. Yet, there were some anecdotal indications; for instance, the high canopy cover in Gap 8 would explain the occurrence of Petit's Cuckoo Shrike there, a strict forest canopy species (Zimmerman *et al.* 1996).

The chi-square test for forest dependence was significant, showing that, in terms of forest dependence (proportion of FF and F species), the within-gap bird species' composition differed from the pattern of forest dependence for the entire forest. In particular, there were fewer FF but more F and f-species than would be expected based on the entire bird species community at Kibale Forest. This is what one would expect in forest gaps because most of the true FF species probably shy away from the openings, as has also been reported from elsewhere (Dale *et al.* 2000; Rail *et al.* 1997; Sekercioglu 2002). Conversely, gaps favour more generalist species (F and f) which take advantage of the superabundance of food due to more light and typically denser foliage cover from increased primary productivity (Greenberg & Lanham 2001, Wunderle *et al.* 2006). For instance, the Black-throated Green Warbler in the US was found to preferentially select gaps in response to there being more insects in gaps (Smith & Dallman 1996). Other studies have also demonstrated differences in assemblages of birds captured in gaps and the surrounding forest understorey, which have been correlated to an increased insect, fruit, and total foliage abundance in forest gaps (Blake & Hoppes 1986, Martin & Karr 1986). Lastly, studies in Costa Rica showed that some gap specialist bird species dominated forest gaps (Levey 1988), as the Black-faced Rufous Warbler, Olive Green

Camaroptera and Olive Sunbird probably did in our study.

Unlike for forest dependence, the gap avian composition in terms of feeding guilds was found to be a subset of the entire forest's feeding guilds composition. The presence of specialized feeders was usually directly attributed to the occurrence of their food requirements e.g. the Great Blue Turaco and Ross's Turaco were observed to be feeding on fruiting trees in Gaps 5 and 3, respectively. This has been found to be the case in other studies too, such as a recent study in Argentina showing that as a consequence of a high abundance of fruits and flowers in gap understory, old gaps were extensively used by understory frugivores-insectivores (Zurita & Zuleta 2008).

In conclusion, given that our gap assemblage differed from the overall forest assemblage, this study demonstrates the importance of gaps for maintaining forest avian diversity. Gaps increase heterogeneity of the vegetation composition and structure, thereby broadening the range of microhabitats and niches for birds to colonize, even if temporarily. Studies on biodiversity of forest gaps remain rather scant in Afrotropical ecosystems. Future studies should aim at getting good controls for vegetation (structure and composition), size and age because this affects the vegetation types present. This would help tease out how each factor affects avian diversity (richness and abundance), as well as enable examination for interactions between them such as gap size and age, gap size and vegetation structure. Finally, long term studies would clarify patterns of utilization of gaps (e.g., species that utilize the gaps year-round), real forest specialists that (almost) never visit gaps, and inter-gap movements by forest birds. A better understanding of the role of small scale disturbances—such as forest gaps—is critical if forest managers are to maintain high quality habitat for forest biota.

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Appendix

Classification of the 55 bird species recorded in eight gaps at Kibale Forest during this study.

English Name	Scientific Name	Family	Forest Dependency	Feeding Guild
Great Blue Turaco	*Corythaeola cristata*	Musophagidae	F	Frugivore
Ross's Turaco	*Musophaga rossa*	Musophagidae	F	Frugivore
Yellowbill	*Ceuthmochares aereus*	Cuculidae	F	Gleaner
Black Bee-eater	*Merops gularis*	Meropidae	FF	Flycatcher
Broad-billed Roller	*Eurystomus glaucurus*	Coraciidae	f	Flycatcher
White-headed Wood-Hoopoe	*Phoeniculus bollei*	Phoeniculidae	FF	Gleaner
African Pied Hornbill	*Tockus fasciatus*	Bucerotidae	F	Mixed
Black and White Casqued Hornbill	*Bycanistes subcylindricus*	Bucerotidae	F	Frugivore
Hairy-breasted Barbet	*Lybius hirsutus*	Capitonidae	F	Frugivore
Speckled Tinkerbird	*Pogoniulus scolopaceus*	Capitonidae	F	Mixed
Golden-rumped Tinkerbird	*Pogoniulus bilineatus*	Capitonidae	F	Mixed
Yellow-crested Woodpecker	*Dendropicos xantholopus*	Picidae	F	Gleaner
Yellow-whiskered Greenbul	*Andropadus latirostris*	Pycnonotidae	F	Mixed
Joyful Greenbul	*Chlorocichla laetissma*	Pycnonotidae	F	Mixed
Little Greenbul	*Andropadus virens*	Pycnonotidae	F	Mixed
Honeyguide Greenbul	*Baeopogon indicator*	Pycnonotidae	FF	Mixed
Cameroon Sombre Greenbul	*Andropadus curvirostris*	Pycnonotidae	FF	Mixed
Common Nicator	*Nicator chloris*	Pycnonotidae	F	Gleaner
Red-tailed Bristlebill	*Bleda syndactyla*	Pycnonotidae	FF	Mixed
Scaly-breasted Illadopsis	*Trichastoma albipectus*	Timaliidae	FF	Ground
Blue-shouldered Robin Chat	*Cossypha cyanocampter*	Turdidae	F	Ground
Rufous Thrush	*Stizorhina fraseri*	Turdidae	F	Ground
African Dusky Flycatcher	*Muscicapa adusta*	Muscicapidae	F	Flycatcher
Grey-throated Flycatcher	*Muscicapa griseigularis*	Muscicapidae	FF	Flycatcher
Northern Black Flycatcher	*Muscicapa edolioides*	Muscicapidae	F	Flycatcher
African Shrike Flycatcher	*Bias flammulatus*	Platysteiridae	FF	Flycatcher
Gray-backed Camaroptera	*Camaroptera brachyura*	Sylviidae	f	Gleaner
Olive Green Camaroptera	*Camaroptera chloronata*	Sylviidae	FF	Gleaner
Black-headed Apalis	*Apalis melanocephala*	Sylviidae	F	Gleaner
Green Hylia	*Hylia prasina*	Sylviidae	F	Gleaner
Buff-throated Apalis	*Apalis rufogularis*	Sylviidae	FF	Gleaner
Black-faced Rufous Warbler	*Bathmocercus rufus*	Sylviidae	FF	Gleaner
Banded Prinia	*Prinia bairdii*	Sylviidae	F	Gleaner
Masked Apalis	*Apalis binotata*	Sylviidae	FF	Gleaner
Yellow White-eye	*Zosterops senegalensis*	Zosteropidae	f	Gleaner
Common Wattle-eye	*Platysteira cyanea*	Platysteiridae	f	Gleaner
Chestnut Wattle-eye	*Dyaphorophyia castanea*	Platysteiridae	FF	Gleaner
Jameson's Wattle-eye	*Dyaphorophyia jamesoni*	Platysteiridae	FF	Gleaner
Bocage's Bush Shrike	*Malaconotus bocagei*	Malaconotidae	F	Gleaner

English Name	Scientific Name	Family	Forest Dependency	Feeding Guild
Lühder's Bush Shrike	*Laniarius luehderi*	Malaconotidae	F	Gleaner
Petit's Cuckoo Shrike	*Campephaga petiti*	Campephagidae	FF	Gleaner
Velvet-mantled Drongo	*Dicrurus modestus*	Dicruridae	F	Flycatcher
Western Black-headed Oriole	*Oriolus brachyrhynchus*	Oriolidae	F	Mixed
Purple-headed Glossy Starling	*Lamprotornis purpureiceps*	Sturnidae	F	Mixed
Green-throated Sunbird	*Nectarinia rubescens*	Nectariniidae	F	Gleaner
Collared Sunbird	*Anthreptes collaris*	Nectariniidae	F	Gleaner
Olive Sunbird	*Nectarinia olivacea*	Nectariniidae	FF	Gleaner
Blue-throated Sunbird	*Nectarinia cyanolaema*	Nectariniidae	FF	Gleaner
Veillot's Black Weaver	*Ploceus nigerrimus*	Ploceidae	f	Mixed
Yellow-mantled Weaver	*Ploceus tricolor*	Ploceidae	FF	Mixed
Red-headed Malimbe	*Malimbus rubricollis*	Ploceidae	FF	Gleaner
Dark-backed Weaver	*Ploceus bicolor*	Ploceidae	F	Gleaner
Gray-headed Negro Finch	*Nigrita canicapilla*	Estrildidae	F	Mixed
Black-bellied Seedcracker	*Pyrenestes ostrinus*	Estrildidae	F	Frugivore
Yellow-fronted Canary	*Serinus mozambicus*	Fringillidae	nf	Mixed