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The avifauna 23 years after logging in Kibale National park, Uganda

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The bird fauna of logged and unlogged forest in Kibale National Park, western Uganda were studied and comparisons made. Species diversity and richness were higher in the logged areas. A single species, the Yellow-whiskered Greenbul *Andropadus latirostris* dominated in the logged compartment. However, the majority of individual birds found in the logged forest were generalist or forest-edge species. Over 84% of the forest interior specialist species that occurred in primary forest had recolonized or persisted in the logged forest; however, there were seven out of 48 understorey forest specialists that had not done so. Although there was moderate species overlap between the two habitats, the logged forest compartment had not fully recovered from logging after 23 years.

Keywords: avifauna; Kibale Forest; forest specialist birds; recolonization.

Introduction

Tropical rainforests are under increasingly severe pressures from deforestation due to agricultural encroachment *and* unsustainable silvicultural practices (Whitemore, 1990; Blockhus *et al.*, 1992). The result of these activities is loss of biological diversity. Currently, detailed information on the ecology and functioning of forest species within secondary or disturbed habitats is very scarce.

Studies on the effects of logging on birds have been documented in South-east Asia and South America (Wong, 1985; Johns, 1986, 1988, 1989a; Lambert, 1992; Thiollay, 1992) but scanty records exist for Africa and Uganda in particular (Kalina, 1988; Obua, 1992; Holbech, 1992; Owiunji, 1996). Some African studies only assessed the effect of forest fragmentation (Newmark, 1990; Fjeldsa and Rabol, 1995). However, majority of the studies concentrated on primates (Struhsaker, 1975; Johns and Skorupa, 1987; Skorupa, 1988; Plumptre and Reynolds, 1994; Plumptre, 1996). The paucity of information on the effects of forest disturbance on understorey birds in Uganda prompted the present study.

It has been suggested that after major disturbances, such as tree felling, bird populations can change in many ways: some species immediately leave the logging area (Crome and Moore, 1988; Johns, 1988), but may re-establish themselves later. Some species decline steadily, while some increase and then decrease with the opposite pattern being found for yet other species. Some other species remain more constant (Johns, 1986, 1987, 1995; Reicher, 1991; Thiollay, 1992; Fortso, 1994). The responses of any species to logging are potentially varied and difficult to predict.

However, the regeneration capacity of the bird community over time is influenced bythe plant community and logging damage. In studies of a Malaysian rain forest, Wong (1985) found that bird populations in areas logged 23–25 years previously were similar to those in primary forests. This was an indicator of resilience of such species to logging. Most

importantly, such a result may indicate the probable availability of a colonizing 'pool' near the logged habitats. In other areas however, forest birds have failed to recover fully after previous logging disturbances (Rappole and Morton, 1985; Thiollay, 1992; Fortso, 1994). Hence, these practices may have far-reaching implications for conservation. The question is why should some bird communities be more resilient to logging than others? According to Bell (1982) and Thiollay (1992) different ecological and environmental factors operating on individual species make them vulnerable or resilient to man-induced disturbances. Some of the important factors included: the species-specific habitat requirements, dietary specialization as well as manoeuvrability or technical skills in obtaining food. A different and most recent line of thinking advanced by Danielsen (1997) is that the resilience of bird communities could be predicted by paleoecological stability of a region. These aspects may determine whether or not an individual species has the capacity to adjust to exploit the changed resources base resulting from logging.

The main aim of this study was to assess the differences in the understorey forest bird community whose habitat was intensively logged 23 years ago. The following questions were asked. What was the diversity more than two decades after the logging operation? Which species may be affected, and how?

Study site

The study was carried out in a tropical rain forest of Kibale National Park, Uganda. Kibale forest is classified as a medium-altitude (within a range of 1590 to 1110 metres above sea level along the North–South axis), moist evergreen tropical forest (Langdale-Brown *et al*., 1964). It lies between 0°13′–0°41′N and 30°32′–30°35′E in the Western part of Uganda and covers an area of 560 km^2. The study sites were located in two forest compartments at Makerere University Biological Field Station, found in the Northern part (Fig. 1). One was in a fairly natural state and the other was selectively logged 23 years ago. The vegetation is dominated by *Parinari excelsa* and the altitude averages to 1500 m.

Unlogged forest compartment

The unlogged forest study site was fairly undisturbed, mature *Parinari* forest (Struhsaker, 1975; Skorupa, 1988). This forest covers an area of about 300 ha characterized by large trees (with dbh of over 50 cm) of *Parinari excelsa, Strombosia* spp, *Olea welwitchii, Mimusops bagschawii, Celtis* spp, *Diospyros abyssinica* and *Uvariopsis congensis*. The commonest understorey plants included *Palisota schweinfurthii* and *Mimulopsis solmsii*.

Pitsawyers extracted a few stems (three/km^2) of the large trees during the early 1950s, which had minimal impact on the general forest structure (Kasenene, 1987; Struhsaker, 1987; Skorupa, 1988). Elsewhere, in West Africa, similar timber offtake had little impact on wildlife (White, 1992).

For over four decades, this site has been used in the comparative studies of primates, small mammals and tree regeneration (Struhsaker, 1975, 1987; Isabirye-Basuta, 1979; Kasenene, 1987; Skorupa, 1988; Muganga, 1989; Lwanga, 1994).

The terrain is steeply undulating (a probable reason that saved it from being logged) as opposed to that of the selectively logged site which is fairly flat. This compartment is surrounded to the West, South and East by grasslands and pine plantation while the North is bordered by lightly logged tropical forest.

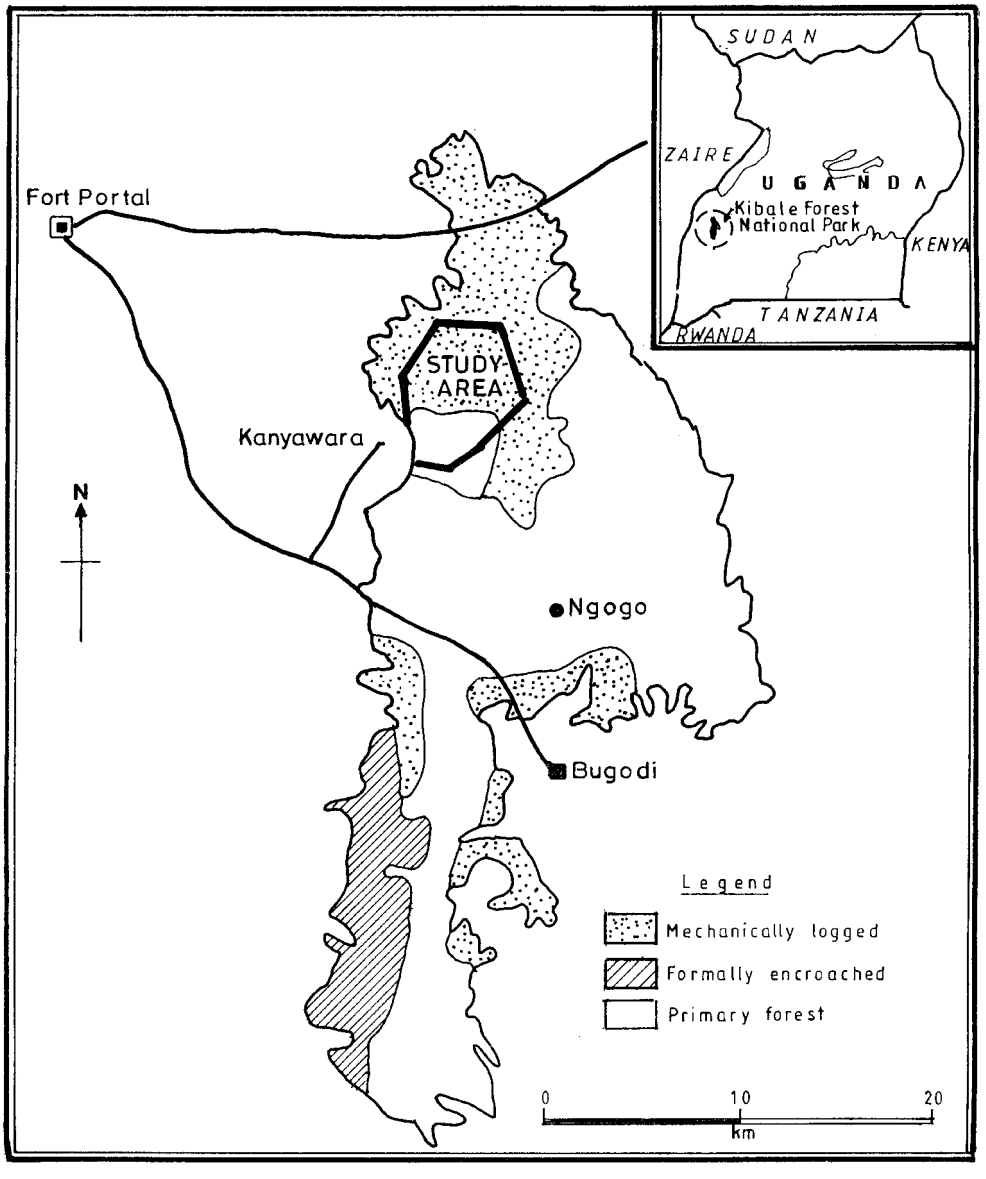


Figure 1. Map of Uganda showing the location of Kibale Forest National Park in relation to other major forests, and the location of the study area.

The 23-year-old selectively logged forest compartment

The selectively logged forest study site covers an area of about 360 ha. However, study sites were located within a 100 ha section that had grid lines. It was heavily logged in the years of 1968–69 (Kasenene, 1987; Skorupa, 1988). From Forest Department records, Skorupa (1988) reported that only 21 m^3 of timber per hectare were extracted. However, it appears that this figure falls below the actual extracted volume, which may not have been

fully recorded, because 62% of the canopy was opened (Kasenene, 1987). This site appears more degraded than areas of Budongo Forest where more than 80 m^3 per ha of timber was removed, and later some residual trees were poisoned (A. Plumptre, pers. comm.). Skorupa (1988) gives details of tree species that were extracted from here in 1968 and 1969. Many other environmental and ecological factors have so far influenced the forest compartment. For example, Tabor *et al.* (1990) found that the gaps in this logged forest continue to enlarge due to increased windfalls. The most common trees are *D. abyssinica*, *Celtis durandii*, *C. africana*, *Milletia dura*, *U. congensis*, *Fagaropsis angolensis* and *O. welwitchii*. *Acanthus pubescens* and *Mimulopsis* spp, together with dense tangles of weed vegetation, form the understorey of this compartment. The logged forest study site consists of more than 30 forest patches ranging from 0.1 to 5.8 ha merged within a 'matrix' of dense secondary vegetation (Dranzoa, 1995). Most of these forest patches were close to one another, separated by a few metres.

This logged site is only 3 km North-East of the unlogged study area. The Southern and Eastern sides, are bordered by very heavily logged forests while the Western and Northern parts are bordered by lightly logged forest. Other forms of disturbance, such as hunting, was negligible in both study areas because hunters avoided research areas.

Methods

In this study, forest birds were placed into three categories (Table 1) adapted from Carlson (1986) and Bennun *et al.* (in press).

Net-lines were established along the slopes and hill tops in the unlogged compartment. In the logged area, which is fairly flat, net-lines were set in flat areas but not in the valley bottom. Each line was separated from the next by at least 200 m.

Trapping was carried out on a regular monthly basis at each site. Birds were trapped using mist-nets of 35 mm mesh. Mist-nets had varying lengths from 9.5 to 12.5 m. The vertical height of each net from ground level was approximately 2.5 m.

Phase one of trapping

From October 1991 to July 1992, the nets were spread at randomly selected sites in the understorey of each forest compartment to establish what was present. A total length of 120 m nets was spread in a continuous mat (i.e. connected end to end). On each trapping day, nets were opened at 0600 hours, before birds started moving, and were closed in the evening at 1800 hours, or earlier if it rained. After 3 days, nets were transferred to another net line for 3 more days because experience showed that the trap rate declined after a second day. The same procedure was followed in each compartment.

Table 1. Forest bird categories

Category	Main habitat requirements
FF-Forest interior specialists	Restricted mainly to undisturbed forests interiors
F-Forest generalists	Characteristically birds of forest edges and gaps
f-Forest visitors	These are birds not dependent on forests at all

Phase two of trapping

During the second phase (from August 1992 to June 1993) there was an attempt in the logged compartment to distinguish the birds found in forest patches from those found in the secondary growth. The nets were connected to each other forming a quadrant (50×50 m) of 0.25 ha. During this period, the nets were left opened for only 4 hours of the early morning. This aimed to provide welfare for trapped birds by lowering the risks of capture-stress of birds whose territory may be partly within the enclosure. Nets were shifted, after the daily 4 hours of netting, to a different locality and set ready (but not opened) for the next morning's netting session. Net lines were checked at hourly intervals, sometimes more often. Each bird caught was tagged with either a numbered coloured plastic ring or a numbered metallic aluminium ring. For each specimen, biometric data were taken.

The taxonomy and nomenclature follow the current East African list (OS-C, in press).

Data analysis

Species richness and diversity were assessed by the use of the Jack-knife estimate and Shannon-Wiener index ($H' = Ep_i \, In(p_i)$) based only on ringing data (Magurran, 1983; Krebs, 1989).

Driscoll (1977) regarded any bird species that contributed at least 0.5% of the total captures as being common. Those contributing less than 0.5% were referred to as uncommon or rare. The same approach was used in this study.

Results

Sampling effort

The total effort in each compartment is summarized in Table 2. Slightly less time was devoted to trapping in the unlogged forest.

To test whether sample effort was adequate, species accumulation curves were plotted against time (Fig. 2). The species accumulation rate was higher in the logged forest than in the unlogged forest. The addition of new species eventually began to level off after November, 1992, within both study sites.

Bird species richness and diversity

Appendix 1 lists all the species and their total number captured, and a summary is given in Table 2. In the logged site, only 22.9% were recaptures whereas recaptures formed about 38.9% of the overall captures in the unlogged forest.

The unlogged forest was poorer than the previously logged forest, both in terms of species numbers and numeric abundance (Table 2). This result is supported by simple species accumulation curves (Fig. 2).

Table 2. Summary of trapping records (from 18 months)

	Unlogged	Logged
Total hours of trapping	550.5	666
Total metre-net-hours	78,860	104,000
Total captures	1608	3809
Number of birds ringed	982	2937
Number of species	64	83

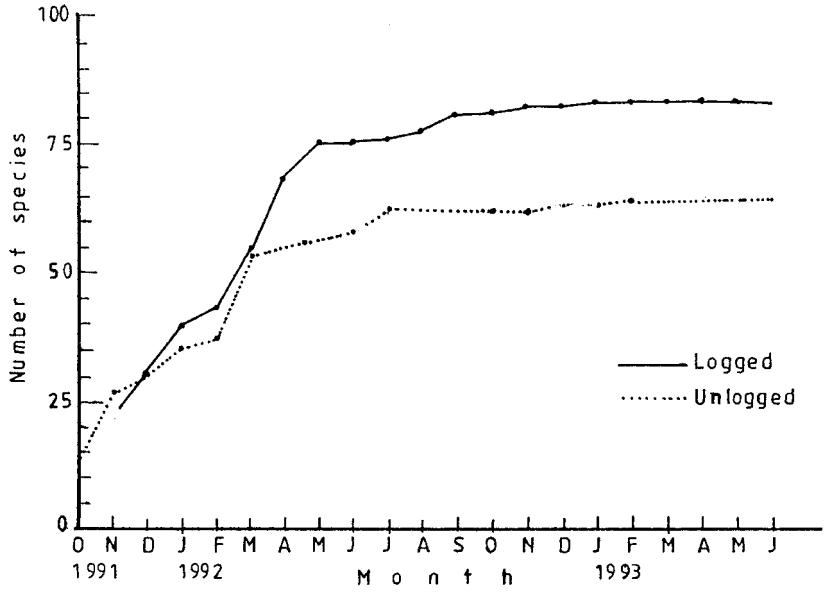


Figure 2. Species accumulation per month, based on monthly captures.

Species richness obtained by the Jack-knife estimate again showed that the logged site was richer than the unlogged site. The maximum estimates of species richness at the 95% confidence level were 89.7 and 116.3 species in the unlogged and logged forests respectively (Table 3).

The Shannon-Wiener index of diversity showed a similarly higher estimate of species diversity in the logged forest (Table 3). When the most common species in the logged compartment, Yellow-whiskered Greenbul, *Andropadus latirostris*, was excluded from the diversity estimates, the results showed no significant differences between the unlogged and logged forests ($t = 0.22,\ p > 0.05$). Similarly, when all the canopy species were excluded in the calculations, the Shannon-Wiener index of diversity was not significantly different between sites ($t = 1.13,\ p > 0.05$).

Table 3. Summary of species diversity

Index	Site unlogged	Logged	Statistical test
(a) Jack-knife	80.20 ± 9.50	101.90 ± 14.36	$\chi^2 = 2.58,\ p < 0.05$
Evenness	10.60	9.82	$p < 0.10$
(b) Shannon-Wiener	2.93	3.02	$t = 2.20,\ p < 0.05$
Yellow-whiskered Greenbul excluded df = 3256	2.66	2.67	$t = 0.22,\ p > 0.05$
Canopy species excluded df = 2274	2.73	2.63	$t = 1.13,\ p > 0.05$

Evenness, which expresses the number of equally common species, was, however, lower in the logged compartment than that in unlogged forest (Table 3).

Relative abundance of understorey birds

Common species in the unlogged forest. There was a more even distribution of most species in unlogged than in the logged forest (Fig. 3). The Olive Sunbird *Nectarinia olivacea,* Brown-chested Alethe *Alethe poliocephala*, *Bristlebill Bleda syndactyla* and White-throated Greenbul *Phyllastrephus albigularis* were among the most abundant species (Appendix 1). The forest interior specialists formed 63.3% ($n = 30$) of the common species, while forest edge species or generalists formed 36.7%. There was no non-forest bird in this category.

Common species in the logged forest. Twenty-nine common species contributed 93.3% of the total captures. Of these species, there was one single particularly abundant species (Fig. 3a), the Yellow-whiskered Greenbul, which contributed 26.6% of the total captures (Appendix 1). The same species also formed 28.5% of the captures of the common species; it was captured more than twice as often as the second commonest species, the Olive Sunbird. Eight other species were numerically abundant, with each contributing at least 2.5% of all the captures. Included in this category were Brown-Chested Alethe, Slender-billed Greenbul *Andropadus gracilirostris*, Cameroon Sombre Greenbul *A. curvirostris*, Little Greenbul *A. virens*, Black-faced Rufous Warbler *Bathmorcercus cerviniventris*, Blue-shouldered Robin Chat *Cossypha cyanocampter*, the Equatorial Akalat *Sheppardia aequatorialis* and Bristlebill.

The forest interior specialists formed 51.7% ($n = 30$) of the common species, while forest edge species or generalists formed 37.9%. The rest were non-forest birds (10.4%).

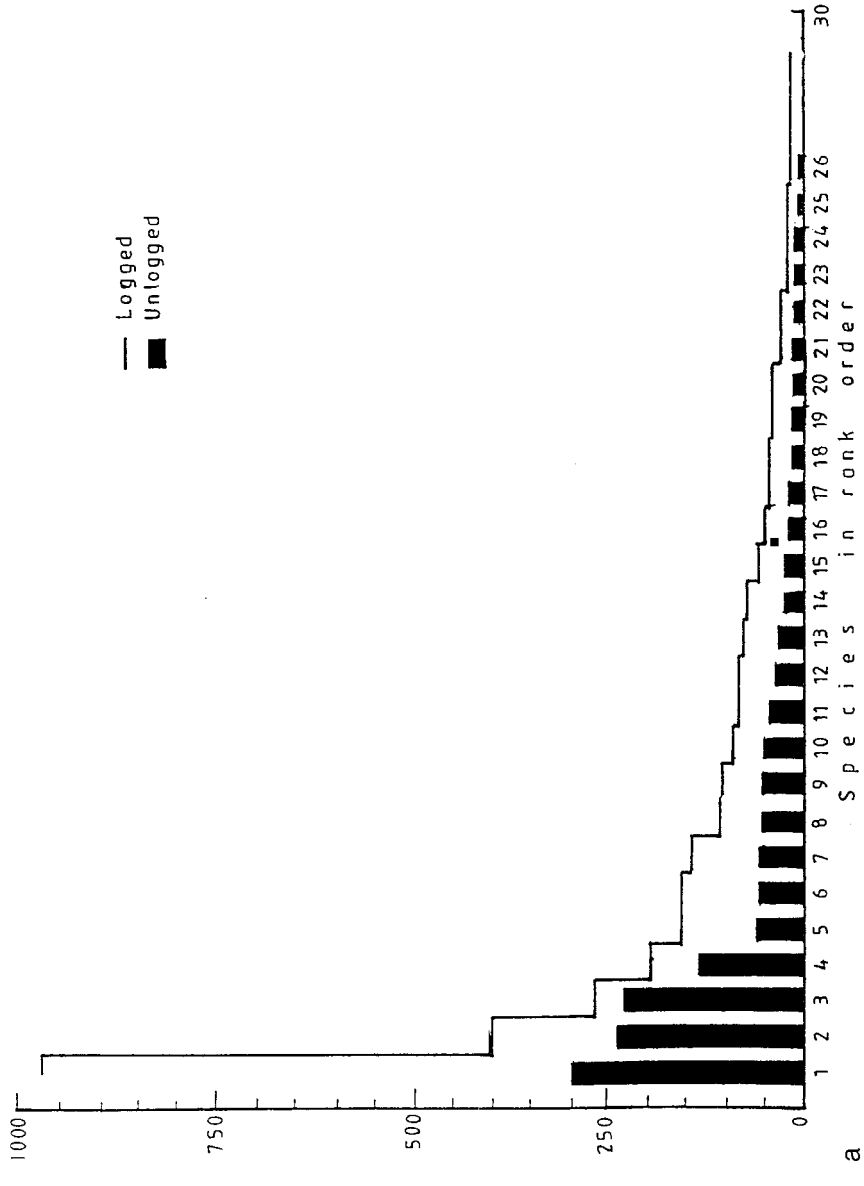
Rare species in the unlogged forest. 53% ($n = 64$) of the total trapped species in the unlogged forest fall in this category of rarity. They included Red-tailed Ant Thrush *Neocossyphus rufus*, Abyssinian Ground Thrush *Zoothera piaggiae*, African Pitta *Pitta angolensis* and others which did not occur in the logged forest. Some 53% of these rare species were represented by single individuals (Appendix 1); the rest had from two to seven individuals per species (Fig. 3b). Forest interior birds formed 56% ($n = 34$) of the rare bird species. 24% were forest generalists and the remaining 20% were non-forest birds.

Rare species in the logged forest. Out of the total understorey community in logged forest, 65.1% were less numerous than those named above, with a majority species being represented by one or two individuals (Fig. 3b). Forest interior birds formed 44.4% ($n = 53$) of the rare bird species. Some 27.8% were forest generalists and the remaining 27.8% were non-forest birds.

Comparison of understorey birds from unlogged and logged forests

In general, capture rates were significantly higher in the logged forest than in the unlogged for all categories except non-forest birds (Table 4). A comparison of capture rates of some common individual species shows marked differences between the two sites (Fig. 4). The largest percentage of forest interior bird species was captured in the primary forest (Fig. 5).

Twenty-three years after logging, there were still some non-forest birds persisting in the logged forest (these are birds that are not associated with forest habitats but are attracted by some of the features created in the concession area by opening up the forest canopy).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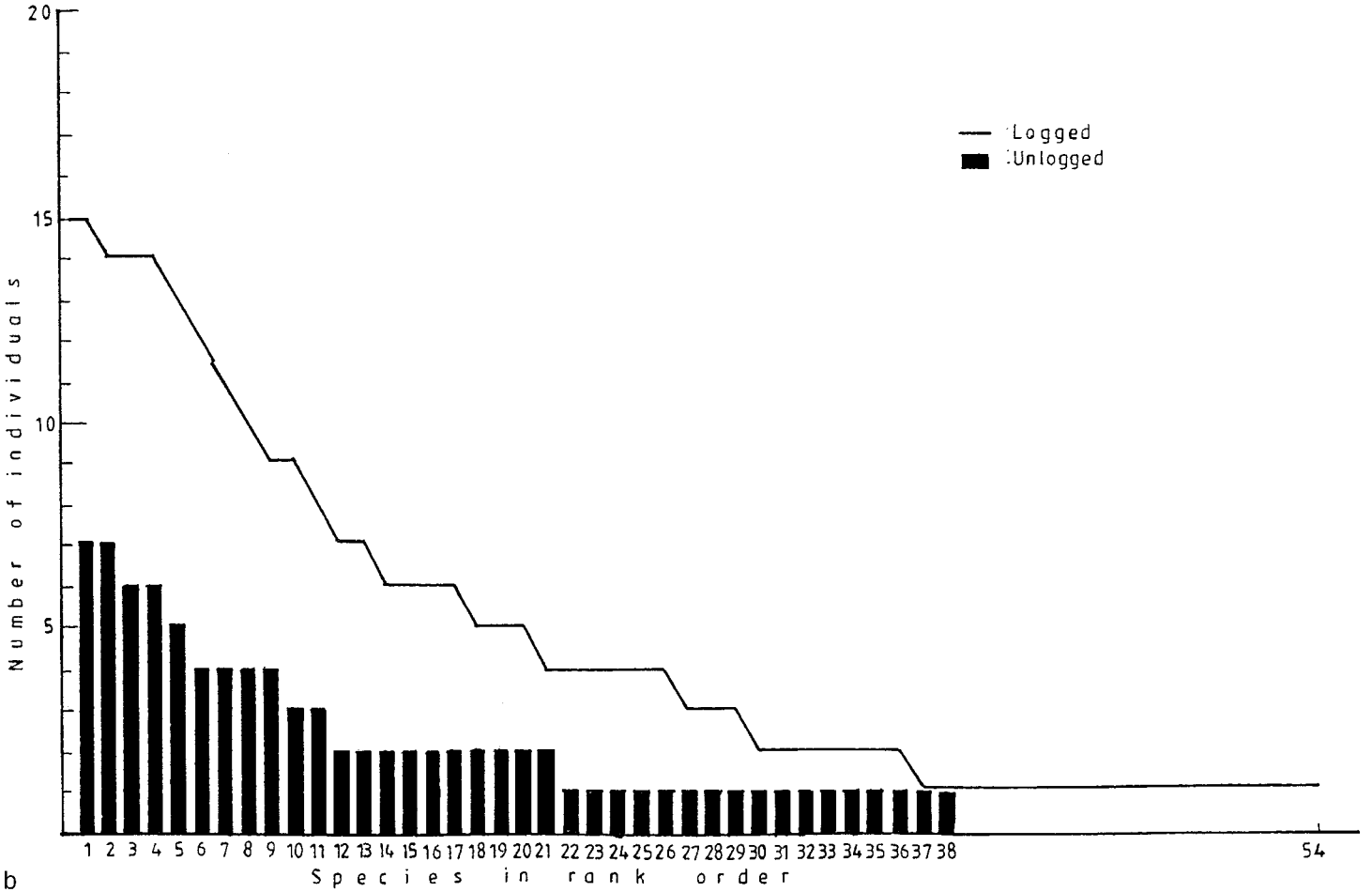

Figure 3. (a) Species rank abundance of common understorey birds. (b) Species rank abundance of rare understorey birds.

Table 4. Capture rates (total number of individuals captured per 100 mnh). The figures in parentheses are percentages of the total captures. The Z-test was used to test whether there were significant increases in capture rates of the different categories of birds in logged forest

	Site			
Species category	Unlogged	Logged	Z-test	*p*
Forest interior specialists	1.41 (69)	1.79 (51)	20.6	***
Forest generalists	0.60 (30)	1.63 (47)	18.9	***
Forest visitors	0.02 (1)	0.08 (2)	128.2	***
Non-forest birds	0.001 (0.1)	0.01 (0.2)	0.001	Ns
Total, all species	2.04	3.51		

Note: Data are pooled from all trap records.
*** = $p < 0.001$; Ns = non-significant.

There were seven forest interior specialists missing from the logged forest study site, i.e. those that have failed to re-colonize the logged forest, namely, Red-tailed Ant Thrush, Abyssinian Ground Thrush, African Pitta, Pale-breasted Illadopsis *Illadopsis rufipennis*, Forest Robin *Stiphrornis erythrothorax*, Mountain Greenbul *Andropadus nigriceps* and White-throated Greenbul. All of these birds are ground feeders and (except for the last) were uncommon in the unlogged forest (Appendix 1).

Although some true forest bird species were missing altogether from logged habitat, species similarity between these two sites was 64.4% (Renkonen index), see Krebs (1989).

Vertical compression. More canopy (including mid-storey and upper canopy foliage) birds were caught in the logged forest, both in terms of species and in total numbers than in the unlogged site (Table 5).

Discussion

Species diversity

This study has shown that the logged forest study site has more diverse understorey birds than the unlogged compartment. A comparative study such as this is open to criticism because of lack of pre-logging data (Wiens, 1989; Johns, 1989a, 1992b; Bierregaard, 1990), since there might have been initial differences between sites before logging took place. In a situation where there is no chance of obtaining pre-logging data, a comparative study can be accomplished only by assessments of biota within both natural and altered habitats. Similar comparative studies from Kibale by Kasenene (1984) and Muganga (1989) showed that logged forests supported a richer rodent community, higher densities and biomass than do unlogged areas. However, frugivorous primate densities plummeted in logged forests, except the unspecialized feeder, Black and White Colubus Monkey *Colubus polykomos* (Skorupa, 1988). The latter case was attributable to socio-ecological factors of the primates and the environmental conditions in logged areas of Kibale.

Both indices of diversity (Jack-knife's estimate, Shannon-Wiener index) and species accumulation curves showed consistently higher understorey bird species diversity and richness in the logged forest than in the unlogged. This result was comparable to that in Budongo forest, Uganda (unpublished observations).

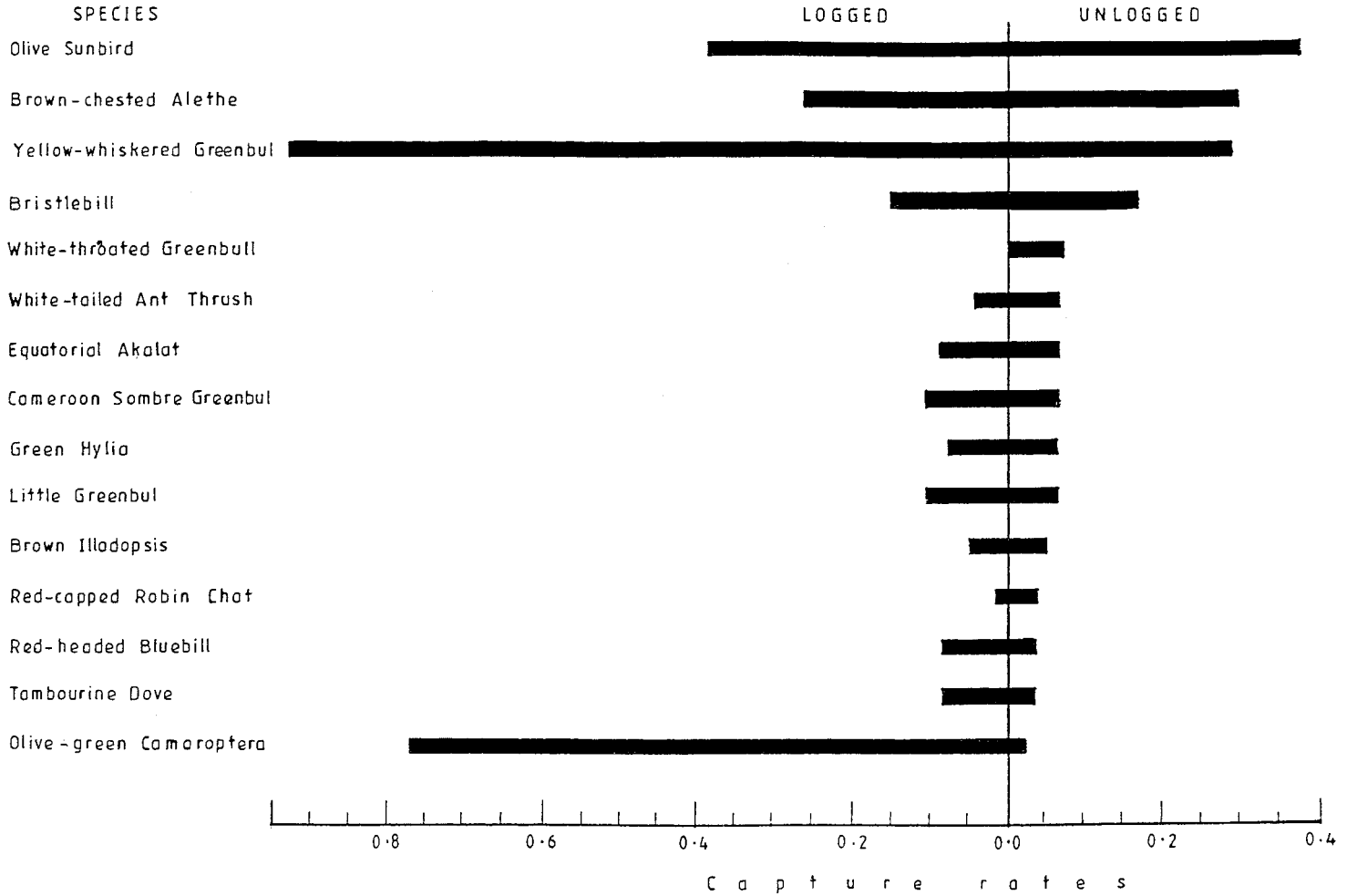

Figure 4. Comparison of capture rates of most common species found in the unlogged and logged forests.

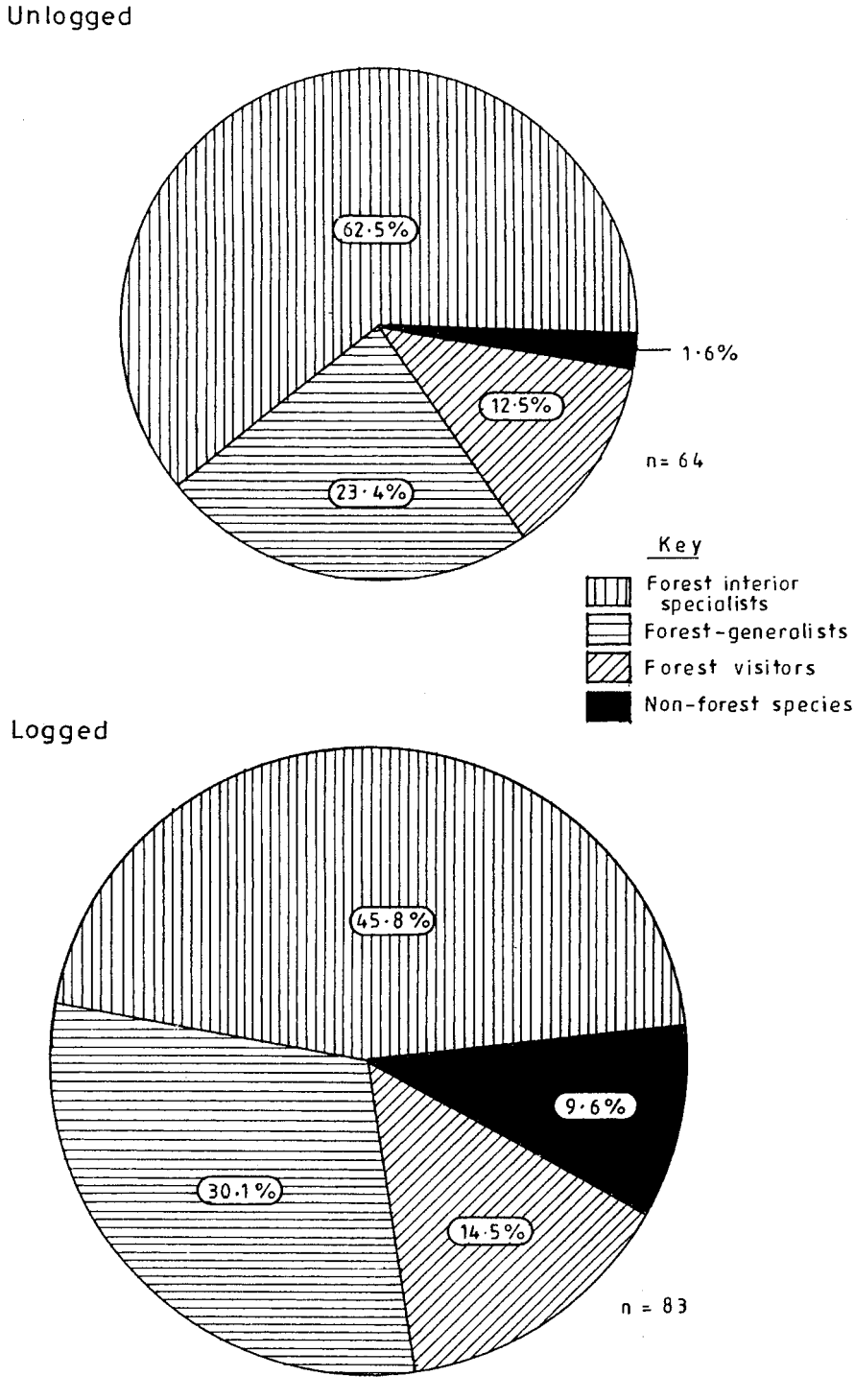

Figure 5. Proportion of each category of understorey birds in the unlogged and logged forests. *Note*: size of the circle reflects the relative number of species in each study area.

Table 5. Ratios of capture rates per 100 mnh of canopy species between logged and unlogged sites (refer to Appendix 1 for scientific names)

Species	Capture rates		Ratio (L:U)
	Logged	Unlogged	
Slender-billed Greenbul	0.188	0.026	7.2
Yellow-rumped Tinkerbird	0.031	0.018	1.7
Yellow White-eye	0.017	–	–
Black-billed Weaver	0.015	0.003	5
Jameson's Hylia Finch	0.014	0.001	14
Masked Apalis	0.012	–	–
Afep Pigeon	0.010	0.006	2.7
Lesser Honey guide	0.006	0.008	0.8
Toro Olive Greenbul	0.006	–	–
Western Black-headed Oriole	0.005	–	–
Joyful Greenbul	0.004	–	–
Grosbeak Weaver	0.003	–	–
Blue-throated Brown Sunbird	0.003	0.001	3
Black Bee-eater	0.002	0.001	2
Cardinal Woodpecker	0.001	–	–
Black-throated Apalis	0.001	0.001	1
Brown-eared Woodpecker	0.001	0.003	0.3
Black Cuckoo Shrike	0.001	0.001	1
Honeyguide Greenbul	0.001	0.003	0.3
Yellow-billed Barbet	0.001	0.003	0.3
Narina's Trogon	–	0.003	–
Black-billed Turaco	–	0.001	–
Total	0.322	0.079	4.1
Mean capture rate	0.016	0.005	3.2

Huston (1979) regarded disturbance as a major contributor to species enrichment due to maintenance of a diversity of microhabitats. The heterogeneous habitat generated by logging has been taken up by large numbers of successional or opportunistic species while precluding some primary forest specialists. This finding contradicts a number of results found in separate studies in Malaysia (Johns, 1985, 1988, 1989a) and Amazonia (Thiollay, 1992) where species richness and diversity were reduced by logging. These differences may have been due to variations in methods and due to the fact that the logged study area in Kibale forest is separated from unlogged forest by a mere 3 kilometres of fairly intact forest: movements between sites is easily facilitated. Further, the logged forest study site still maintains a substantial number of non-forest birds, invaders, which can be regarded as opportunistic, increasing the total diversity and species richness there.

My study and other major studies, e.g. Johns (1989a), Lambert (1992), Thiollay (1992) and Fortso (1994), reached similar conclusions: logging generally alters the structure of the bird community, with a few abundant species occupying a higher proportion of the total sample (e.g. in this study it was the Yellow-whiskered Greenbul). Each species reacts differently to forest disturbance, depending on habitat and food specialization, physiological sensitivity and foraging behaviour (Bell, 1982; Begon *et al*., 1990; Thiollay, 1992).

Much of the change in abundance results from changes in the structure of the vegetation as well as reduction in foraging space within the logged forest (Dranzoa, 1995). The study in Ghana (Holbech, 1992) did not show any major impact on the structure of the bird community following logging. This could have been due to the fact that the selective logging in Ghana did not cause a significant structural alteration in the vegetation.

Exclusion of the Yellow-whiskered Greenbul and omission of the canopy species from the calculation (Table 3) showed no significant differences in the measures of diversity between the two study areas. Diversity indices are useful in making rapid biological assessments (Beehler *et al*., 1987) but results in this study and others (Karr, 1976; Johns, 1985, 1986), suggest that a single index may be of limited value in making management decisions because (a) it does not recognize the fact that different subsets of the community react to habitat disturbances in a different manner, and (b) it overlooks changes in community structure following disturbance.

The diversity in the logged forest reflects the structural alteration of the logged area which has reduced canopy cover but left dense undergrowth (Dranzoa, 1995). Such conditions attract many understorey and canopy species (with a few exceptions) to exploit new niches created by the logging, hence creating an impression of increased understorey species diversity. Therefore precautions must be taken in using diversity indices to examine such data.

Recolonizers

Observations made during the logging activities and after logging in Malaysia (Johns, 1985) revealed that many species vacate the area as soon as logging starts and subsequently avoid it. Over time, some recolonize when regeneration takes place, but invaders may also come into the disturbed habitat. Although the dispersal abilities of rain forest birds are not well documented, there are some indications that distant movements occur among understorey birds. For example, Dranzoa (1990) showed that a Rufous Thrush moved 5 kilometres from the site of ringing to another forest fragment in southern Uganda. During this study a Brown-chested Alethe and Yellow-whiskered Greenbul that were ringed in the unlogged forest were re-trapped in the logged forest a minimum distance of 3 kilometres (Dranzoa, 1995). As logged forest regenerates, conditions become more suitable for species which may survive poorly in forest immediately after logging (Johns, 1992a).

Johns (1989b) showed that after 12 years, the previously logged forest had more or less recovered fully: only about 2–5% of the species has completely disappeared. Wong (1985) also showed that in an advanced regenerating forest (25 years after the logging operations) most of the forest specialists had recovered. In this study, 15% of the forest interior specialists (Appendix 1) were not found in the 23-year regenerating forest. This implies that recolonization in the logged forest study site is very poor compared to that in Malaysia. The understorey forest bird community in the logged forest study site had large transient populations as indicated by high overall capture rates and lower recapture rates. This may indicate that the conditions in the 23-year-old logged forest were still different from those of primary forest where birds occurred in low density but where the majority were residents.

The low regeneration of forest trees in logged forest study site does not improve the situation for those species that are not favoured by degraded habitats. This poor regeneration is enhanced by abiotic factors such as increased windthrows due to the openness (Skorupa and Kasenene, 1984; Kasenene, 1987; Tabor *et al*., 1990) and other ecological

factors such as increased elephant populations and trampling activities in logged forest study site (Nummelin, 1990; Lwanga, 1994). Elephants and other herbivores are attracted by the large herbaceous foliage that dominate this logged forest, hence further increasing damage to the seedlings and other vegetation (Lwanga, 1994).

Five of the missing species (African Pitta, Red-tailed Ant Thrush, Pale-breasted Illadopsis, Abyssinian Ground Thrush and Forest Robin) are ground-feeding insectivores. The most probable explanation for their absence may be their lack of adaptability to the high volume of understorey vegetation found in the logged forest study site. The altered microclimatic conditions within the logged forest may not favour the survival of such species (Thiollay, 1992). Local migrants such as the Pitta and some thrushes (Mackworth-Praed and Grant, 1964; Keith *et al*., 1992) may not be well adjusted to alterations of habitats. Lack of adjustment has also been documented in winter migratory species in the Americas (Terborgh, 1964; Robins, 1979). On the other hand, the absence of White-throated Greenbul and Mountain Greenbul from the logged site or their failure to re-establish themselves could be explained by the theory of 'niche contraction' (Wiens, 1989) and take-over of congeners' space by one or a few successful species. This happens among antwrens, *Myrmotherula*, in disturbed habitats in Malaysia (A.G. Johns, pers. comm.). It appears that the Yellow-whiskered Greenbul may have been prominent among the initial recolonizers, and, because of its omnivorous feeding habits and social system of lekking (Brosset, 1982; Keith *et al*., 1992), it may have taken up the niches of forest interior species such as the White-throated and the Mountain Greenbuls. Of these two species, the White-throated Greenbul was one of the most common species in the unlogged study site, hence their absence is all the more surprising and may be explained by competitive exclusion by the numerically superior Yellow-whiskered Greenbul.

Conservation implications

The logged forest study site retained a moderate number of forest birds after logging. However, logged areas cannot be a substitute to the primary forest because a large proportion of the bird fauna is generalist species that are of low conservation significance since they are widely distributed.

As a result of large entry of forest generalist birds into the logged forest, the diversity and richness appeared higher therein. However, 15% of primary forest birds had not yet recolonized or had failed to adapt to the logged forest habitat. There is no guarantee that more stenotypic forest birds will not disappear in the long run if the regeneration level of this habitat remains in the present state. In the same study, Dranzoa (1995) showed that substantial numbers of crevice nest sites were lost, and the existence of large numbers of forest interior species in the logged forest study site was owed to the presence of small but fairly intact forest patches.

The disturbance caused by the past logging in this part of Kibale forest triggered a series of negative interactions, whose long-term effect on forest interior birds and birds with specialized needs (i.e. crevice nesters, roosters) is still not well known and cannot be adequately predicted. Therefore there is a need to generate more information on the long-term effects of logging on forest bird species.

In order to safeguard against the loss of biological diversity, the retention of a mosaic of primary forest patches in logged tropical ecosystems should be made mandatory in any management system. At the same time, restoration of degraded tropical ecosystems should be supported as a means of recovery schemes for both the flora and fauna.

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Appendix 1. The total captures (N) and the recaptures (%) in unlogged and logged forests

Species (common/scientific name)	Category	Unlogged		Logged	
		N	%	N	%
Olive Sunbird *Nectarinia olivacea*	FF	295	12.7	570	38.9
Brown-chested Alethe *Alethe poliocephala*	FF	234	40.2	258	39.1
Yellow-whiskered Greenbul *Andropadus latirostris*	F	228	24.5	969	14.8
Bristlebill *Bleda syndactyla*	FF	132	28.8	156	41.0
White-throated Greenbul *Phyllastrephus albigularis*	FF	57	38.6	0	0
White-tailed Ant Thrush *Neocossypha poensis*	FF	55	38.2	44	25.0
Equatorial Akalat *Sheppardia aequatorialis*	FF	53	26.4	89	26.9
Green Hylia *Hylia prasina*	F	52	25.0	75	37.3
Cameroon Sombre Greenbul *Andropadus curvirostris*	FF	52	7.7	144	10.4
Little Greenbul *A. virens*	F	51	11.8	106	10.4
Scaly-breasted Illadopsis *Illadopsis albipectus*	FF	42	14.3	48	10.4
Red-capped Robin Chat *Cossypha natalensis*	FF	34	14.7	14	21.4
Red-headed Bluebill *Spermophaga ruficapilla*	F	31	16.1	83	8.4
Tambourine Dove *Turtur tympanistria*	F	30	3.3	84	3.6
Olive-green Camaroptera *Camaroptera chloronota*	FF	22	18.2	80	21.3
Slender-billed Greenbul *Andropadus gracilirostris*	FF	21	14.3	194	17.5
Rufous Thrush *Stizorhina fraseri*	FF	20	10.0	4	0
Brown Illadopsis *Illadopsis fulvescens*	FF	17	11.8	46	10.9
Ashy Flycatcher *Muscicapa caerulescens*	F	16	6.3	21	14.3
Chestnut Wattle-eye *Dyaphorophyia castanea*	FF	15	6.7	25	8.7
Yellow-rumped Tinkerbird *Pogoniulus bilineatus*	F	14	14.3	32	6.3
Blue-shouldered Robin Chat *Cossypha cyanocampter*	F	13	7.7	104	17.3
Red-bellied Paradise Flycatcher *Terpsiphone rufiventer*	FF	10	20.0	8	0
Dusky Long-tailed Cuckoo *Cercococcyx mechowi*	FF	9	22.2	13	15.4
Black-faced Rufous Warbler *Bathmocercus rufus*	FF	9	0	156	11.5
Blue-breasted Kingfisher *Halcyon malimbica*	F	8	12.5	0	0
Jameson's Wattle-eye *Dyaphorophyia jamesoni*	FF	7	14.3	52	13.5
Forest Robin *Stiphrornis erythrothorax*	FF	7	0	0	0
Lesser Honeyguide *Indicator minor*	F	6	0	6	0
Nicator *Nicator chloris*	F	6	0	7	0
Afep Pigeon *Columba unicincta*	FF	5	0	10	10
Pygmy Kingfisher *Ispidina picta*	F	4	25.0	1	0
Pale-breasted Illadopais *Illadopsis rufipennis*	FF	4	25.0	0	0
Red-chested Owlet *Glaucidium tephronotum*	FF	4	25.0	1	0
Red-faced Crimsonwing *Cryptospiza reichenovii*	FF	4	0	23	8.7
Grey-backed Camaroptera *Camaroptera brachyura*	f	3	0	30	3.3
Vieillot's Black Weaver *Ploceus nigerrimus*	f	3	0	1	0
Black-necked Weaver *P. nigricollis*	f	2	0	9	0
Black-billed Weaver *P. melanogaster*	FF	2	0	15	13.3
Yellowbill *Ceuthmochares aereus*	F	2	0	1	0
Black and White Mannikin *Lonchura bicolor*	f	2	0	*	–
Yellow-billed Barbet *Trachylaemus purpuratus*	F	2	0	1	0
Narina's Trogon *Apaloderma narina*	F	2	0	*	–
Brown-eared Woodpecker *Campethera caroli*	F	2	0	1	0
Honeyguide Greenbul *Baeopogon indicator*	FF	2	0	1	0
Green-headed Sunbird *Nectarinia verticalis*	F	2	0	6	0

Appendix 1. *Continued.*

Species (common/scientific name)	Category	Unlogged		Logged	
		N	%	N	%
Green-backed Twinspot *Mandingoa nitidula*	FF	1	0	19	5.3
Black Cuckoo *Cuculus clamosus*	FF	1	0	1	–
Elliot's Woodpecker *Dendropicos elliottii*	FF	1	0	1	0
Dark-backed Weaver *Ploceus bicolor*	F	1	0	11	9.1
Red-fronted Antpecker *Parmoptila woodhousei*	FF	1	0	14	14.3
Abyssinian Ground Thrush *Zoothera piaggiae*	FF	1	0	0	0
Red-tailed Ant Thrush *Neocossyphus rufus*	FF	1	0	0	0
Black-throated Apalis *Apalis Jacksoni*	FF	1	0	1	0
Black-billed Turaco *Tauraco schuettii*	FF	1	0	*	–
African Broadbill *Smithornis capensis*	FF	1	0	9	0
Yellow-crested Woodpecker *Picoides obsoletus*	F	1	0	*	–
African Pitta *Pitta angolensis*	FF	1	0	0	0
Mountain Greenbul *Andropadus nigriceps*	FF	1	0	0	0
Blue-throated Brown Sunbird *Nectarinia cyanolaema*	FF	1	0	2	0
African Hill Babbler *Pseudoalcippe abyssnica*	FF	1	0	1	0
African Thrush *Turdus pelios*	f	1	0	1	0
White-chinned Prinia *Prinia leucopogon*	F	1	0	42	19.1
Black-crowned Waxbill *Estrilda nonnula*	f	1	0	4	0
Grey-headed Negrofinch *Nigrita canicapilla*	F	*	0	4	0
Banded Prinia *Prinia bairdii*	F	*	–	59	13.6
Luhder's Bush Shrike *Laniarius leuhderi*	F	*	–	21	4.8
Yellow White-eye *Zosterops senegalensis*	f	*	–	18	0
Collared Sunbird *Antreptes collaris*	F	*	–	18	11.1
White-browed Crombec *Sylvietta leucophrys*	F	*	–	14	14.3
Masked Apalis *Apalis binotata*	FF	*	–	12	0
White-collared Oliveback *Nesocharis ansorgei*	F	*	–	7	0
Toro Olive Greenbul *Phyllastrphus hypochloris*	FF	*	–	6	0
Buff-spotted Woodpecker *Campethera nivosa*	FF	*	–	6	6.3
Common Bulbul *Pycnonotus barbatus*	f	*	–	5	0
Olive-bellied Sunbird *Nectarinia chloropygia*	F	*	–	5	0
Speckled Tinkerbird *Pogoniulus scolopaceus*	FF	*	–	4	0
Chubb's Cisticola *Cisticola chubbi*	F	0	0	4	0
Western Black-headed Oriole *Oriolus brachyrhynchus*	F	*	–	4	0
Joyful Greenbul *Chlorocchla laetissima*	FF	*	–	4	0
White-breasted Negrofinch *Nigrita fusconota*	F	*	–	3	0
Grosbeak Weaver *Amlyospiza albifrons*	f	*	–	3	0
Paradise Flycatcher *Terpsiphone viridis*	f	*	–	2	0
Black Bee-eater *Merops gularis*	FF	*	–	2	0
Lemon Dove *Aplopelia larvata*	FF	*	–	2	0
White-tailed Crested Flycatcher *Trochocercus albonotatus*	FF	–	–	2	0
Grey-capped Warbler *Eminia lepida*	f	0	0	2	0
Tawny-flanked Prinia *Prinia subflava*	nf	0	0	2	0
Wattle-eye *Platysteira cyanea*	f	*	–	1	0
White-browed Coucal *Centropus superciliosus*	nf	0	0	1	0
Dusky Tit *Parus funereus*	FF	*	–	1	0

Appendix 1. *Continued.*

Species (common/scientific name)	Category	Unlogged		Logged	
		N	%	N	%
Brown-headed Tchagra *Tchagra australis*	nf	0	0	1	0
Grey-headed Bush Shrike *Malconotus blanchoti*	nf	0	0	1	0
Cardinal Woodpecker *Dendropicos fuscescens*	nf	0	0	1	0
Bronze Mannikin *Lonchura cucullata*	nf	0	0	1	0
Scarlet-chested Sunbird *Nectarinia senegalensis*	nf	0	0	1	0
Total captures	–	1603	–	3809	–