
The influence of forest variation and possible effects of poaching on duiker abundance at Ngogo, Kibale National Park, Uganda

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Abstract

Duikers were censused at the Ngogo study area, Kibale National Park, Uganda, between July 2002 and August 2004. Censuses were conducted along three transects, of which, two (colonizing forests 1 and 2) were located in colonizing forests naturally replacing anthropogenic grasslands and one in old growth forest. Colonizing forest 1 was more prone to poaching than both colonizing forest 2 and the old growth forest that were closest to the research camp. Duikers that were actually sighted were identified to species, red or blue. However, on some occasions, duikers were detected by alarm calls and/or movements as they fled; these were simply recorded as duikers. Duiker abundance, regardless of species or mode of detection, was higher in colonizing forest 2 than colonizing forest 1 and the old growth forest. However, when the analysis was restricted only to duikers that were sighted, and hence identified to species, red duiker abundance was highest in colonizing forest 2 followed by the old growth forest and was lowest in colonizing forest 1; all these differences were significant. Blue duiker abundance was lowest in the old growth forest despite its proximity to the research camp; however, this was only significantly lower than in colonizing forest 2. Apart from colonizing forest 1, red duikers were significantly more abundant than blue duikers in the other two forest sections. This study suggests that forests colonizing anthropogenic grasslands may support more duikers than old growth forests; poaching in colonizing forest 1 has a severe impact on the duiker population and, red duikers are affected more severely by poaching than blue duikers.

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Résumé

Les duikers furent recensés dans la zone d'étude de Ngogo dans le Parc National de Kibale en Ouganda entre juillet 2002 et août 2005. Les recensements furent menés le long de trois transects, desquels deux (forêts colonisatrices 1 et 2) furent situés dans les forêts colonisatrices en train de remplacer naturellement la prairie anthropogène, et un dans la forêt surannée. La colonisation de forêt 1 fut plus enclin au braconnage que la forêt 2 et la forêt surannée qui était les plus près du camp de recherche. Les duikers vraiment aperçus furent identifiés par espèce - le céphalophe du natal ou le céphalophe bleu. Par contre, les duikers décelés par alarme, ou entrevus en train de s'enfuir furent simplement enregistrés comme duikers. L'abondance de duikers, sans regarder l'espèce ou le mode de détection, fut plus élevée dans la forêt colonisatrice 2 que dans la forêt 1 et la forêt surannée. Cependant, quand l'analyse fut contrainte aux duikers vraiment aperçus, et donc identifiés par espèce, l'abondance du céphalophe du natal fut plus élevée dans la forêt colonisatrice 2, suivi par la forêt surannée, et fut plus bas dans la forêt colonisatrice 1 ; toutes ces différences furent importantes. L'abondance du céphalophe bleu fut plus bas dans la forêt surannée malgré sa proximité du camp de recherche ; cependant, ce fut seulement beaucoup plus bas que dans la forêt colonisatrice 2. A part dans la forêt colonisatrice 1, les céphalophes du natal furent plus abondants que les céphalophes bleus dans les deux autres sections forestières. Cette étude impliquent que les forêts colonisant la prairie anthropogène peuvent soutenir un plus grand nombre de duikers que les forêts surannées ; le braconnage dans la forêt colonisatrice 1 entraîne des conséquences sévères pour la population de

duikers et les céphalophes du natal sont plus gravement touchés que les céphalophes bleus.

Introduction

The importance of bush meat as source of animal protein for some sections of the human population in sub-Saharan Africa is well documented (e.g. Wilkie, Sidle & Boundzanga, 1992; Feer, 1993; Fitzgibbon, Mogaka & Fanshawe, 1995; Noss, 1998, 2000; Wilkie *et al.*, 1998; Muchaal & Ngandjui, 1999; Wilkie & Carpenter, 1999; Hart, 2000; Remis, 2000). Contribution to animal protein consumed by local people can be as high as 98% in some areas (Muchaal & Ngandjui, 1999). The annual commercial value of wild meat for five West African countries varied between US\$22 and 205 million between 1989 and 1997 (Davis, 2002). West and Central African studies (e.g. Feer, 1993; Wilkie *et al.*, 1998; Wilkie & Carpenter, 1999; Hart, 2000) indicate that duikers were the most hunted animals. Contrary to these reports, a study conducted in Kenya, East Africa (Fitzgibbon *et al.*, 1995) indicated that duikers were caught rarely. This may however, represent a situation where the duiker population has already been overharvested. Although there are no hunting records for Kibale National Park, Uganda; anecdotal observations suggest that duikers are the prime targets of hunters in this area as in the West African forests. Over 90% of the wire snares recovered in this area are of the size suitable for catching small animals such as duikers.

The importance of duikers and other forest ungulates is not only limited to being sources of animal protein and income for humans, these animals are an integral component of the forest ecosystem. The decimation of forest ungulates will have deleterious effects on the long-term viability of the forest ecosystem; these animals serve as seed dispersers for some plants as well as food for forest predators (Redford, 1992; Wilkie *et al.*, 1998). If the harvesting of bushmeat is to continue contributing to the livelihood of mankind, it must be done on a sustainable basis. Unfortunately, most studies on the exploitation of bushmeat (e.g. Redford, 1992; Feer, 1993; Noss, 1998, 2000; Wilkie & Carpenter, 1999) indicate that current levels of exploitation are unsustainable for most prey species. In spite of all the evidence indicating that the harvesting of bushmeat is not sustainable in most parts of the world, international development agencies can still make a link between bushmeat exploitation and poverty alleviation (Bennett, 2002; Davis,

2002; Rao & McGowan, 2002; Rosser & Mainka, 2002; Sanderson & Redford, 2003). Faced with this situation, conservationists must either provide more convincing evidence that this exploitation is not sustainable or develop sustainable harvest models. However, the latter may be very difficult in the face of increasing human population and declining wildlife habitats.

In Uganda, duikers have not received much conservation attention. No effort has been made to determine their abundance or threats on a nationwide or park-wide scale as has been done for the more charismatic species such as chimpanzees (Plumptre, Cox & Mugume, 2003) and gorillas (Uganda Government, 2004). Studies on duikers in Uganda are very few, of short duration and cover relatively small areas (e.g. Nummelin, 1990; Plumptre, 1994; McCoy, 1995; Struhsaker, 1997). This is perplexing because in Uganda duikers are among those species that are targeted by poachers and hence, are directly affected by human activities. It is therefore necessary to monitor their populations, habitat changes and human threats that may affect them.

My ongoing research has two short-term objectives: (i) to compare duiker abundance in old growth forest and colonizing forests; (ii) to assess the impact of poaching on duiker abundance, and one long-term objective, i.e. assessing the impact of regular patrols by park rangers on duiker conservation. This paper focuses on the short-term objectives.

Methods

The study area and study subjects

Kibale National Park covers 766 km² in western Uganda between 0°13'N to 0°41'N and 30°19'E to 30°32'E. The park is a mixture of forest, colonizing bush, grassland and swamp surrounded by land dominated by agriculture (Struhsaker, 2002). Human population density in the parishes adjacent to the park is quite high – about 300 persons per square kilometre in the year 2000 (Struhsaker, 2002). Altitude within the park ranges from 1590 m in the north to about 990 m in the south, with Ngogo at about 1350 m. Rainfall in the park, generally follows a bimodal pattern with the months of March–May and September–November wet, while June–July and December–February are dry. Mean annual rainfall at Ngogo was 1492 mm for the period between 1977 and 1991 (Struhsaker, 1997). (For more details on the park, see

Struhsaker, 1997 and Chapman & Lambert, 2000.) The Ngogo study site is described in detail by Ghiglieri (1984) and Struhsaker (1997). The two colonizing forests studied were floristically similar. Both were grasslands as of 1955 (Uganda Government, 1965). The two areas were different in that colonizing forest 1 was more distant from the research camp and closer to the park boundary than colonizing forest 2. This situation rendered colonizing forest 1 more prone to poaching than colonizing forest 2. Unfortunately, poaching is difficult to quantify because it is an illegal activity and poachers endeavour to conceal evidences. Nevertheless, anecdotal observations such as presence of human and dog footprints, cuttings, snares and old snare sites indicate that poaching was more prevalent in colonizing forest 1 than colonizing forest 2.

Two species of duikers live in the park (Struhsaker, 1997). The blue duiker *Cephalophus monticola* is the smaller of the two and the smallest of the Cephalophinae; adults weigh about 5 kg (Struhsaker, 1997). The taxonomy of the red duiker in Kibale is uncertain (McCoy, 1995; Struhsaker, 1997). It has been referred to as *C. natalensis*, *C. harveyi*, *C. callipygus* and *C. weynsi* by various authors (McCoy, 1995; Struhsaker, 1997). The weight of one adult female (15.4 kg) recovered from poachers is within the range reported for *C. callipygus* and *C. weynsi* but about 2 kg heavier than that given for *C. natalensis* and *C. harveyi* (Struhsaker, 1997). Colour variation of the Kibale red duikers adds to the confusion, some animals having black muzzles and foreheads like those of *C. nigrifrons* (Struhsaker, 1997). It is not clear whether there are two or one polymorphic species of red duikers. For the purpose of this paper, duikers will be referred to as blue or red duikers.

Data collection

I collected data along three line transects (Fig. 1) between July 2002 and August 2004 inclusive. One transect was located in old growth forest. Duiker censuses have been conducted along this transect since 1975 (McCoy, 1995; Struhsaker, 1997). I established the transects in the colonizing forests in 2002 and conducted two monthly censuses along each transect for all the months except for July 2002 and August 2004. During these months, I completed only one census for each transect. Censuses along the same transect were separated by at least 7 days and those along different transects were conducted on consecutive days except when interrupted by rain or the presence of elephants.

In order to allow direct comparison, I used methods similar to those used by McCoy (1995) and Struhsaker (1997) to census duikers in the same forest. Similar methods have been used to estimate forest primate densities (National Research Council, 1981; Whitesides *et al.*, 1988). I conducted censuses between 7.30 and 13.30 hours. During each census I walked slowly at about 1 km h⁻¹, regularly stopping at intervals of 10 to 20 m to scan the forest floor for as far as I could see and listened for duiker alarms and/or movements. On detecting a duiker, I recorded whether it was actually seen (sighted), detected by alarm (flushed alarm) or simply detected by fleeing movements (flushed no alarm). Fleeing duikers make characteristic movements, gallop followed by a short run, that are easily distinguished from other terrestrial animals in the forest. Inclusion of animals detected this way counters the effects of poor visibility especially in colonizing forests that usually have thick ground vegetation cover. For animals sighted, I visually estimated sighting distance (animal to observer), measured sighting angle using a compass, and calculated perpendicular distance using the preceding measurements. Transect lengths were 3.9 km in colonizing forest 1 (southern transect), 3.75 km in colonizing forest 2 (northern transect) and 4.4 km in the old growth forest (central transect).

Data analysis

In general, the aim of conducting line transect censuses is to estimate and compare animal densities. However, this was not possible because several of the assumptions outlined by Buckland *et al.* (1993) which are crucial to the accuracy of density estimates obtained using DISTANCE are unlikely to be fulfilled in duiker censuses. The major ones are outlined below:

1 Objects on the census line are always detected; this assumption was most likely not met all the times because duikers naturally avoid approaching humans, sometimes they elude detection by moving away quietly and this is especially true for blue duikers. The large number of sightings on the trail reflects greater visibility on the trail, but this does not necessarily mean that all duikers on the trail were seen.

2 Objects are detected at their initial location, prior to any movement in response to the observer; as mentioned above, duikers tend to avoid approaching humans by moving away quickly and oftentimes quietly. Even when they alarm as they flee, they are usually seen several

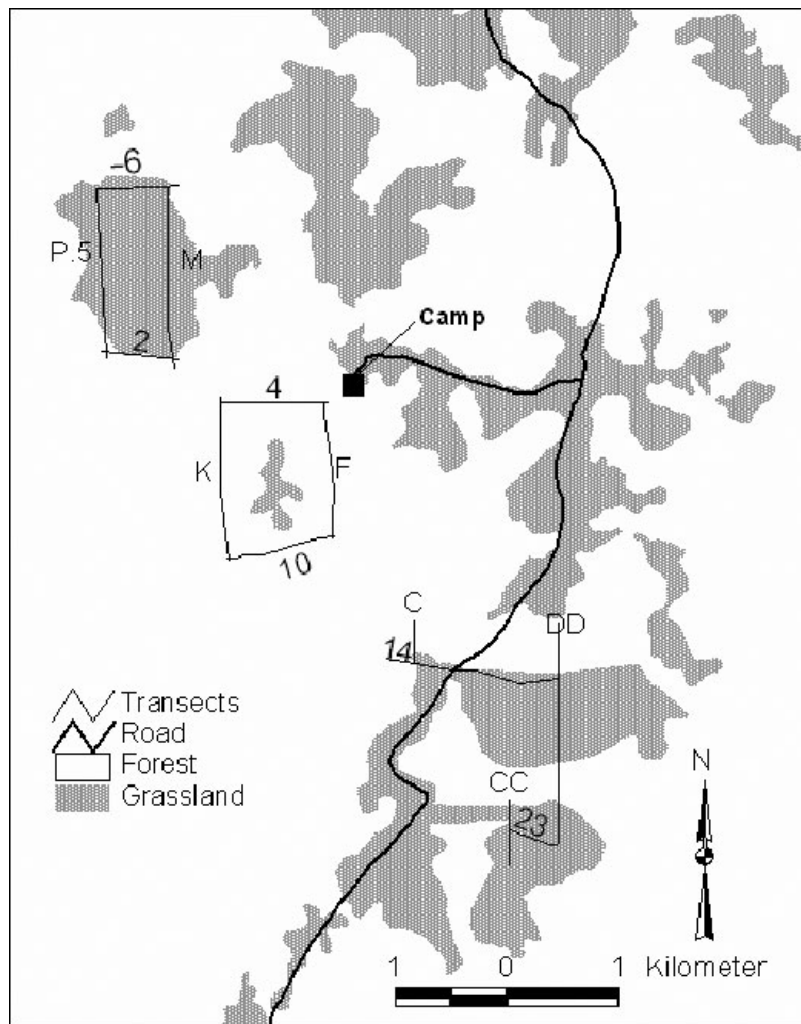


Fig 1 Map of the Ngogo Study Area showing vegetation as of 1955 and census routes used for censusing duikers. Census trails are represented with lines labelled with numbers or letters; areas covered by the northern and southern routes have now reverted to colonizing forest.

meters from the initial location. Therefore, this assumption does not seem to apply.

3 Census lines are placed at random with respect to the distribution of the animals under consideration. Previous studies in Kibale (Nummelin, 1990; McCoy, 1995) indicate that duikers prefer cut trails in forests with thick undergrowth; it is therefore unlikely that this assumption was met in colonizing forests.

Furthermore, comparison of animal densities across habitat types may be problematic if detection is affected by differences in vegetation cover. I therefore tested whether sighting and perpendicular distance estimates were not biased by habitat differences among the three forest sections, using ANOVA. Separate tests were conducted for each duiker species. Where significant differences were

detected, I used the LSD multiple range tests to determine which mean values were different. Additionally, I compared the shapes of the frequency distributions of sighting and perpendicular distances between transects in a pairwise manner using the two-sample Kolmogorov–Smirnov test. Differences in distance estimates among transects render use of density estimates (animals ha^{-1}) inappropriate.

Given the above limitations, I compared relative abundances (animals detected km^{-1}) among transects instead of densities because the former does not make assumptions that are likely to be violated. Furthermore, this also allows inclusion of animals detected by sounds in the analysis because vegetation cover does not bias this mode of detection.

Table 1 Analysis of variance results comparing sighting and perpendicular distances for blue and red duikers among the three transects

Species	Distance	Colonizing forest 1	Colonizing forest 2	Old-growth forest	F-value	P-value
Blue	Sighting	17.44 (8.27)	17.94 (10.44)	20.06 (10.18)	0.748	0.475
	Perpendicular	7.33 (8.41)	5.95 (5.87)	9.30 (10.14)	1.717	0.184
Red	Sighting	19.69 (10.93)	21.64 (13.27)	20.33 (11.33)	0.606	0.546
	Perpendicular	6.47 ^a (6.66)	5.55 ^a (6.51)	10.56 ^b (8.75)	14.293	<0.001

Mean distances and standard deviations (in parentheses) are presented.

Sample sizes were 43, 51, and 33 in colonizing forest 1, colonizing forest 2 and old growth forest, respectively, for blue duikers. Corresponding sample sizes for red duikers were 51, 132, and 111.

Superscripts indicate that mean values that were different ($a < b < c$) at $P < 0.05$ LSD.

For each of the forest section sampled, I computed the precision of my estimates of mean number of each duiker species sighted, and for all duikers detected. Precision was computed as 95% confidence limits of estimated mean values expressed as the percentage of those mean values (National Research Council, 1981). This was done to determine if the number of censuses completed were adequate to detect differences in the relative abundance of duikers among the sections of the forest sampled. The Kruskal–Wallis test was used to determine if duiker relative abundance (duikers detected km^{-1}) differed among forest sections. Where differences were detected, *post hoc* procedures (Siegel & Castellan, 1988) were computed to ascertain which two mean values were different. This analysis was conducted separately for each species where the animals were detected by sight. Analyses including all duikers detected by sight, vocalization or movements were also performed. The Mann–Whitney test was used to test if the abundances of blue and red duikers were different in any of the forest sections sampled. These analyses were limited to sighted duikers only.

Results

Sighting and perpendicular distances

Average sighting and perpendicular distances are presented in Table 1. For blue duikers, both sighting and perpendicular distances did not differ significantly among the three transects. Similarly, sighting distance for the red duikers did not differ among transects; however, perpendicular distances differed significantly. On average, perpendicular distances for red duikers were longer in the old growth forest than in colonizing forests (Table 1). The difference between the two colonizing forests was not

significant. These differences were also reflected in the shapes of frequency distribution of sighting and perpendicular distances.

The shapes of frequency distribution of perpendicular distances did not differ between any pair of transects for blue duikers (all comparisons $P > 0.1$). However, for the red duikers, significant differences between shapes of frequency distribution of perpendicular distances were detected between colonizing forest 1 and the old growth forest ($Z = 1.786$, $P = 0.003$) and between colonizing forest 2 and the old growth forest ($Z = 2.318$, $P < 0.0001$). The difference between colonizing forest 1 and 2 was not significant. On the other hand, the shapes of frequency distribution of sighting distances did not differ between any pair of transects for neither blue nor red duikers (all comparisons $P > 0.1$).

Adequacy of sample sizes

Per cent precision of mean number of duikers detected plotted as a function of cumulative number of censuses approached an asymptote after 20–30 censuses. This suggests that the number of censuses conducted in each forest section were adequate to detect differences among these forest sections. Curves reached an asymptote much quicker where encounter rates with duikers were higher. Consequently, curves that included all duikers regardless of species or mode of detection were the most asymptotic in any forest section. Table 2 shows precision estimates after the 50th census in each of the forest sections sampled. These are based on duikers that were detected visually and hence identified to species, duikers that were detected visually or by alarm calls, and the last category includes all duikers including those detected from movements without vocalizations. Precision was higher for red duikers than

Table 2 Precision of estimated mean number of duikers per census after 50 censuses along each of the three transects

Transect	Blue duiker	Red duiker	Visual or vocal	Visual, vocal or movement
Colonizing forest 1 (%)	±36.5	±32.9	±25.3	±23.5
Colonizing forest 2 (%)	±34.5	±17.6	±15.2	±15.0
Old growth forest (%)	±41.0	±21.3	±20.2	±20.1

Values under blue and red duikers are based on animals that were detected visually, while those under visual or vocal are based on animals that were detected visually or from alarm calls regardless of species and the category visual, vocal or movement includes all duikers detected including those detected by movement without alarm calls.

blue duikers in all forest sections. Overall, precision was highest in colonizing forest 2.

Comparison of duiker abundance among forest sections

When duiker abundance, regardless of species or mode of detection, was compared across forest sections, a significant difference was detected (Table 3). *Post hoc* tests revealed that duikers were more abundant in colonizing forest 2 than in colonizing forest 1 and the old growth forest. Although more duikers were detected in the old growth forest than in colonizing forest 1, this difference was not significant. Results followed exactly the same trend when the analysis was restricted to only animals that were detected visually or by vocalizations (Table 3). However, when the analysis was restricted to only animals that were detected visually and hence identified, a somewhat different picture emerged. The abundance of blue duikers differed significantly among the three forest sections. *Post hoc* multiple comparisons revealed that the

abundance of blue duikers in the old growth forest was lower than in either of the two colonizing forests. However, the difference between the two colonizing forests was not significant. For the red duikers, the overall test also detected a significant difference in the abundance of this species among the forest sections. Red duiker abundance was different in all the three forest sections; it was highest in colonizing forest 2 followed by the old growth forest and lowest in colonizing forest 1 (Table 3).

Blue versus red duiker abundance

The comparison between the abundance of blue and red duikers in each forest section revealed that although red duikers were slightly more abundant than blue duikers in colonizing forest 1, this difference was not significant (Table 4). On the other hand, in colonizing forest 2, red duikers were more than twice as abundant as blue duikers, and this difference was highly significant. In the old growth forest, red duikers were more than three times as abundant as blue duikers. This difference was also highly significant (Table 4).

Discussion

The secretive nature of duikers coupled with their small size and poor visibility on the forest floor rendered the estimation of duiker densities impossible. This is because, under these conditions, several assumptions underlying models for density estimation were very likely violated (see Methods). Furthermore, density estimates were complicated by inconsistencies in perpendicular distances (Table 1). Average perpendicular distances for blue duikers were very short because many duikers were sighted on the trail, which could lead to overestimation of density for this

Species	Colonizing forest 1	Colonizing forest 2	Old-growth forest	Kruskal–Wallis statistic	P-value
All detected	0.56 ^a (0.47)	1.11 ^b (0.61)	0.70 ^a (0.53)	27.17	<0.001
Visual or alarm	0.53 ^a (0.47)	1.05 ^b (0.58)	0.68 ^a (0.52)	27.17	<0.001
Blue	0.22 ^{ab} (0.29)	0.26 ^b (0.31)	0.15 ^a (0.25)	6.86	0.032
Red	0.26 ^a (0.30)	0.69 ^c (0.45)	0.49 ^b (0.39)	32.03	<0.001

Averages for the all detected category are based on duikers of both species that were either actually seen or detected by alarm calls or movements during the census. Averages for blue and red are based on duikers that were actually seen.

Figures in parentheses are standard deviations and superscripts indicate mean values that were shown by the *post hoc* test as different (a < b < c) $P < 0.05$.

Table 3 Kruskal–Wallis results comparing average number of duikers per km of transect in colonizing forests 1 and 2 and in the old growth forest

Table 4 Result from Mann-Whitney test comparing differences between average number of blue and red duikers sighted per km in colonizing forests 1, colonizing forest 2 and old growth forest

Transect	Blue	Red	Z-value	P-value
Colonizing forest 1	0.22 (0.29)	0.26 (0.30)	-0.763	0.446
Colonizing forest 2	0.26 (0.31)	0.69 (0.45)	-5.105	<0.001
Old growth forest	0.15 (0.25)	0.49 (0.39)	-4.926	<0.001

Figures in parentheses are standard deviations.

species. For red duikers, perpendicular distance varied significantly among forest sections; results in Table 1 suggest that visibility was better in the more open old growth forest.

Nonetheless, some questions of great importance to conservation such as habitat preference, population changes over time, impact of hunting or the response of duikers to conservation efforts can be adequately addressed using relative abundance. This method does not make assumptions that are likely to be violated. Furthermore, the method does not stress the animals compared with methods that involve capturing of the animals (e.g. Wilkie & Finn, 1990) although the latter method can yield more precise density estimates.

Precision (the repeatability of a sample estimate) was consistently better for the more abundant species, the red duiker, than blue duiker in all forest sections (Tables 2 and 3). Similarly, precision was consistently highest in colonizing forest 2 where duiker abundance was highest and lowest in colonizing forest 1 where duiker abundance was lowest. The precision of line transect methods is directly related to population density (National Research Council, 1981) and interobserver reliability (Mitani, Struhsaker & Lwanga, 2000). Other factors that are likely to influence precision include home range size and mobility of the species under consideration. Assuming that home range size and mobility were not influenced by habitat, the only factor that affected precision in this study was difference in density because I was the only observer.

The influence of habitat and hunting on duiker abundance

When duiker abundance, regardless of mode of detection and species, was compared among the three forest sections, results were rather ambiguous. Duiker abundance in colonizing forest 1 and the old growth forest was not significantly different (Table 3). However, duiker abundance in colonizing forest 2 was significantly higher than either colonizing forest 1 or the old growth forest. One would expect duiker abundance in the two colonizing forests to be

similar. The higher abundance of duikers in colonizing forest 2 compared with the old growth forest suggests that young forests may be better habitats for duikers. This observation lends support to Wilkie & Finn's (1990) impression that secondary forests (replacing slash-and-burn agriculture) are more productive compared with old growth forests in terms of hunted species including duikers. In the Ituri forest of the Democratic Republic of Congo (former Zaire) they did not find the relative densities of duikers and other hunted species in colonizing forest to be significantly lower than in the old growth forest, despite the continuous high hunting intensity in the former. The difference between duiker abundance in colonizing forests 1 and 2 suggests that hunting may be affecting the duiker population in colonizing forest 1. Although I did not quantify hunting pressure systematically, anecdotal observations suggest that hunting pressure was higher in colonizing forest 1. Signs such as bare foot and sandal prints (all workers wear rubber or jungle boots), cuttings, paths used by humans, and wire snares or old snare sites were not uncommon in colonizing forest 1.

Proximity to active research camps serves as a deterrent to poachers (Remis, 2000; Fischer & Linsenmair, 2001; Struhsaker, 2002). Results from this study are consistent with these findings. In spite of the relatively high abundance of duikers in the old growth, signs of poaching were extremely infrequent. This area is very close to the research camp and is the center of activity for chimpanzee researchers. Although colonizing forest 2 is further away from the research camp, it is between two research camps and workers walk through this section of the forest on regular basis. This activity apparently confers some protection to the duikers in this area against poachers. Colonizing forest 1 on the other hand is located between the Ngogo camp and the park boundary and is very accessible to poachers.

When the comparison of duiker abundance was restricted to only animals that were sighted, it became apparent that blue and red duikers were affected differently by habitat type and possibly poaching (Table 3). In spite of

the higher likelihood of poaching incidence in colonizing forest 1, blue duiker abundance in this forest section was not significantly different from that in colonizing forest 2. This observation suggests that the current level of poaching does not affect the blue duiker population greatly. Studies from elsewhere (Muchaal & Ngandjui, 1999; Hart, 2000) lend support to this suggestion. Blue duikers are capable of maintaining their populations under exploitation because of their rapid growth rates; in particular, females in exploited areas attain sexual maturity at a young age (Hart, 2000). In spite of close proximity to the research camp, and hence more protection from poaching, the old growth forest had the lowest abundance of blue duikers; the difference between the relatively protected forest, colonizing forest 2 was significant (Table 3). This observation suggests that the old growth forest may be a less favourable habitat for blue duikers than colonizing forests.

Data on duikers sighted indicate that red duikers were least abundant in colonizing forest 1 (Table 3). The difference between the two colonizing forests suggests that the red duiker population in colonizing forest 1 is severely affected by poaching. Because the vegetation in both forest sections is considerably similar, composed of forest replacing former grasslands, one would expect the abundance of red duikers to be similar; the apparent difference between the two areas is poaching intensity. Considering that there are fewer red duikers in colonizing forest 1 than colonizing forest 2, and that the abundance of blue duikers in these two forest sections did not differ significantly, yet both species are experiencing similar conditions, it is safe to conclude that red duikers are more affected by poaching than blue duikers. The same conclusion was reached in Makokou, Gabon (Lahm, 1994, see Wilkie & Carpenter, 1999), Lobéké, Cameroon (Wilkie & Carpenter, 1999; Fimbel, Curran & Usongo, 2000) and Ituri forest, Congo (Hart, 2000). A similar situation may prevail in the Budongo Forest in Uganda; Plumptre (1994) reported that the density of red duikers was far less than that of blue duikers in this forest. Although he did not discuss poaching, other studies from Budongo indicate that snaring is a serious problem in this forest (Quiatt, Reynolds & Stokes, 2002; Plumptre *et al.*, 2003).

In spite of the fact that the old growth forest section was closest to the research camp, and that researchers were always active in this section, thus offering more protection, the abundance of sighted red duikers was higher in colonizing forest 2 than in the old growth forest. This obser-

vation suggests that colonizing forest may provide better habitat for red duikers than old growth forest. In the Ituri forest, Democratic Republic of Congo, Wilkie & Finn (1990) inferred that secondary forests replacing abandoned cultivated areas were more productive and could sustain higher levels of hunting (duikers were among the hunted species) than mature uncut forests.

In forest sections that received more protection from poachers, that is old growth forest and colonizing forest 2, red duikers were significantly more abundant than blue duikers (Table 4). On the other hand, in colonizing forest 1 that was more prone to poaching, the abundance of both species was about the same. These results suggest that in Kibale, in the absence of hunting, red duikers are more abundant than blue duikers. In the un hunted areas of the Ituri forest, the opposite was observed; blue duikers were more abundant than red duikers (Hart, 2000). However, at the Ituri study site, blue duikers were less vulnerable to leopard predation, the main predator, than red duikers (Hart, Katembo & Punga, 1996; Hart, 2000). Probably in the absence of predation by leopards, red duikers would have been more abundant than blue duikers as at Ngogo where leopards no longer exist. The lack of significant difference between the abundance of blue and red duikers in colonizing forest 1 unlike in the other two forest sections (Table 4) suggests that red duikers are more severely affected by poaching than blue duikers. Studies from elsewhere lend support to this suggestion. For example, the density of blue duikers was higher than that of red duikers in the heavily hunted area of Mossapoula, Central African Republic (Noss, 2000); in the western Dja Reserve, Cameroon, the capture rate of a red duiker species was higher in the less intensively hunted area whereas that of blue duikers was higher in more intensively hunted area (Muchaal & Ngandjui, 1999). Similarly, in the Ituri Forest, the frequency of red duiker tracks in the un hunted area was significantly higher than in the hunted area while no significant difference was detected for blue duikers in both areas (Koster & Hart, 1988).

Compared with two previous duiker censuses (McCoy, 1995; Struhsaker, 1997) conducted in the old growth forest at Ngogo along the same transect as I did, our results were very similar. Duiker abundance (based on duikers detected per kilometre) was 0.796, 0.705 and 0.70 during Struhsaker's, McCoy's and my study, respectively. Struhsaker conducted his study between 1973 and 1978, while McCoy conducted hers in 1993. In all studies, we used the same methods thus allowing direct comparisons. These results

suggest that the duiker population in the old growth forest at Ngogo is relatively stable. However, this apparent stability in duiker population is attributable to the active research camp in the area. Poaching up to the fringes of the trail system, as evidenced by bare footprints, cuttings, wire snares and campfire sites were common prior to the establishment of a ranger post at Ngogo in April 2004. Active research camps are known to deter illegal activities in their vicinity (Remis, 2000; Fischer & Linsenmair, 2001; Struhsaker, 2002), therefore the presence of signs of poaching at the fringes of the Ngogo study site seems to indicate depletion of duikers further away from the research camp rather than boldness of poachers. This impression is supported by the low abundance of red duikers in colonizing forest 1 that was furthest away from the camp.

Conclusion

In conclusion, duiker abundance varied across forest sections. This variation is apparently influenced by differences in habitat type, poaching, and proximity to the research camp. Colonizing forests that are not affected by poaching may provide better habitats for duikers than old growth forests. Therefore, forest conservation should pay attention to both colonizing and old growth forests. The presence of an active research camp at Ngogo seems to deter poachers; it is therefore important to extend research activities further away from the camp or conduct frequent patrols in distant areas.

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References

BENNETT, E.L. (2002) Is there a link between wild meat and food security? *Cons. Biol.* **16**, 590–592.

- BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P. & LAAKE, J.L. (1993) *Distance Sampling*. Chapman & Hall, London.
- CHAPMAN, C.A. & LAMBERT, J.E. (2000) Habit alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. *Am. J. Primatol.* **50**, 169–185.
- DAVIS, G. (2002) Bushmeat and international development. *Cons. Biol.* **16**, 587–589.
- FEER, F. (1993) The potential for sustainable hunting and rearing of game in tropical forests. In: *Tropical Forests, People and Food* (Eds C. M. HLADIK, A. HLADIK, O. F. LINARES, H. PAGEZY, A. SEMPLE and M. HADLEY). UNESCO, Paris, pp. 691–708.
- FIMBEL, C., CURRAN, B., USONGO, L. (2000) Enhancing the sustainability of duiker hunting through community participation and controlled access in the Lobéké region of southern Cameroon. In: *Hunting for Sustainability* (Eds J. ROBINSON, and E. BENNETT). Columbia University Press, New York. pp. 356–374.
- FISCHER, F. & LINSENMAIR, K.E. (2001) Decreases in ungulate population densities. Examples from the Comoe National Park, Ivory Coast. *Biol. Cons.* **101**, 131–135.
- FITZGIBBON, C.D., MOGAKA, H. & FANSHAW, J.H. (1995) Subsistence hunting in Arabuko-Sokoke Forest, Kenya, and its effects on mammal populations. *Cons. Biol.* **9**, 1116–1126.
- GHIGLIERI, P.M. (1984) *The Chimpanzee of Kibale Forest*. Columbia University Press, New York.
- HART, J. (2000) Impact and sustainability of indigenous hunting in the Ituri Forest, Congo-Zaire: a comparison of un hunted and hunted duiker populations. In: *Hunting for Sustainability* (Eds J. ROBINSON, and E. BENNETT). Columbia University Press, New York, pp. 106–153.
- HART, J.A., KATEMBO, M. & PUNGA, K. (1996) Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *Afr. J. Ecol.* **34**, 364–379.
- KOSTER, S.H. & HART, J.A. (1988) Methods for estimating ungulate populations in tropical forests. *Afr. J. Ecol.* **26**, 117–126.
- MCCOY, J. (1995) Responses of blue and red duikers to logging in the Kibale Forest of Western Uganda. M.Sc. Thesis, University of Florida, Gainesville, FL.
- MITANI, J.C., STRUHSAKER, T.T. & LWANGA, J.S. (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *Int. J. Primatol.* **21**, 269–286.
- MUCHAAL, P.K. & NGANDJUI G. (1999) Impact of village hunting on wildlife populations in western Dja Reserve, Cameroon. *Cons. Biol.* **13**, 385–396.
- National Research Council (1981) *Techniques for Study of Primate Population Ecology*. National Academy Press, Washington D.C.
- NOSS, A. (1998) Cable snares and bushmeat markets in a central African forest. *Environ. Cons.* **25**, 228–233.
- NOSS, A. (2000) Cable snare and nets in the Central African Republic. In: *Hunting for Sustainability in Tropical Forests* (Eds J. ROBINSON, and E. BENNETT). Columbia University Press, New York, pp. 282–304.

- NUMMELIN, M. (1990) Relative habitat use of duikers, bush pigs, and duikers in virgin and selectively logged areas of the Kibale Forest, Uganda. *Trop. Zool.* **3**, 111–120.
- PLUMPTRE, A. (1994) The effects of long-term selective logging on blue duikers in the Budongo Forest Reserve. *Gnusletter* **13**, 15–16.
- PLUMPTRE, A.J., COX, D. & MUGUME, S. (2003) *The Status of Chimpanzees in Uganda*, Albertine Rift Technical Report Series no 2. Wildlife Conservation Society, Kampala.
- QUIATT, D., REYNOLDS, V. & STOKES, E.J. (2002) Snare injuries to chimpanzees (*Pan troglodytes*) at 10 study sites in east and west Africa. *Afr. J. Ecol.* **40**, 303–305.
- RAO, M. & MCGOWAN, P.J.K. (2002) Wild-meat use, food security, livelihoods, and conservation. *Cons. Biol.* **16**, 580–583.
- REDFORD, K.H. (1992) The empty forest: many large mammals are already ecologically extinct in vast areas of neotropical forest where the vegetation still appears intact. *BioScience* **42**, 412–422.
- REMIS, M.J. (2000) Preliminary assessment of the impact of human activities on gorillas *Gorilla gorilla* and other wildlife at Dzanga-Sangha Reserve, Central African Republic. *Oryx* **34**, 56–65.
- ROSSER, A.M. & MAINKA, S.A. (2002) Overexploitation and species extinctions. *Cons. Biol.* **16**, 584–586.
- SANDERSON, S.E. & REDFORD, K.H. (2003) Contested relationships between biodiversity conservation and poverty alleviation. *Oryx* **37**, 389–390.
- SIEGEL, S. & CASTELLAN, N.J. (1988) *Nonparametric Statistics for Behavioral Sciences*. McGraw-Hill, New York.
- STRUHSAKER, T.T. (1997) *Ecology of an African Rain Forest*. University Press of Florida, Gainesville, FL.
- STRUHSAKER, T.T. (2002) Strategies for conserving forest national parks in Africa with a case study from Uganda. In: *Making Parks Work: Strategies for Preserving Tropical Nature* (Eds J. TERBORGH, C. van SCHAIK, L. DAVENPORT, and M. RAO), Island Press, Washington, DC, pp. 97–110.
- Uganda Government (1965) *Maps of Fort Portal and Kahunge, Series Y 732, Edition 3 U. S. D.*. Department of Lands and Survey, Entebbe, Uganda.
- Uganda Government (2004) *Conservation Action Plan for Uganda Mt. Gorillas 2006–2010*. Uganda Wildlife Authority, Kampala, Uganda.
- WHITESIDES, G.H., OATES, J.F., GREEN, S.M. & KLUBERDANZ, R. P. (1988) Estimating primate densities from transects in a West African rain forest: a comparison of techniques. *J. Anim. Ecol.* **57**, 345–367.
- WILKIE, D.S. & CARPENTER, J.F. (1999) Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodiv. Cons.* **8**, 927–955.
- WILKIE, D.S. & FINN, J.T. (1990) Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaire. *Biotropica* **22**, 90–99.
- WILKIE, D.S., SIDLE, J.G. & BOUNDZANGA, G.C. (1992) Mechanized logging, market hunting, and a bank loan in Congo. *Cons. Biol.* **6**, 570–580.
- WILKIE, D.S., CURRAN, B., TSHOMBE, R. & MORELLI, G.A. (1998) Modeling the sustainability of subsistence farming and hunting in the Ituri Forest of Zaire. *Cons. Biol.* **12**, 137–147.

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