Research Article

Relative densities of mammals in response to different levels of bushmeat hunting in the Udzungwa Mountains, Tanzania.

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Abstract

Bushmeat hunting constitutes the most immediate threat to wildlife populations in the Udzungwa Mountains of the Eastern Afromontane biodiversity hotspot. This study assesses the impact of hunting by comparing densities of mammalian species between the little hunted West Kilombero Scarp Forest Reserve (WKSFR), the medium-hunted Udzungwa Scarp Forest Reserve (USFR) and the intensively hunted New Dabaga Ulongambi Forest Reserve (NDUFR). Of the 22 species recorded, 20 were present in WKSFR, 17 in USFR and 12 in NDUFR. Most large species (>40 kg) were absent from hunted areas, while medium-sized species were reduced more than smaller species. Few traces of Abbott's duiker were observed in hunted areas and bush pig were reduced by more than 85% in hunted areas. Hunting appears to have had little effect on relative abundance of primates, blue duiker, Harvey's duiker, aardvark, eastern tree hyrax, and giant pouched rat in USFR, at least for those areas surveyed. In NDUFR relative abundance of most mammals are reduced compared to the less hunted reserves. The exception is the red colobus which were no less abundant than USFR. However in NDUFR, transects were placed in the best quality habitat for these habitat-sensitive monkeys, thus emphasising the additional role of habitat degradation. The effect of hunting appears to be proportional to the size of the species and the intensity of hunting, although effects of life history strategy, forest fragment size, isolation, and previous logging cannot be excluded. Reduction of hunting levels are paramount to the survival of large bodied species in USFR and for the continued presence of most species in NDUFR. This study furthermore constitutes an important baseline for monitoring the effect of current efforts to implement joint forest management in the Udzungwa Mountains.

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Introduction

Hunting of wildlife for food (i.e., bushmeat hunting) is today considered a significant threat to conservation of biodiversity [1]. Available information indicates that hunting is often not sustainable, and wildlife populations in west and central Africa have shown consistent declines or have become locally extirpated [2], whereas the situation has been less studied in East Africa. In Tanzania, bushmeat is becoming increasingly important as a source of protein and cash income [3]. The illegal bushmeat trade is developing fast in urban areas and is beginning to drive demand [3].

The Eastern Arc forests of Kenya and Tanzania have, as a component of the Eastern Afromontane biodiversity hotspot, been ranked among the 34 most biologically diverse areas in the world [4]. The Udzungwa Mountains have the largest area of forest cover within the Eastern Arc and have been considered of particular importance for the protection of biodiversity [5, 6]. Despite the now fragmented nature of forested areas, the Udzungwa Mountains support populations of five mammal species and two subspecies that are endemic to the Eastern Afro-Montane and the Coastal Forests biodiversity hotspot [4] as well as 12 IUCN Red-listed larger mammals (>400 g). A considerable number of new vertebrate species have also been discovered in recent years (see [6]). The larger endemic mammal species in the Udzungwa Mountains include Abbott's duiker (*Cephalophus spadix*), Lowe's servaline genet (*Genetta servalina lowei*) [75], the newly discovered grey-faced sengi or elephant shrew (*Rhynchocyon udzungwensis*) [7], and three endemic primates: Udzungwa red colobus (*Procolobus gordonorum*) (Fig. 1), Sanje mangabey (*Cercocebus galeritus sanjei*), and the kipunji (*Rungwecebus kipunji*), a newly described genus [8]. It is assumed that forest cover was continuous in recent historical time [5]. Previous logging and agricultural encroachment has fragmented the forests (median natural forest patch area 8.74 km^2, [9]), reduced available habitats, and led to the threatened status of many of these species.

Fig. 1. Udzungwa red colobus (*Procolobus gordonorum*) endemic to the Udzungwa Mountains. Photo by M.R. Nielsen taken in NDUFR.

A considerable proportion of Udzungwa forests are legally protected in forest reserves, and since the early 1990s Tanzania's national forest policy has introduced a stop to all logging in government reserves. Although illegal logging still occurs in the Udzungwas, it is now on a much lower scale, but subsistence hunting is widespread. Thus, in areas where the forest is still standing, bushmeat hunting is considered the greatest threat to wildlife populations [10]. Bushmeat hunting for commercial as well as subsistence use can drive species to the point of local extinction [1, 2]. It is therefore urgently necessary to assess the spatial effect of hunting and address this in management plans that can ensure the survival of large mammal species in the Udzungwa Mountains.

Due to a lack of monitoring of population trends, studies of the impact of hunting on mammal populations in tropical forests primarily consist of market analyses of carcasses on sale (e.g., [11]), comparisons of abundances between sites differing in level of hunting (e.g., [10, 12]) and comparison of harvest rate with sustainable yield calculations based on reproductive characteristics of wildlife species (e.g., [12, 13]). While some studies indicate that bushmeat hunting can be sustainable for some species [14], most studies find that hunting is unsustainable for larger and preferred game species and primates [15, 16]. Hunting pressure also interacts with factors such as forest size to affect sustainability so that populations in small reserves are at particularly high risk of local extinction [17, 68, 69].

There are fundamental problems in the approaches for assessing hunting effort and impact [18]. In surveys of bushmeat markets, the size of the affected wildlife population is often not known, and the harvest level is underestimated if some carcasses are not brought to market [11]. Assessing harvest levels directly in the Udzungwa Mountains is complicated, as hunting is illegal and people are reluctant to share information. Estimation of potential sustainable harvest yields requires detailed knowledge of ecology and abundance [19]. This method is therefore not suitable in areas like the Udzungwa Mountains where little information is available on density and breeding ecology of wildlife populations. Comparison of animal abundances between areas differing in hunting level may be biased by natural variability in habitat quality. If however, similar habitats are compared, the method can provide a rapid assessment of the direct effect of hunting on wildlife populations [20]. Combined with indirect measures of hunting levels, this can provide rough estimates of the effect and long-term sustainability of varying hunting intensities and methods.

This study aims to evaluate the effect of hunting in montane forests of the Udzungwa Mountains by comparing the relative density of mammals in three Forest Reserves subjected to different levels of hunting: the little-hunted West Kilombero Scarp Forest Reserve (WKSFR), the medium-hunted Udzungwa Scarp Forest Reserve (USFR) and the intensively hunted New Dabaga Ulongambi Forest Reserve (NDUFR; often referred to incorrectly as Ulangambi; Iringa Forest Office, pers. comm.). The manuscript combines previously published results, showing significant impacts of human disturbance on monkeys and duikers [21, 42] with previously unpublished data on monkeys, ungulates, and rodents. The study constitutes an important baseline for monitoring and evaluating the effect of ongoing efforts to implement joint forest management (JFM) involving patrols [22].

Methods

Study Sites

The three forest reserves are located in the Udzungwa Mountains, Iringa and Kilolo district, Iringa Region (Fig. 2) in the same general habitat (montane and upper montane forest), and were presumably connected in recent historical time [5]. The forests are exposed to similar rainfall (1,500-2,000 mm per year) and temperature regimes (10-27 °C with minimum daily temperatures of 21°C) [23].

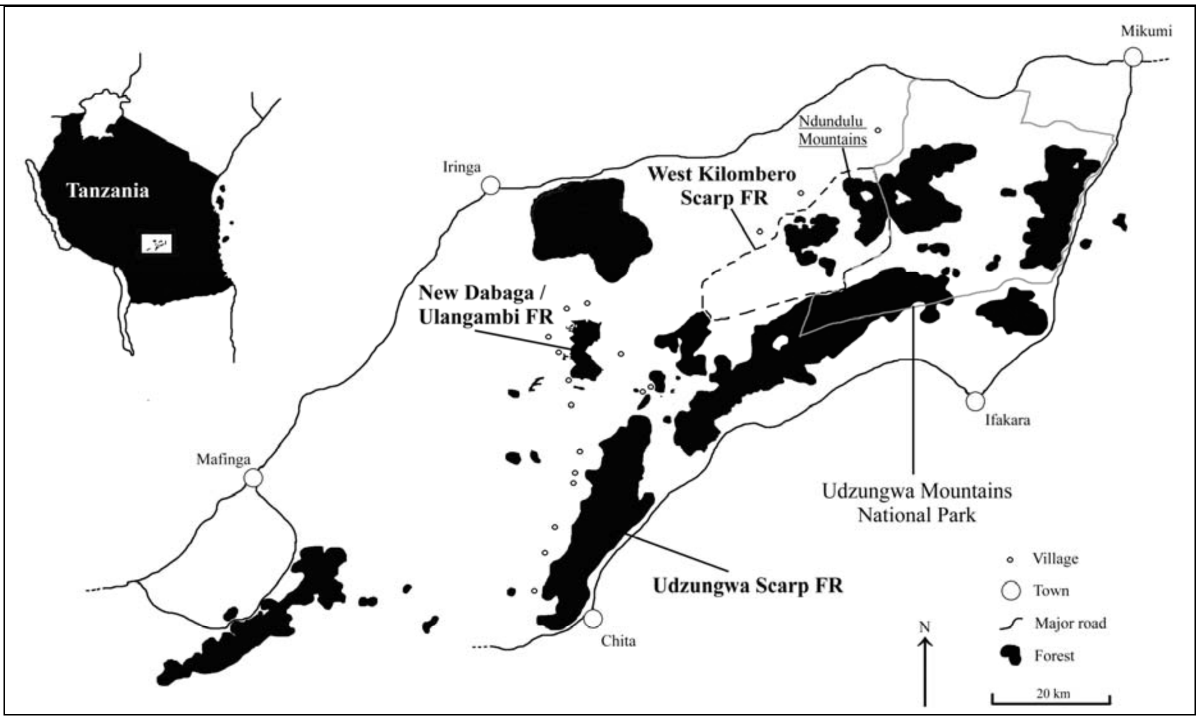

Fig. 2. Map of the Udzungwa Mountains showing the location of the focal forest reserves WKSFR, USFR and NDUFR. Since the survey WKSFR has been incorporated into the new Kilombero Nature Reserve [62]. Adapted from [21].

1. West Kilombero Scarp Forest Reserve

WKSFR is among the least disturbed areas in the Udzungwa Mountains and surveys have recorded the presence of a diverse large mammal assemblage [5, 24]. The study site in WKSFR (36°29'E; 7°45'S) is located near Mufu camp in the Ndundulu Mts in the 240 km^2 large Luhombero forest east of Udekwa village. The census area was in closed canopy forest more than 1 km from the forest edge at altitudes ranging from 1,540 to 1,820 m. The northern part of Ndundulu was subjected to sporadic selective logging until the mid 1990s [25]. However, no such activity was observed near the census area. Wildlife is subjected to very low levels of exploitation, which, according to villagers and surveys of signs of human disturbance, is concentrated along forest edges in the area between the forest fragments [10, 26, 27]. On one occasion, poachers carrying meat of elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus scriptus*) and hyrax (Hyracoidea) were encountered in the reserve (Andrew Perkin, pers. comm.). With the exception of species with large home ranges like elephant, buffalo and the large carnivores, it is therefore assumed that mammal populations in the census area are not influenced by hunting. Since the survey WKSFR has been incorporated into the new Kilombero Nature Reserve [62].

2. Uzungwa Scarp Forest Reserve

The study site in USFR (35°58'E; 8°22'S) was located in the northernmost area of the reserve, known as Kihanga. The overall size of USFR is 207km^2 [23], of which 100km^2 is closed canopy [68,69], with an altitude range of 1,530 to 1,760 m. Two often-used trails run through the survey area, leading from the villages Mbawe and Masisiwe on the plateau, to Ikule in the Kilombero Valley. During 36 days of fieldwork, 31 people were encountered on these trails (twice with dogs) and gunshots were heard twice. Signs of hunting observed during this study include nine pitfalls (two active), 19 snares (five active), two huts containing snare strings, and 15 trees cut to drive eastern tree hyrax (*Dendrohyrax validus*) from their holes. A rough estimate of the density of active traps based on transect surveys is 17.6 per km^2.

3. New Dabaga Ulongambi Forest Reserve
NDUFR (35°55'E; 8°04'S) is located on the undulating plateau on the northwest side of the Udzungwa Mountains near the village of Kidabaga. The forest is 37 km^2 and the altitude of the census area ranges from 1,800 to 1,980 m. NDUFR was logged in the 1970-80s [5]. To reduce the potential effect of different habitat quality on the results, a survey area with intact forest cover was selected. Numerous paths cross the reserve leading from villages along the western side of the reserve to fields on the eastern side and many people traverse the forest regularly. Hunting is evident over most of the reserve and a density of 32.6 active traps per km^2 has been recorded [28]. The level of arboreal hunting is unclear, but one shotgun shell was found and four baited log-fall traps set for primates were observed.

Forest Density and Tree Species Composition
The comparability of tree density and tree species composition for the three reserves was assessed based on studies using the 20-tree variable-area plotless technique and from tree species lists from published accounts [23, 29-33]. To begin to discern habitat differences, tree species lists were compiled from various sources (including unverified identifications [29,30,33 and Pedersen and Topp-Jørgensen unpublished data). Given that many of these identifications have not been verified by expert botanists, results should be treated with caution and regarded only as indicative of potential differences. The comparability of the degree of vegetation cover at knee height was assessed at a radius of 10 meters to evaluate differences in the probability of detecting animals and tracks.

Relative Densities
Surveys to estimate relative densities of animals were conducted in WKSFR and USFR from January to March 1998, and in NDUFR from October to November 2000. In addition to the systematic surveys, more complete species lists were obtained for the three reserves through casual observations of animals and their tracks. Differences in the basic ecology of the surveyed species meant that three methods were employed to assess the relative densities.

Line transects [34] were used to assess densities of diurnal primates. Transects were established perpendicular to the altitudinal gradient totalling 4,420, 4,256, and 6,243 m in WKSFR, USFR and NDUFR, respectively. Surveys were conducted by ETJ and UBP in WKSFR and USFR and by ARM in NDUFR. Surveys were conducted between 7:00 and 11:30 a.m.. Walking speed was 0.7 km/h and transect walks were repeated 22, 19 and 10 times in WKSFR, USFR and NDUFR, respectively. Statistical tests were conducted by pairwise numeric resampling with 500,000 permutations.

Group counts of all primate species (excluding solitary individuals) were also made to supplement relative density data, mostly during transect walks. However due to inherent difficulties in counting groups over the short timeframe necessitated by transect survey which typically underestimate group size [38,70,71], these should be treated as approximations. Due to the non-parametric nature of the data, group size confidence intervals were determined from 999 bootstrapped samples [72]. Kruskal-Wallis tests were used to test for statistically significant differences.

The line intersect method [35] was used to assess the relative density of duikers and bush pig (*Potamochoerus larvatus*). A total of 4,260, 4,086, and 4,650 m transects were surveyed in WKSFR, USFR and NDUFR, respectively. Surveys were conducted moving along the transect line recording all intersecting animal trails. The observer was accompanied by two trackers with local knowledge from the specific areas. Census speed was adjusted to vegetation structure and topography to ensure detection of all spoors. Trails were attributed to a species based on footprints and dung. If no clear footprints or dung piles were found, the path was discarded as being old. If different-sized duiker prints occurred on the same path, only the largest species was recorded to avoid bias from young individuals. Furthermore to avoid known problems of identification by dung in the Udzungwa Mountains [73], we were careful not to differentiate between dung of similar-sized species. No attempt was made to distinguish between blue duiker (*Cephalophus monticola*) and suni (*Neotragus moschatus*) which both occur in the Udzungwa Mountains and they are hereafter referred to combined as blue duiker/suni. Abbott's duiker and the similar-sized bushbuck also both occur in the Udzungwa Mountains. The latter is more common in forest edge areas and woodlands than in moist forest [20]. As results were collected more than 1 km inside the forest we tentatively assume that the large antelope recordings were Abbott's duiker. The relative density was calculated as the number of trails intersecting the transect line per km. A Mann-Whitney U-test was used for pair-wise statistical comparison between locations due to the non-parametric nature of the data.

Fixed area searches [35] were conducted along the transects established for primate surveys to assess the relative density of aardvark (*Orycteropus afer*) and giant pouched rat (*Cricetomys gambianus*) using the number of burrows within five meters to either side of the transect. Only active burrows were recorded, based on uncovered trails and holes. A distance of 25 m between entrance holes was applied to discern between den systems to avoid overestimation, since burrowing animals may have several entrance holes. This allowed for the estimation of the number of den systems rather than number of holes alone and is considered sufficiently precise for a comparison of relative densities between the three locations. A t-test was used for statistical comparison where both sets of data had equal variance and normal distribution.

Results

Forest Density and Tree Species Composition

Our review of tentative lists of plant species found 159 species in WKSFR, 214 in USFR and 88 in NDUFR. Of the 214 species recorded from USFR, 55 species and seven additional genera were shared with NDUFR, and 88 species plus four additional genera were shared with WKSFR. Of the 88 species recorded in NDUFR, 52 species and three additional genera were shared with WKSFR. The density of trees with DBH above 20 cm was 19,700 trees per km^2 in WKSFR and 19,760 per km^2 in NDUFR. Tree density was not assessed in USFR.

Significant difference in ground vegetation density was observed between WKSFR and USFR (U_{181} = 2981, $P<0.001$). The structure of ground vegetation affects the probability of detecting animals and spoors (e.g. [20, 36, 37]). Transect sections with very dense ground vegetation were therefore excluded from the analysis (160 m in WKSFR and 155 m in USFR).

Relative Densities

Udzungwa red colobus, Angolan black and white colobus (*Colobus angolensis palliatus*), and Sykes' monkey (*Cercopithecus mitis* subsp.) were recorded in all three reserves. Of the three reserves, Sanje mangabeys are only known from USFR and were only seen on two occasions. Previously reported observations of Sanje mangabey in WKSFR were mistaken identity of the newly discovered kipunji [74].

In total, 93 primate groups combined were observed in WKSFR, 54 in USFR, and 28 in NDUFR, averaging 1.73, 0.97, and 0.58 groups per kilometer transect, respectively (Table 1). Primate groups combined per km transect were significantly higher in WKSFR compared to USFR and NDUFR ($P<0.001$ both cases). Groups per km transect were also significantly higher in WKSFR compared to USFR for Udzungwa red colobus and Sykes' monkey ($P<0.001$ both cases). Similarly, groups per km transect were significantly higher in WKSFR compared to NDUFR for all three species (red colobus: P<0,009, black and white colobus: $P<0.001$, Sykes' monkey: $P<0.001$). Furthermore, groups per km transect of black and white colobus were significantly higher in USFR compared to NDUFR ($P<0.005$).

Mean group sizes of Udzungwa red colobus decreased inversely to the level of hunting, however the difference was not significant between the three reserves (Kruskal-Wallis $p=0.44$; Table 1). Angolan black and white colobus groups were of similar size in all three reserves (Table 1). No group size estimates were made for Sykes' monkey.

Table 1. Relative density of primates in terms of average number of groups per kilometer transect, and mean group size. Surveyed transects were 4,42 km, 4,26 km, and 6,00 km in WKSFR (22 repetitions), USFR (19 repetitions) and NDUFR (10 repetitions), respectively. Numbers in brackets are 95% confidence intervals.

	WKSFR	USFR	NDUFR
Groups per km			
Udzungwa red colobus (*Procolobus gordonorum*)	0.52 (±0.14)	0.23 (±0.11)	0.24 (±0.12)
Angolan black and white colobus (*Colobus angolensis palliatus*)	0.57 (±0.15)	0.46 (±0.14)	0.15 (±0.10)
Sykes' monkey (*Cercopithecus mitis*)	0.64 (±0.15)	0.28 (±0.12)	0.18 (±0.08)
Total	1.73 (±0.29)	0.97 (±0.23)	0.58 (±0.22)
Mean group size			
Udzungwa red colobus	14.4 (9.0-20.4)	11.69 (4.6-10.6)	9.3 (5.0-13.8)
Angolan black and white colobus	7.0 (5.1-8.8)	6.28 (4.7-8.3)	6.3 (4.9-7.4)

Recorded ungulates include blue duiker/suni, Harvey's duiker, Abbott's duiker, bush pig, buffalo, and elephant, and the number of trails per kilometer is presented in Table 2. Relative density of blue duiker/suni, Harvey's duiker, and Abbott's duiker was significantly higher in WKSFR compared to USFR ($U_{33} = 46.0$, $P<0.001$, $U_{33} = 72.5$, $P<0.021$ and $U_{33} = 17.0$, $P<0.001$). Blue duiker/suni trails occurred significantly less often in NDUFR compared to USFR ($U_{34} = 70.0$, $P<0.006$). Harvey's duiker trails were also less frequent in NDUFR although not significantly so ($U_3 = 93.0$, $P<0.069$). Only once was a path assigned to Abbott's duiker in USFR, and in NDUFR this species was only recorded from two casually observed dungpiles during four months of fieldwork. However we are cautious about identifying this species with certainty from dung alone due to similarity in size to bushbuck.

Relative density of bush pig was significantly higher in WKSFR compared to USFR (U_{33} = 54.5, P<0.001), but slightly higher in NDUFR compared to USFR although not significantly so and still significantly lower compared to WKSFR (U_{35} = 66.0, P<0.001). Spoors of elephant and buffalo were only recorded in WKSFR. No significant differences were found in densities of burrows of giant pouched rat or aardvark between areas with different hunting levels. The density of active giant pouched rat burrows was, however, highest in USFR, while few burrows were found in NDUFR (Table 3). Similarly the relative density of aardvark was lower in USFR than WKSFR and the species was absent from NDUFR where no burrows, new or old, were observed.

Table 2. Number of intersecting trails per kilometer in WKSFR, USFR and NDUFR. Surveyed transects were 4,26 km, 4,10 km, and 4,65 km in WKSFR, USFR, and NDUFR, respectively.

		WKSFR	**USFR**	**NDUFR**
Blue duiker/suni	(*Cephalophus monticola / Neotragus moschatus*)	45.3	19.0	3.0
Harvey's duiker	(*Cephalophus harveyi*)	22.8	11.9	5.4
Abbott's duiker	(*Cephalophus spadix*)	16.9	0.2	0
Bush pig	(*Potamochoerus larvatus*)	11.0	1.2	1.5
Buffalo	(*Syncerus caffer*)	11.7	0	0
Elephant	(*Loxodonta africana*)	1.2	0	0

A total of 22 mammal species (<400 g) were recorded in the three locations: 20, 17, and 12 species in WKSFR, USFR, and NDUFR, respectively (Appendix 1). All relevant forest-dependent species were recorded in WKSFR and USFR (not considering the subsequently discovered Lowe's servaline genet, kipunji and grey-faced sengi). The only two species that were not recorded in WKSFR were small and not typical of forest habitat: chequered elephant shrew (*Rhychocyon cirnei*) and yellow-spotted bush hyrax (*Heterohyrax brucei*). Surveys in USFR, in addition to the yellow-spotted bush hyrax, failed to record four out of five large species known from WKSFR while two IUCN threatened species (Sanje mangabey and Zanj elephant shrew (*Rhynchocyon petersi*)) were absent from NDUFR. The results furthermore illustrate that larger mammals such as hyena (*Crocuta crocuta*), lion (*Panthera leo*), elephant, and buffalo, which are not considered forest species, may use forest habitat in non-hunted locations. No signs of these species were observed in either USFR or NDUFR.

Table 3. Number of active giant pouched rat and aardvark burrow systems per hectare in WKSFR, USFR, and NDUFR.

		WKSFR	**USFR**	**NDUFR**
Giant pouched rat	*Cricetomys gambianus*	2.11	2.45	1.29
Aardvark	*Orycteropus afer*	1.41	0.49	0

Discussion

Primate Densities and Group Sizes

The line transect method has been criticized for not complying with assumptions for density estimation (e.g., [38]). To avoid bias from unsatisfactory fulfilled assumptions this study applied the number of visually observed primate groups per kilometer transect as a measure of relative density [20]. This does not, however, account for differences in visual detection probabilities between census areas [38]. However since most primate observations (80.7% in WKSFR and 69.8% in USFR) were initiated by hearing shaking of branches, the effect of habitat structure becomes less important.

The observation that group sizes were not different between reserves is contrary to previous comparison between WKSFR and NDUFR [21]. The difference is most likely due to group counts from WKSFR and USFR in the present study being made largely during line-transect counts. This supports previous studies showing that group counts made during line-transect surveys tend to underestimate true group size [73, 74]. Studies in other locations have found that primate social organization can be affected by degradation of habitat and hunting [20]. This can result in the reduction of social group size and the frequent splitting of groups into smaller foraging parties [20, 39].

Densities of monkeys are also directly affected by the level of hunting off-take and it was found that the combined primate group and individual species densities, with the exception of Udzungwa red colobus in NDUFR, were roughly proportional to hunting intensity. Comparison with the non-hunted WKSFR indicates that relative densities of Udzungwa red colobus and Sykes' monkey were significantly smaller in the medium-hunted USFR (both 56% less abundant) and the intensively hunted NDUFR (54% and 72%, respectively). The more terrestrial behavior of Syke's monkey makes this species particularly prone to snaring and log-fall trapping and high catches has been recorded through hunter interviews in the villages surrounding NDUFR [10] (see Fig. 3). The reason why densities of Angolan black and white colobus in USFR have not declined proportionally to the other two species (19%) is at this point unclear.

Despite higher hunting intensity in NDUFR, densities of Udzungwa red colobus and Syke's monkey are comparable to USFR. This is likely because the number of ground traps applied as an indicator of hunting intensity in this study does not accurately reflect the actual level of hunting for the predominantly arboreal primates in the two reserves. Alternatively it reflects the positioning of the transects in NDUFR, which was biased towards closed-canopy forest and therefore contained the highest densities of monkeys in the reserve [21].

A number of factors support that the observed differences among locations are a result of hunting. This includes low levels of predation in USFR and NDUFR by natural predators such as leopard (*Panthera pardus*) and African crowned eagle (*Stephanoaetus coronatus*) that are common in WKSFR, very rare in USFR and do not occur in NDUFR. Low predation rates may, on the other hand, reduce the benefits of group foraging and lead to more frequent splitting up of groups and thus lower group size [39, 40] as observed in the two hunted areas. NDUFR in particular also differs in terms of previous logging intensity and size. Monkeys may, however, benefit from the emergence of pioneer species 10-17 years after logging [41]. This has been suggested to occur for Udzungwa red colobus and Angolan black and white colobus in Ndundulu forest [21] and is likely to apply also in NDUFR. Finally, forest fragments smaller than NDUFR are able to support densities comparable to the largest forest fragments in the Udzungwa Mountains [5, 21]. It is therefore unlikely that the large size difference between WKSFR, USFR, and NDUFR are the primary determinant of the low densities in NDUFR although effects of difference in habitat quality cannot be excluded. Thus, with the potential exception of Angolan black and white colobus, results indicate that primate group densities and sizes decrease in proportion to increasing hunting intensity.

Ungulates

Attempts to determine actual densities of forest antelopes based on direct observations are fraught with uncertainty mainly due to differences in visibility and flight response [37, 42]. This study therefore applies the line intersect method and number of trails per km as a measure of relative densities. This constrains the conclusions that can be drawn from the results due to the non-proportional relationship between trails and population size [43]. Nevertheless, the results are roughly comparable to those obtained using trails and dung piles as measures of relative densities, respectively [10, 42]. Illustrating the methodological difficulties in evaluating duiker densities, considerable difference occurred in densities of dung piles observed in NDUFR in these two studies, as the former found no dung piles whereas the latter estimated 764 (95% CI±53) and 522 (95% CI±371) blue duiker/suni and Harvey's duiker dung piles per km^2, respectively.

The results indicate that blue duiker/suni and Harveys duiker in USFR have been reduced to 41.9% and 52.2% of non-hunted densities, which may be within the boundaries of optimal population size assuming that maximum sustainable off-take level for duikers occurs at 60% of carrying capacity [44]. Blue duiker/suni and Harvey's duiker populations in NDUFR are, however, reduced to 6.6% and 23.6% of non-hunted densities. Several studies have shown duiker abundance to decrease as a result of hunting (e.g., [10, 45, 46]) and that the scale of reduction depends on the level of hunting [13, 20] and distance to human settlements [47]. The result that blue duiker/suni is more sensitive to hunting than Harvey's duiker is contrary to results of other studies [10, 48] and may be an artefact of the method applied and differences in these species' territoriality. Blue duiker and suni both have relatively small non-overlapping home ranges and are very territorial, while the Natal red duiker, which is very similar to Harvey's duiker, have much larger and overlapping home ranges [37]. Home ranges of blue duiker/suni may therefore expand more than those of Harvey's duiker when populations are reduced below a certain level. The likelihood of bisecting a Harvey's duiker home range is therefore higher than for blue duiker/suni even though blue duiker/suni may be equally or somewhat more abundant. It is therefore likely that changes in number of trails do not reflect changes in densities proportionally for blue duiker/suni and Harvey's duiker. Considerable precaution should therefore be taken in comparing relative densities of species with differences in ecology such as territoriality. Results indicate that Abbott's duiker is threatened by current hunting levels in both USFR and NDUFR. This is of concern since hunting takes place in most protected areas in the Udzungwas [5, 49] and probably also in other Eastern Arc reserves. Abbott's duiker is endemic to Tanzania, restricted to isolated montane forests and known from only six sites in the Eastern Arc and adjacent mountains, including a recently discovered population in the Rubeho Mountains [50].

That the observed differences among locations are a result of hunting is supported by many duiker species having a wide tolerance for logging disturbance, with the direct effect of habitat alteration having only negligible consequences on densities compared to associated losses from hunting (see [51] for a review). In some cases the density of duikers may even increase in degraded or secondary forest due to increased availability of food sources [36, 51]. Thus, comparison between locations indicates that the duiker population has been reduced by hunting, although effects of differences in habitat quality related to previous logging activities cannot be excluded.

Bush pigs are, according to villagers, a preferred catch, pursued to reduce crop damage, and results indicate that the species is reduced more than 85% in the hunted reserves compared to WKSFR. Bush pig could, however, constitute an important source of bushmeat to local communities if off-take was closely managed for sustainable use, due to the species' high reproductive potential [52].

Aardvark and Giant Pouched Rat

This study used a fixed area search based on long and narrow plots to compare relative densities of aardvark and giant pouched rat among locations. This is considered more efficient than square plots that often represent local extremes [53]. The observed number of active giant pouched rat and aardvark den systems is relatively low, indicating small sampling intensity and making it difficult to exclude effects of natural local variation. Results may thus not enable firm conclusions but still indicate trends in relative densities.

Although no significant difference was found, the relative density of active aardvark den systems was lower in the medium-hunted USFR compared to the non-hunted WKSFR, and the species is absent from the intensively hunted NDUFR. This is considered a result of this species' low reproductive rate [52], small forest size that enables high human activity throughout the reserve, and the ease with which the aardvark can be caught once an inhabited den is found. Although not a typical moist forest species, aardvark appears abundant in WKSFR and it is therefore likely that hunting has led to extinction of this species in NDUFR although effects of the isolated nature of this reserve cannot be excluded.

Densities of active giant pouched rat burrows were highest in USFR. Nielsen [10] in comparison found a higher density in NDUFR compared to WKSFR and attributed this to differences in natural predator assemblage, reduced interspecific competition from depleted populations of most other species, and potential benefits of the more disturbed habitat in NDUFR. Nevertheless it is likely that the high trap density in NDUFR also has a considerable effect on densities of giant pouched rat. Like the aardvark, the giant pouched rat is trapped at its burrows. Snares are often placed at all entrances leaving little chance for the animal to escape. However, contrary to the aardvark, a high reproduction rate probably allows this species to persist in the reserve.

Large Mammal Assemblage

The high number of species recorded in WKSFR can be attributed to the low level of hunting. This enables large species like elephants, buffaloes, and three large carnivores that are particularly sensitive to overexploitation due to their life history characteristics [54] to persist in the area. The only two species that have not been recorded in WKSFR are small and not typical of forest habitat (not considering the subsequently discovered grey-faced sengi). Surveys in USFR indicate that a number of large species are absent whereas the high level of hunting in NDUFR has led to the disappearance of most large species. Bush pig and a medium-sized antelope (probably Abbott's duiker but maybe bushbuck due to uncertainty in identification from dung) appear to be the only larger species (>16 kg), that still occur in NDUFR. Differences in forest size and distance to potential sources of replenishment, however, make the comparison of presence-absence between NDUFR and the other reserves unjustified for species with large home ranges.

Habitat Quality or Hunting Pressure?

Comparison of habitat quality among the three locations reveals a high degree of overlap in tree species composition. Furthermore, WKSFR and USFR both cover a considerable altitude range (>1000 m) compared to NDUFR (300 m), and tree species composition in moist forests in Tanzania has been shown to change with altitude [55]. Species lists from WKSFR and USFR are therefore likely to include tree species that will not occur within the relevant altitude range of NDUFR. Species accumulation curves for WKSFR and NDUFR in addition do not reach an asymptote, suggesting that additional species can be found [29, 30]. Tree densities in WKSFR and NDUFR were similar [29, 30]. Tree density was not assessed in USFR, but is likely to be similar to WKSFR due to identical climatic conditions, large overlap of tree species and because both areas have not previously been subject to logging. Thus, results suggest similar habitat quality in the three reserves. But due to the coarse-grained nature of the comparison, not considering tree species density specifically, and not considering tree size or species, it cannot be excluded that variation in habitat quality affects the results. The much-depleted status of populations and the high hunting intensity in NDUFR in comparison to WKSFR, however, indicates that this is not a result of variation in habitat quality alone.

The trap density of 17.6 traps/km^2 recorded in USFR in this study is comparable to the highest trap densities observed in African tropical forest ([13] (5.9-16.6 traps/km^2); [45] (4.2 traps/km^2)), while the density of 32.6 traps/km^2 recorded in NDUFR [28] is almost twice as high. Furthermore, all recorded terrestrial species are likely subject to hunting due to the non-selective nature of the predominant method, cable snare hunting [45] (see Figure 4). In contrast, no traps have been observed in the forested areas of WKSFR by this or other surveys [10, 26, 27]. Interviews with hunters in WKSFR, however, indicate that hunting of most relevant species does occur [27]. Records of catch from 46 hunters from Udekwa indicate that catch is skewed towards larger species [27]. In combination with the lack of observations of traps, this suggests that hunting in WKSFR is conducted primarily with rifles outside or on the edge of the forests. Although hunting is considered low especially within forested areas in WKSFR, the fact that wildlife is hunted indicates that relevant species in USFR and NDUFR are more severely depleted than the comparison indicates and therefore at high risk of extirpation from continued hunting and stochastic variation [56]. Moreover, the isolated nature of NDUFR may prevent successful re-colonization when species become extinct.

Implications for Conservation

Hunting has reduced the density of wildlife populations in USFR and NDUFR and the effect seems to depend on the intensity of hunting and the size of the species, although effects of differences in habitat quality as well as forest size and isolation cannot be excluded. Hunting intensity was in turn probably determined by distance to and size of surrounding human population [10, 13, 47] under the low efforts of law enforcement at the time of the study. Variations between the three locations in the opportunity costs of hunting [19, 57], access to markets [58, 59], local preferences and traditions for hunting [60, 61] may also influence hunters' incentives and contribute to the difference in hunting intensity.

Elephants, buffaloes, lions, and hyenas were recorded only in WKSFR. Medium-sized species (>16 kg) such as bush pig, Abbott's duiker, and aardvark were significantly less abundant in both hunted areas. Smaller ground-living species had the lowest relative density in the area with the highest level of hunting, while two of three primate species were approximately equally abundant in the two hunted areas. To protect the astounding biodiversity of WKSFR, the Ndundulu, and Nyanbanitu forests and the adjacent Matundu and Iyondo forest reserves have recently been gazetted as the Kilombero Nature Reserve [62]. The status as nature reserve is the highest protection under the Tanzanian Forestry and Beekeeping Division legislation, equivalent to the National Park status of the Tanzania National Parks Authority.

Fig. 3. Sykes monkey on the menu. Photo by M.R. Nielsen taken in one of the villages surrounding NDUFR.

Fig. 4. Suni (*Neotragus moschatus*) caught with a cable snare. Photo by M.R. Nielsen taken in one of the villages surrounding NDUFR.

Despite a reduction in relative density of mammals in the hunted areas, all forest-dependent species were present in USFR. At the time of survey, the hunting level in the northern part of this reserve seems not to pose an immediate threat for primates (Sanje mangabey not assessed), blue duiker/suni, Harvey's duiker, aardvark, and giant pouched rat, but appears to be unsustainable for Abbot's duiker and bush pig. A survey based on point counts of auditory cues in addition found relative densities of eastern three hyrax in USFR significantly lower than in WKSFR but without this being a threat to the species persistence in the reserve [63]. The large size of USFR and its proximity to other areas with diverse and relatively undisturbed wildlife populations indicate that there is scope for a return of larger terrestrial mammal species if hunting is reduced significantly and connectivity to other wildlife areas is maintained and improved [49]. If the Udzungwa Mountains become isolated from adjacent protected areas, mammal populations of the Kilombero valley will lose an important dry-season refuge while isolation of elephant populations within the Udzungwa forests potentially could constitute a threat to habitat structure and rare tree species diversity [68]. Failure to include USFR in the Kilombero Nature Reserve therefore seems to be a significant oversight considering the rich biodiversity of the reserve (particularly high herpetological diversity) and high levels of threat [62]. This should be rectified or alternatively USFR could be given national park status while the Mngeta corridor linking the reserve to the southern forests of Udzungwa Mountain National Park should be defined and managed [49].

The isolation and small size of NDUFR likely means that the reserve at best can maintain the present wildlife species. Hunting seems unsustainable for terrestrial mammals with the exception of giant pouched rat, while primates were significantly reduced. Densities of eastern tree hyrax were in addition too low to enable sufficient records of auditory cues to enable estimation of a relative density in NDUFR [63]. Reduction of hunting intensity is therefore paramount for the survival of present mammal populations in NDUFR.

Subsequent to data collection for this study, JFM involving patrolling and monitoring of biodiversity and forest quality by local communities was implemented in WKSFR and NDUFR [64]. The government of Tanzania is furthermore in the process of scaling up and implementing participatory forest management approaches on a national basis [65]. However, there appears to be very little hard evidence on to what extent this and related approaches have been successful in achieving their conservation objectives [66] (but see [67]). JFM in forests with few opportunities for income generation through extraction, in consideration of national and international priorities for protecting valuable ecosystem services and biodiversity, represents a particular problem in relation to maintaining community interest and incentives for protection [10, 64, 65]. This study therefore constitutes an important baseline for evaluating conservation outcomes of JFM initiatives [22] as well as establishment of the new Kilombero Nature Reserve.

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Appendix 1. Recorded mammal assemblage (>400g) for study areas in WKSFR, USFR and NDUFR, their forest dependency and IUCN status. This is not a comprehensive list for the reserves as a whole. Species endemic to Tanzania in bold.

Species	Latin	Forest dependent	WKSFR	USFR	NDUFR	IUCN Status
Udzungwa red colobus	***Procolobus gordonorum***	**F**	×	×	×	**VU**
Angolan black and white colobus	*Colobus angolensis palliatus*	F	×	×	×	DD
Sanje crested mangabey	***Cercocebus galeritus sanjei***	**F**		×		**EN**
Sykes' monkey	*Cercopithecus mitis* [subsp.]	F	×	×	×	
Zanj elephant shrew	*Rhynchocyon petersi*	F	×	×		EN
Chequered elephant shrew	*Rhynchocyon cirnei*	N		×	×	
Giant pouched rat	*Cricetomys gambianus*	f	×	×	×	
Tanganyika mountain squirrel	*Paraxerus lucifer lucifer*	F	×	×	×	
Porcupine	*Hystrix cristata*	f	×	×		
Spotted hyena	*Crocuta crocuta*	F[¤]	×			LR/cd
Leopard	*Panthera pardus*	F[¤]	×	×[1]		
Lion	*Panthera leo*	N[¤]	×			VU
Aardvark	*Orycteropus afer*	f	×	×		
Eastern tree hyrax	*Dendrohyrax validus*	f	×	×	×	VU
Yellow-spotted bush hyrax	*Heterohyrax brucei*	f			×[#]	
African elephant	*Loxodonta africana*	f	×			EN
Bush pig	*Potamochoerus larvatus*	f	×	×	×	
African buffalo	*Syncerus caffer*	f	×			LR/cd
Bushbuck	*Tragelaphus scriptus*	f	×	×[2]		
Blue duiker/Suni	*Cephalophus monticola/ Neotragus moschatus*	f	×	×	×[#]	LR/cd
Harvey's duiker	*Cephalophus harveyi*	F	×	×	×	LR/cd
Abbott's duiker	***Cephalophus spadix***	**F**	×	×	×	**VU**

Forest dependency: F = forest dependent; f = found in forest as well as other habitats; N = normally regarded as a non-forest species. Based on Burgess *et al*. (2000), Kingdon (1974, 1997) and Kingdon & Howell (1993). IUCN Status: EN = endangered, VU = vulnerable, LR/CD = lower risk/conservation dependent, DD = data deficient.
[1]=David Moyer *pers. comm*.; [2]=Jon Fjeldså, *pers. comm*. .
[¤]: May not be subjected to hunting, but clearly avoid areas of human activity.
[#]: Suni and *Heterohyrax* skulls identified by Dieter Kock, Zoological Museum, Frankfurt.